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# Effects of radiation, especially ultraviolet B, on conidial germination and mycelial growth of grape powdery mildew

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## Abstract

Conidia of *Uncinula necator* inoculated on vine leaf disks were exposed to different irradiation conditions during various combinations of irradiation periods. In controlled experiments at constant leaf temperature spore germination and mycelial growth were negatively affected by the UV B doses, irrespective of the exposition duration. In semi-controlled condition experiments, conidia were exposed to shaded, sunny and sunny without UV B radiation conditions. Shaded conditions were always more favourable to spore germination and mycelial growth than sunny conditions. Under two different ranges of temperature (20–24 and 26–31 °C for shaded conditions), the effect of radiation on germination and mycelial growth differed. Thus, the effect of radiation on spore germination and mycelial growth seems to be affected by temperature. In general, radiation effects increased as the number of exposition periods increased, indicating that both spore germination and mycelial growth were reduced, but not totally stopped by the different exposures. Germination was most affected by exposures applied just after inoculation, whereas mycelial growth was most affected by exposures applied one day after inoculation. These results indicate that radiation is an important factor to consider for a better understanding of the relationships between climate and grape powdery mildew epidemics.

## Introduction

Powdery mildew, caused by *Uncinula necator* (Schweiniz) Burrill, is a major disease of vine (*Vitis vinifera* L.) in many areas of grape production (Pearson and Goheen, 1988). The disease develops better under shaded conditions provided by e.g. the presence of trees nearby the vineyard, or by vigorous vines (Bulit and Lafon, 1978). Since shading is associated with reduced irradiation, reduced temperatures and increased humidity, these effects can not be dissociated under field conditions. High temperature and low humidity are unfavourable for the fungus (Delp, 1954; Heintz, 1988; Toma, 1978; Weltzien-Stenzel, 1959). In contrast, little is known about the effect of radiation and contradictory results have been reported. According to Toma (1978), spore germination of *U. necator* is higher under diffuse light than under direct sunlight. On the contrary, investigations by Weltzien-Stenzel (1959) showed that this process is affected by total obscurity, but is independent of the light intensity. The influence of radiation on the development of *U. necator* thus remains unclear. Studies conducted on several aerial fungi showed that radiation could be a limiting factor for their development, the spectral part corresponding to UV B being mainly responsible of this effect (Fargues et al., 1988; Fargues et al., 1989; Maddisson and Manners, 1973; Rotem et al., 1985; Rougier et al., 1993; Smits, 1992; Stevenson and Pennypacker, 1988). Spore survival can also be affected by increasing surface temperature caused by radiation (Rotem et al., 1985; Rougier et al., 1993; Smits, 1992; Smits et al., 1992). In the case of *U. necator*, the relative importance of photic effect (specially caused by the rays), and thermic effect (caused by the increase of temperature) of

radiation on the development of the fungus remains unknown.

In this work, we assessed the effect of radiation and its UV B portion on the spore germination and the mycelial growth of *U. necator* on grapevine leaves, in controlled and semi-controlled conditions.

## Materials and methods

*Fungal material*

A monoconidial strain (R7) of *U. necator* isolated in 1990 in Carregado, Portugal was used in all the experiments. It was maintained by successive transfers every 5 to 6 weeks on one month-old *in vitro* cuttings of grapevine cv. Cinsault rooted on Murashige-Skoog (21 g/l) and agar (6 g/l) medium (Murashige and Skoog, 1962).

*Plant material*

Methods described by Steva and Clerjeau (1990) to prepare leaves, slightly modified, were used. Leaves from one-eye cuttings were removed from 2 month-old plants (cv. Cinsault) grown in a greenhouse on a compost and sand-based substrate. The plants were kept free from powdery mildew by sulfur powdering every 10 days. The second or third fully expanded leaves from the apex were chosen for their high susceptibility. Leaves were rinsed under permuted water, disinfected in a calcium hypochlorite bath (50 g/l) for 10 min, rinsed in sterilized water and dried between two sheets of sterilized filter paper.

*Inoculum production*

Leaves were placed in Petri dishes on agar medium (20 g/l) supplemented with benzimidazole (30 mg/l) (Steva and Clerjeau, 1990). Inoculations were performed in a plexiglass square section settling tower (20 or 30 cm large, 60 cm high). Petri dishes containing leaves or 14 mm diameter leaf disks to be inoculated were placed at the bottom of the tower. Inoculation was performed by dispersing spores from a sporulating leaf placed on the top of the tower ; air was blown over the conidia from the tip of a Pasteur pipet connected to an oxygen pump. The sporulating leaf was infected 12 to 14 days before by the same way and incubated at 21 °C (30 $\mu$E $m^{-2}$ $s^{-1}$, 8 h/16 h photoperiod). The density of conidia deposited, controlled with a haemocytometer placed at the bottom of the tower, ranged from 300 to 600 spores/$cm^2$.

*Solar simulation experiments*

Leaf disks, cut from leaves prepared as described above, were placed in Petri dishes on a wet filter paper (with 0.5 ml of water), and inoculated. Irradiation took place in an illuminated incubator, described in detail elsewhere (Rougier et al., 1993; Rougier et al., 1994); the light source consisted of two halogenure lamps, equiped with interchangeable long-pass glass filters blocking shorter wavelengths at either 320 nm or 295 nm. These two lamps emitted a continuous spectrum from 270 to 1100 nm at a power of 400 W. Preset levels of irradiance were obtained by varying the distance between the radiation source and the inoculum. Inoculum temperature was regulated at 25 °C by circulating cool water through the platform supporting the samples to be irradiated. Temperature regulation was monitored with an electronic system connected with a thermocouple measuring the surface temperature of a leaf disk placed in a Petri dish, on a wet filter paper, on the beam. Another thermocouple, placed on the same disk, was connected to a 21X micrologger (Campbell Scientific Ltd, Loughrough, UK) to estimate the temperature at the level of conidia during the experiments. A close thermal contact between the Petri dishes and the thermally-regulated plate surface was provided by silicone paste. The irradiance within the UV B waveband (from 280 to 320 nm) was measured prior and after each experiment with a UV Centra radiometer (OSRAM, Molsheim, France). Experiments consisted of exposing fungal samples to three conditions varying according to waveband and irradiance (Table 1). Under the first condition (HI B+), the UV B irradiance (1.3 W $m^{-2}$) was similar to that measured in the Paris area from 10 a.m. to 2 p.m. in a cloudless summer day (Rougier et al., 1994) and the duration of exposure was 4 h. Under the second condition (LI B+), the fungus received the same UV B dose, but in increased exposure time (8 h) and reduced UV B irradiance (0.7 W $m^{-2}$). In the last experimental condition (HI B−), the inoculum was exposed for 4 h to the higher flux but without UV B.

For each of the three irradiation conditions, 7 combinations of irradiation periods (CIP) were compared (Table 2), including 1 to 3 light exposures applied between 0 and 48 h after inoculation. During each experiment, uninoculated control and inoculated samples not to be irradiated were transferred to a growth chamber at 25 °C in darkness. The samples to be irradiated were exposed to radiation in Petri dishes, on a filter paper kept wet by regular deposits of 1 ml water.

*Table 1.* Specifications of the different irradiation conditions tested under solar simulation

| Irradiation condition | Abreviation | Wavelength range of transmission (nm) | Distance between the lamps and the inoculum (m) | UV B irradiance applied to the inoculum (W $m^{-2}$) |
|---|---|---|---|---|
| Broad band radiation, High Intensity | HI B+ | 295–3000[a] | 0.5 | 1.3 |
| Broad band radiation, Low Intensity | LI B+ | 295–3000[a] | 1 | 0.7 |
| Radiation without UV B, High Intensity | HI B− | 320–3000[b] | 0.5 | –[c] |

[a,b] Transmittance of Schott ling pass filters [a]WG 295 and [b]WG 320.
[c] UV B irradiance non significant.

*Table 2.* Combinations of irradiation periods (CIP) applied to leaf disks inoculated with *U. necator* conidia

| CIP | Irradiation applied after inoculation | | |
|---|---|---|---|
| | Immediately | 24 h | 48 h |
| D0 | X | | |
| D1 | | X | |
| D2 | | | X |
| D0D1 | X | X | |
| D0D2 | X | | X |
| D1D2 | | X | X |
| D0D1D2 | X | X | X |

Between exposures and after the last one, the leaf disks were transferred to a filter paper placed on agar medium supplemented with benzimidazole on Petri dishes, and previously wetted with 1 ml of water. They were incubated at 20 °C (25 $\mu$E $m^{-2}$ $s^{-1}$, 12 h/12 h photoperiod).

*Sunlight experiments*

Samples consisted of inoculated leaf disks placed in Petri dishes on 5 superposed filter papers wetted with 1 ml of water. Samples were horizontally exposed between 10 a.m. and 2 p.m., in the Bordeaux area, on an open site. This experiment was conducted twice, in the summer of 1993, during clear sunny days. Three conditions of exposure were tested. In the first experimental condition, samples were exposed to incident sun radiation (SUN). In the second one, they were submitted to sunlight without the UV B waveband (SUNB−) by using a plexiglass plate mounted above the irradiated platform. In the last condition, samples were placed in the shade of a white oilcloth mounted as the plexiglass screen (SHAD). The surface temperature of leaf disks was not controlled, but was monitored for each of the 3 radiation conditions with a thermocouple placed under a leaf disk (placed on 5 wet superposed filter papers disposed on a Petri dish), connected with a 21X micrologger. Intensity of solar radiation data were provided by the INRA Laboratory of Bioclimatology, and were collected with a pyranometer located 200 m from the experimental site.

For each of the three exposure conditions, a CIP design similar to that of laboratory experiments (Table 2) was used. During each exposure, control and samples not to be exposed were transferred to a growth chamber (21 °C, 30 $\mu$E $m^{-2}$ $s^{-1}$). The samples to be exposed were transferred to the appropriate exposure site and filter papers were kept wet by regular deposits of 1 ml water. Between exposures and after the last one, the samples were incubated at 21 °C (30 $\mu$E $m^{-2}$ $s^{-1}$, 8 h/16 h photoperiod).

*Conidial germination and mycelial growth*

72 h after inoculation, fungal organs were removed from leaf disks to glass slides and prepared for microscopic observation (× 100) as described by Steva (1994). For each leaf disk, the spore germination was estimated from the observation of 100 spores. A conidium was considered germinated when the germ tube was at least as long as the width of the spore (Manners, 1966). For each leaf disk, mycelial growth was assessed from the average of the longest hyphae developed by 20 spores.

*Experimental design and data analysis*

Both laboratory and sunlight experiments were repeated twice. A complete randomized block design with 7 replications was used to assess the CIP effect within the same irradiation condition. The experimental units consisted of leaf disks, and each leaf used to provide the disks was considered as a block. The same source of inoculum was used for each irradiation condition tested. To facilitate the comparison between the effects of the different irradiation conditions tested, germination and mycelial length were expressed as the

fraction relative to the control. Analysis of variance was performed with the SAS GLM procedure (SAS, 1988).

To describe the effects of UV B and temperature on the infection processes (germination and mycelial growth), regression analyses were performed with the SAS REG procedure (SAS, 1988). Two linear models were tested, with the shape: (1) GF = f(Ri, T, $T^2$, $R_i$*T, Ri*$T^2$) and (2) MF = g(Ri, T, $T^2$, Ri*T, Ri*$T^2$), where GF = germination (fraction relative to the control) assessed 72 h after inoculation, MF = mycelial length (fraction relative to the control) assessed 72 h after inoculation, T = average leaf temperature experienced during the exposure periods, Ri (i = 0, 1, 2) were binary variables representing the presence of UV B for each day of exposure; R0, R1 and R2 were equal to zero for all the samples submitted to SUNB- and SHAD conditions. For the SUN condition, Ri = 1 if the observation corresponded to a sample exposed to direct sunlight during the day 'i' of exposure (Di), and 0 if not.

## Results

In all experiments, the germination in controls ranged from 70 to 90% and mycelial length ranged from 450 to 600 $\mu$m. These values reflected a good and uniform quality of the inoculum used.

*Exposure to artificial light*

Except for D0D1D2, spore germination was not significantly affected by artificial radiation without UV B (HI B−) (Figure 1A). Nevertheless, germination fractions for samples exposed immediately after inoculation (D0, D0D1, D0D2, D0D1D2) ranged around 0.7 instead of 1 in the case of irradiation 24 h and 48 h after inoculation. Samples submitted to radiation including the UV B waveband showed a significant decrease in germination, when exposed to both levels of UV B irradiance (HI B+ and LI B+) immediately after inoculation of leaf disks. Their germination fractions ranged from 0.36 (D0) to 0.06 (D0D1D2), without significance corresponding to level of UV B irradiance. In contrast, irradiation only applied 24 h and 48 h after inoculation did not induce any significant detrimental effect on germination.

Mycelial growth was not affected by irradiation without UV B, since fractions relative to control were close to 1 for all CIP tested (Figure 1B). As for

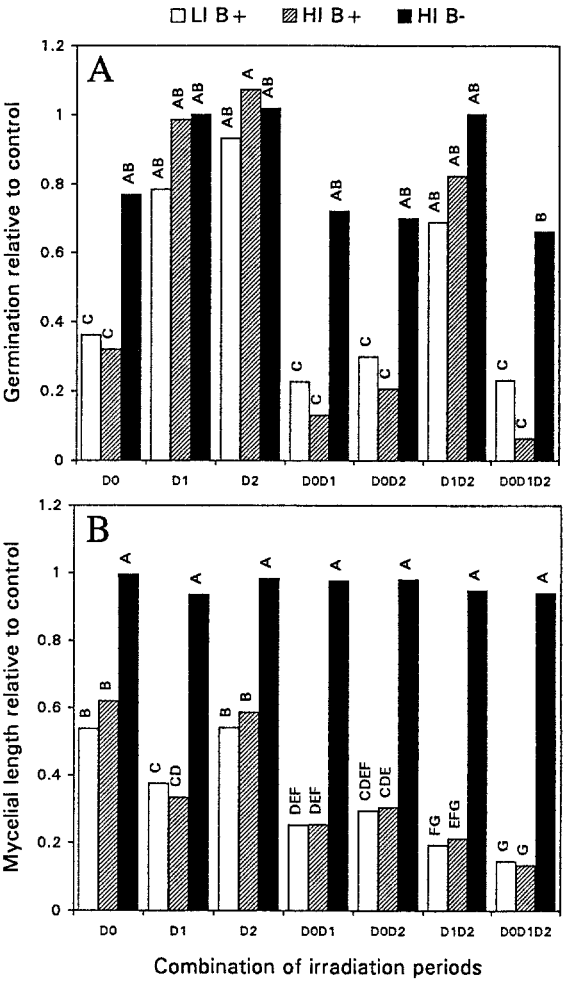


*Figure 1.* Effect of irradiation treatments on conidial germination (A) and mycelial growth (B) tested under solar simulation. Data recorded 72 h after inoculation. LI B+: 0.7 W $m^{-2}$ UV B irradiance, irradiation period of 8 h; HI B+: 1.3 W $m^{-2}$UV B irradiance, irradiation period of 4 h; HI B−: 0.2 W $m^{-2}$ UV B irradiance, irradiation period of 4 h. Treatments corresponding to the different combinations of irradiation period are given in Table 2. Means in each figure are based on data recorded from 7 leaf disks by treatment averaged over 2 experiments. In each figure, bars labeled with the same letter are not significantly different from each other according to Student-Newman-Keuls multiple range test ($P = 0.05$).

the spore germination, no significant differences were found between both irradiation conditions with UV B, whatever the CIP applied. Irradiations including UV B applied 24 h after inoculation seemed to be the most unfavourable conditions for mycelial growth, since values obtained for CIP D1 were significantly inferior to that observed for both CIP D0 and D2. Moreover, mycelial growth slowed significantly according to the number of exposures.

*Table 3.* Surface temperature of leaf disk (minimum-maximum) (°C) recorded during the three conditions of exposure tested under sunlight

| Exposure day | SHAD | SUNB- | SUN |
|---|---|---|---|
| 17 Aug | 26.8–29.3 | 32.4–36.2 | 32.5–36.2 |
| 18 Aug | 29.0–31.4 | 32.4–39.2 | 31.8–38.6 |
| 19 Aug | 26.2–27.5 | 33.3–38.4 | 32.5–36.6 |
| 30 Aug | 20.1–22.6 | 25.9–30.2 | 28.2–30.9 |
| 31 Aug | 21.5–24.3 | 26.2–31.3 | 27.0–31.3 |
| 1 Sept | 21.3–22.8 | 26.3–30.6 | 27.8–30.5 |

*Exposure to sunlight*

The first experiment took place on 17, 18 and 19 August 1993, the second one on 30, 31 August and 1 September 1993. During all exposure periods, the global radiation (300–3000 nm) values were similar (hourly averages of 755, 758, 746, and 747, 721, 739 W $m^{-2}$, respectively). Leaf disk temperatures, however were 5 to 10 °C lower in the second experiment (Table 3). For each exposure period, temperature of samples placed under plexiglass were similar to that of samples directly exposed to the sun, and were 3 to 10 °C higher than that of shaded samples.

In the first experiment, both spore germination and mycelial growth were significantly affected by sunlight, and sun radiation including the UV B waveband was the most unfavourable condition (Figure 2A and C). The differences of germination fractions between SHAD and SUNB- conditions could reach up to 0.74 (for CIP D0D1D2). Between SUN and SUNB- conditions, differences were smaller, and significant only for CIP D1, D0D2 and D1D2. Differences in mycelial length fractions between SHAD and SUNB- conditions varied between 0.19 (D0) and 0.77 (D1D2). In all cases, samples directly exposed to the sun showed a mycelial growth inferior to that of samples under SUNB- conditions, but significant differences were observed only for 3 CIP (D0, D0D1 and D0D2).

The second experiment showed a smaller detrimental effect of natural radiation despite a similar global irradiance (Figure 2B and D). These results indicated that temperature interacts in the effect of natural radiation. For the first and the second experiments, the lowest germination fractions were 0.04 (SUN, CIP D0D1D2) and 0.42 (SUN, CIP D0D1), respectively. Mycelial length relative to the control was also higher in the second experiment, under SUNB- and SUN conditions (Figure 2D). On the contrary, mycelial length fraction of shaded samples was slightly lower, and was on average 0.8. For each CIP tested, mycelial growth was similar under SUNB- and SHAD conditions, whereas samples directly exposed to the sun showed a significantly lower mycelial growth.

For both experiments, under SUNB- and SUN conditions, germination and mycelial growth decreased as the periods of exposure accumulated; three exposures (D0D1D2) to direct sunlight lead generally to the lowest fractions, less than 0.2 and 0.4 for the first and second experiment, respectively. As found previously in laboratory trials, exposure of fungal spores immediately after leaf inoculation (D0) induced the highest germination inhibition, and 48 h post-inoculation irradiation did not affect germination at all.

The contributions of the interaction terms between the binary variables representing the presence of UV B and temperature or squared temperature (Ri*T and Ri*$T^2$) were not found to significantly improve the description of variation in germination and mycelial growth. The resulting regressions were thus of the shape: GF = f(Ri, T, $T^2$) and MF = g(Ri, T, $T^2$). These regression models allowed to predict a fair fraction of variation in germination ($R^2 = 0.52$) and a large fraction of variation in mycelial growth ($R^2 = 0.81$) (Table 4). In the case of spore germination, only one variable representing radiation, R0, contributed significantly to the regression, with a relatively large and negative parameter (−0.4). This reflected the detrimental effect of UV B on germination only when irradiation is applied just after inoculation. In contrast, UV B exposures on the very day, and the day following inoculation significantly affected mycelial growth (R0 and R1). This was reflected by regression parameters that were comparatively smaller in absolute values (−0.15 and −0.24, respectively). Both germination and mycelial growth processes were significantly and positively related to temperature and negatively to squared temperature. From the regression equations, the estimated optimal temperature for germination and mycelial growth were 25.5 and 26.2 °C, respectively.

## Discussion

*Experimental conditions*

In most of studies conducted to determine the effect of light on pathogens (e.g. Maddisson and Manners, 1973; Rotem et al., 1985), the samples were kept in darkness after exposure in order to avoid the effect of photoreactivation (Jagger, 1958). In our experiments, samples were incubated with alternating light/dark

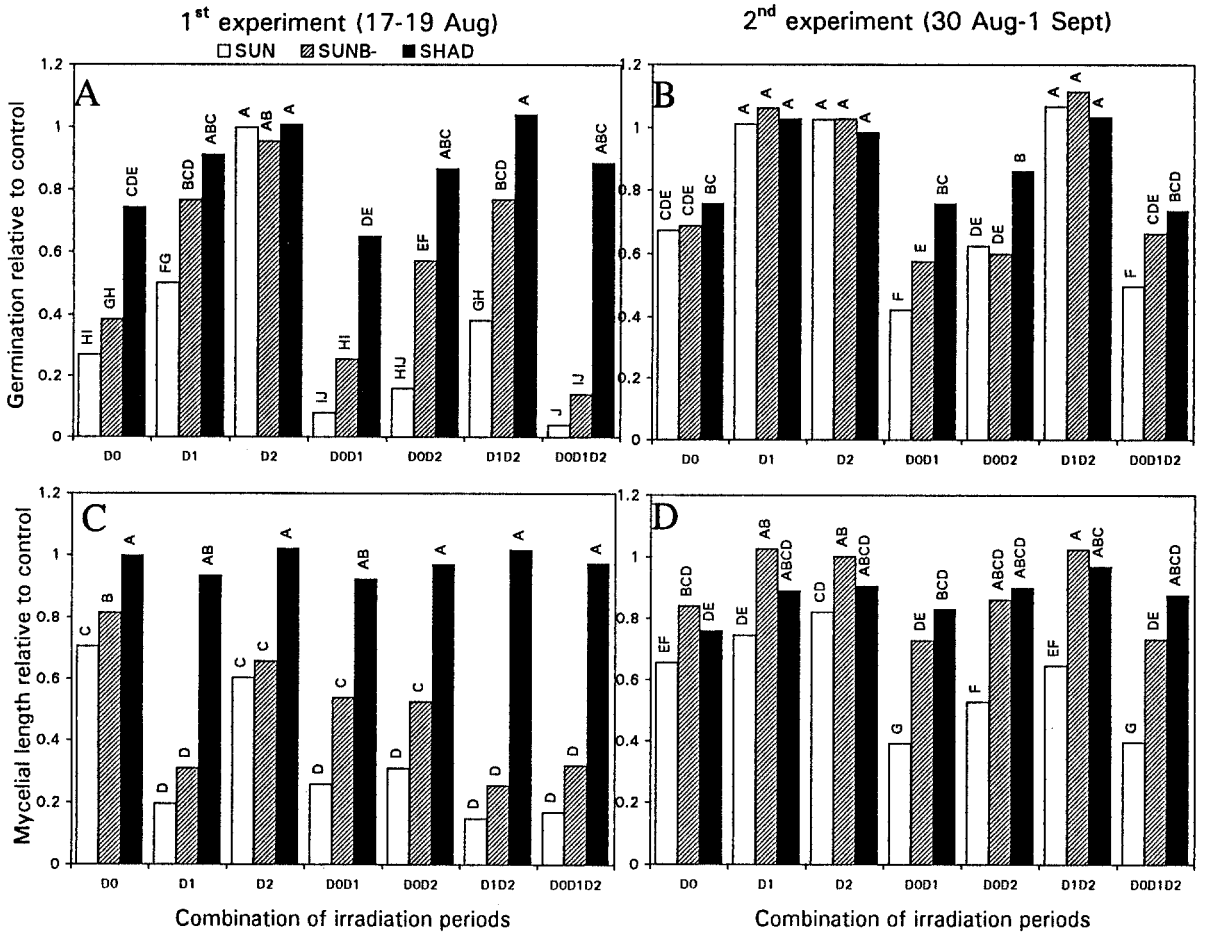


*Figure 2.* Effect of irradiation treatments on conidial germination (A, B) and mycelial growth (C, D) tested under sunlight. Data recorded 72 h after inoculation. SUN: Full sunlight; SUNB-: Sunlight without UV B; SHAD: Shade. Treatments corresponding to the different combinations of irradiation period are given in Table 2. Means in each figure are based on 7 leaf disks by treatment. In each figure, bars labeled with the same letter are not significantly different from each other according to Student-Newman-Keuls multiple range test ($P = 0.05$).

conditions between irradiation exposure periods. Thus, the results obtained reflect the combined effects of radiation and also photoreactivation, but represent more realistic conditions than complete darkness until the assessment.

Since conidia were deposited on vine leaf disks before irradiation, spore germination and mycelial growth reflect the combined effects of the radiation on the fungus and on the plant. UV B exposure can increase the susceptibility of plants (Runeckles and Krupa, 1994). At the same time, adverse effect of UV B on the microorganisms is well known (Leach, 1971). As a result, depending on the pathosystem, UV B exposure timing, pathogen inoculum level and crop cultivar and age, the UV B effects on the disease can be contrasted (Runeckles and Krupa, 1994). For example, preinfectional treatment with UV B enhanced the sensitivity of cucumber to scab, caused by *Cladosporium cucumerinum* and anthracnose, caused by *Colletotrichum lagenarium*, but the disease was less enhanced when a postinfectional treatment was added (Orth et al., 1990). In the case of rice blast, caused by *Magnaporthe grisea*, depending on the cultivar, preinfectional UV B irradiations either had no effect, or induced an increase of the disease (Finckh et al., 1995). In our work, the effect of UV B on the plant was not assessed, but we can state that the overall effect of UV B on both *U. necator* and *V. vinifera* led to a noticeable reduction in fungal development. However, this trend may be biased as UV B action on leaf disks is different from that on the whole grapevine plant.

*Table 4.* Regression analysis of germination fraction (GF) and mycelial length fraction (MF) on temperature and UV B radiation

| Dependant variables[a] | Independent variables[b] | Parameter estimate | Standard error | Prob > \|T\|[c] | |
|---|---|---|---|---|---|
| GF | intercept | −1.5447 | 1.3308 | 0.2534 | DF = 41 |
| | R0 | −0.4020 | 0.0934 | 0.0001 | $R^2$ = 0.52 |
| | R1 | −0.0752 | 0.0933 | 0.4256 | CV = 29.62 |
| | R2 | 0.1056 | 0.0932 | 0.2650 | |
| | T | 0.1934 | 0.0925 | 0.0438 | |
| | $T^2$ | −0.0038 | 0.0016 | 0.0215 | |
| MF | intercept | −2.6923 | 0.7558 | 0.0011 | DF = 41 |
| | R0 | −0.1502 | 0.0530 | 0.0075 | $R^2$ = 0.81 |
| | R1 | −0.2410 | 0.0530 | 0.0001 | CV = 17.05 |
| | R2 | −0.0960 | 0.0530 | 0.0781 | |
| | T | 0.2788 | 0.0530 | 0.0001 | |
| | $T^2$ | −0.0053 | 0.0009 | 0.0001 | |

[a] GF = germination (fraction relative to the control) assessed 72 h after inoculation, MF = mycelial length (fraction relative to the control) assessed 72 h after inoculation.
[b] Ri (i = 0,1,2) = binary variables representing the presence of UV B for each day of exposure. R0, R1 and R2 = 0 for all the samples submitted to SUNB- and SHAD conditions. For the SUN condition, Ri = 1 if the observation corresponded to a sample exposed to direct sun light during the day 'i' of exposure (Di), and 0 if not. T = average leaf temperature experienced during the exposure periods.
[c] T for H0: parameter = 0.

*Controlled conditions experiments*

The experiments conducted under controlled conditions suggest that the photic effect of radiation on both spore germination and mycelial growth is mainly determined by the total UV B dose, irrespective to the duration of exposition. These results are consistent with reports on other fungi, as *Puccinia* spp. (Maddisson and Manners, 1973) and *Paecilomyces fumosoroseus* (Smits, 1992).

*Semi-controlled conditions experiments*

Since temperature of samples placed under plexiglass in semi-controlled experiments were similar to that of samples directly exposed to the sun, we may assume that differences in spore germination and mycelial growth observed between these two conditions were mainly due to the effect of UV B. Temperature of shaded samples were 5 to 10 °C lower. Differences between shaded samples and those exposed to sunlight without UV B may thus reflect the combined effects of temperature and radiation without UV B. This last component may be neglected, as results obtained in controlled condition experiments indicated that the effect of radiation on both infection processes was mainly caused by UV B. Hence, in the first series of experiments, temperature had a strongly detrimental effect, whereas for the second one, no significant effect was observed. Furthermore, from the regression analysis, the optimal temperature we found reached 25–26 °C. These results are in agreement with previous studies which reported that optimal temperature for the infection of *U. necator* was between 20 and 27 °C (Delp, 1954; Oku et al., 1975; Weltzien-Stenzel, 1959; Yossifovitch, 1923). Temperature ranges observed for the second experiment under SHAD and SUNB- conditions thus represented similar stimuli for the infection processes. In contrast, during the first experiment SHAD temperature (29 °C) was more favourable than SUNB- one (35 °C).

The effect of UV B on spore germination appeared to be more important in the first than in the second experiment. This may reflect an interaction of UV B radiation and temperature, leading to the enhancement of the lethal effect of UV B on the spore germination at high temperatures. If differences in mycelial growth between SUNB- and SUN were higher for the second experiment, the ratio SUN/SUNB- was quite similar for all the CIP tested. For this process, UV B effect seemed thus to be similar for the two ranges of temperature experienced.

Germination and mycelial growth were less affected by UV B during the 30 August/1 September experiment than under controlled conditions, where the temperature was optimal. As the UV B dose

received during the semi-controlled experiments can be assumed to be equal or higher than that applied in the controlled experiments, these results suggest that for the same UV B dose applied, the measured effect is more important under controlled conditions. A similar discrepancy has been reported for the survival of *P. fumosoroseus* spores (Smits, 1992). Under controlled conditions, either a higher frequency of shortwave UV B, or a lower light intensity received by samples (thus associated with a lower photoreactivation effect), may be the source of the differences of UV B dose effect observed.

*Effect of the exposure timing*

In general, spore germination and mycelial growth decreased as the number of irradiation periods increased. These results suggest that both processes are only slowed by irradiation, and not stopped. Irradiation applied just after the inoculation was most unfavourable for spore germination, as shown by analysis of variance and regression analysis. Such a result is consistent with the dynamics of the fungus germination: this process takes place very quickly after spore deposition, and can be achieved in a few hours under favourable conditions (Delp, 1954; Toma, 1978). Mycelial growth seemed to be most affected by irradiation applied 24 h after inoculation. We may assume that under these conditions, the whole population of conidia was affected, whereas for the treatment D0, only the mycelial length of conidia able to germinate after the irradiation were measured, thus concerning the fraction of the population the most resistant to radiation.

*Implications in the vineyard*

The detrimental effect of radiation on the infection process is likely to affect the development of the disease in the vineyard. At the beginning of the growing season, when the canopy density is low and the temperatures are moderate, radiation may represent a limiting factor for the disease, especially on the upper side of leaves. In these conditions, the lower sides of leaves, which do not receive direct light, are more favourable for infection. As the vine shoots grow, shaded zones could represent the most favourable infection sites, with lower temperature and radiation. Bunches directly exposed to sunshine are also less likely to be infected by *U. necator* than shaded ones. From these results, training systems providing less shade can be helpful to reduce powdery mildew infections. In this respect, Chellemi and Marois (1992) have shown that removal of leaves localized nearby clusters lead to less infection.

As both thermic and photic effects of radiation can affect fungal infection, surface temperature as well as incident radiation can be considered as relevant microclimatic factors to take into account for a better understanding of the disease development in the vineyard. Further investigations are needed to quantify the radiation effect on the other processes of the fungal infection cycle, particularly sporulation. Complementary studies on entire plants could also assess radiation effects on the grapevine in a more realistic way.

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