# Effect of Water Stress on Reproduction and Colonization of *Podosphaera aphanis* of Strawberry

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## ABSTRACT

In a number of pathosystems involving the powdery mildews (Erysiphales), plant stress is associated with decreased disease susceptibility and is detrimental to pathogen growth and reproduction. However, in strawberry, anecdotal observations associate severe powdery mildew (*Podosphaera aphanis*) with water stress. In a 2017 survey of 42 strawberry growers in Norway and California, 40 growers agreed with a statement that water-stressed strawberry plants were more susceptible to powdery mildew compared to non-stressed plants. In repeated *in vitro* and *in vivo* experiments, we found that water stress was consistently and significantly unfavorable to conidial germination, infection, and increases in disease severity. Deleterious effects on the pathogen were observed from both pre-inoculation and post-inoculation water stress in the host. Soil moisture content in the range from 0 to 50% was correlated ($R^2$ = 0.897) with germinability of conidia harvested from extant colonies that developed on plants growing at different levels of water stress. These studies confirm that *P. aphanis* fits the norm for biotrophic powdery mildews and hosts under stress. Mild water stress, compared to a state of optimal hydration, is likely to decrease rather than increase susceptibility of strawberry to *P. aphanis*. We believe it is possible that foliar symptoms of leaf curling due to diffuse and inconspicuous infection of the lower leaf surfaces by *P. aphanis* could easily be mistakenly attributed to water stress, which we observed as having a nearly identical leaf curling symptom in strawberry.

Keywords: abiotic stress, powdery mildew, small fruits,

## INTRODUCTION

Powdery mildew, caused by *Podosphaera aphanis,* can be a devastating disease of strawberry (*Fragaria* x *ananassa*). The pathogen infects all aboveground organs and results in malformed or aborted fruit (Daubeny 1961, Peres and Mertely 2009). Conidia of *P. aphanis* are dispersed by wind (Blanco et al. 2004; Strand 2008), and germination is most favorable when temperatures are between 15 and 25ºC (Amsalem et al. 2006; Peries 1962) and humidity is above 75% (Jhooty and McKeen 1965). Germination and colony development, however, are inhibited by free water, particularly when supplied as rain or overhead irrigation (Peries 1962).

Abiotic stresses, including extreme temperatures and water stress, generally reduce host suitability for biotrophic plant pathogens, in particular powdery mildews (Gadoury and Pearson 1988, Moyer et al. 2010, Weldon et al. 2017). The effect of water stress on *P. aphanis* has not been thoroughly investigated. However, substantial research on water stress and powdery mildews of other crops has been reported. Water stressed barley (Ayres and Woolacott 1980, Wiese et al. 2004), cereals (Bencze et al. 2008), garlic mustard (Enright and Cipollini 2011), grapevine (Austin and Wilcox 2011), pepper (Caesar and Clerk 1984, Caesar and Clerk 1985), and tomato (Achuo et al. 2006) are less susceptible to powdery mildew compared to well-watered plants. Water stress has been found to have an adverse impact on the development and vigor of various powdery mildews. The length and width of conidia of *Leveillula taurica* on pepper plants decreased

with decreased relative water content in the leaves, as did conidiophore length (Caesar and Clerk 1984). Similarly, germination and appressorium formation by *Blumeria graminis* f. sp. *hordei* were inhibited in barley grown in dry soil, and the rate of colony expansion was reduced compared with plants grown in wet soil (Ayres and Woolacott 1980). In severely water stressed garlic mustard (*Alliaria petiolata*), the colony size of *Erysiphe cruciferarum* was one-fifth that of well-watered plants (Enright and Cipollini 2011). Increased thickness of epidermal cell walls induced by water stress was negatively correlated with colony size in powdery mildew of barley (Ayres and Woolacott 1980). Water stress resulted in a two-fold increase in foliar levels of abscisic acid (ABA) and an increased resistance to *Oidium neolycopersici* on tomato (Achuo et al. 2006).

Despite the foregoing, we encountered a widespread belief among strawberry producers that severity of powdery mildew is causally related to water stress. In a 2017 survey of 42 strawberry growers in California and Norway, 40 agreed with a statement that water stressed strawberries were more susceptible to powdery mildew than non-stressed plants. Our goal in the present study was to reconcile the foregoing perception among strawberry growers and reveal whether or not powdery mildew is a disease enhanced by water stress. Based on experimental evidence spanning a diversity of powdery mildews on other crops indicating decreased susceptibility to infection and decreased severity of disease due to water stress, we hypothesize that water stress will reduce the colonization and reproduction of the obligate biotroph powdery mildew in strawberry, just as water stress is debilitating to the plant. Our objectives were: (i) to determine the degree to which timing and duration of water stress affected the incidence

87 and severity of *P. aphanis*; and (ii) to assess the effect of water stress on germination of
88 *P. aphanis* conidia.

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91 **MATERIALS AND METHODS**

92 **Plant production.** Strawberry plug plants of cv. Korona were obtained from a
93 certified nursery. Plants were potted in 11-cm-diameter plastic pots containing a standard
94 limed fertilized peat medium (Go'jord Proff from Degernes Torvstrøfabrikk, Degernes,
95 Norway). The growth medium contained 80 and 10% peat moss (*Sphagnum* spp.)
96 classified as H1 – H4 and H4 – H6, respectively, on the von Post scale of humification,
97 and with 10% fine sand. Potted plants were contained and monitored for 2 weeks before
98 transfer to the greenhouse to ensure that the plants did not have virus-vectoring insects.
99 During quarantine, plants were kept at a minimum air temperature of 20°C, 16 h daylight
100 period, and 80% relative humidity (RH). All watering during quarantine and later for the
101 experiments was done with fertilized water with an electric conductivity of 1.7 mS/cm, with
102 a mixture from stock solutions of Superba™ Rød (7-4-22 NPK + micronutrients) and
103 Calcinit™ (15.5% N, 19% Ca).

104 **Inoculum preparation.** Emergent powdery mildew-free and ontogenically
105 susceptible strawberry trifoliate leaves (approximately one-half mature size, phenological
106 stages 3 to 4 *sensu* Asalf et al. 2014) were used for the maintenance and multiplication
107 of *P. aphanis* for experiments on pathogen growth. Absence of powdery mildew prior to
108 inoculation was confirmed by examining the leaves using a stereomicroscope at 10 to

30x magnification. Trifoliate leaves were surface-sanitized in 0.5% sodium hypochlorite for 5 min, rinsed twice in distilled water for 2 min, and then air dried for 3 min under a laminar flow hood. The petiole was removed, and the leaves were divided into single leaflets, unfolded gently, and placed within 9-cm diameter Petri dishes containing 0.5% water agar amended with 0.03% benzimidazole with the abaxial surface of the leaflets facing upward. The abaxial surface of the leaflets was then inoculated with conidia of *P. aphanis,* by touching them with leaves bearing 8- to 10-day-old sporulating colonies obtained from donor plants maintained as a source of inoculum. Each Petri dish contained four leaflets selected from four different leaves. Inoculated leaflets were then incubated in a growth chamber (20°C, 16 h light: 8 h dark photoperiod, and 80% RH). To maintain a source of inoculum, colonies were transferred to new sanitized leaflets every 8 to 10 days.

**Severity of powdery mildew on leaves subjected to water stress *in vivo*.** Following the two-week quarantine, sixty mildew-free 'Korona' plants were transferred to the greenhouse (18 to 20°C, 16 h daylight period, 80% RH). A 15-cm-diameter tray was placed beneath each plant, which was potted into an 11-cm diameter plastic pot containing the growth medium previously described. Approximately 45 ml of fertilized water (previously specified) was added daily to the tray for three weeks. The daily amount of water needed was determined by calculating average water lost by transpiration. Prior to the experiment, twenty 'Korona' plants were used to calculate the average water loss by transpiration. Initially, the weight of the potted plants at soil water holding capacity, which was measured by adding 100 ml of water to the pot and then allowing the excess water to drain before weighing the pot, was subtracted from the weight after 24 h. Enough

132 water was added to account for the weight loss. After sufficient water was added, the
133 potted plants were weighed again and then weighed once more after 24 h. The process
134 was repeated for one week.

135 After three weeks in the greenhouse, the plants were then divided into two groups
136 of 30 plants each. One group continued to be watered as above while the other was water
137 stressed. Water stress was attained using a watering regime adapted from Enright and
138 Cipollini (2011). Water stressed plants were observed daily and deprived of water until
139 wilting occurred. Plants were then supplied with approximately 45 ml water and allowed
140 to wilt again. Two weeks later, following approximately four cycles of wilting in the water
141 stressed plants, leaves of both treatment groups were inoculated. One to two leaves per
142 plant were tagged at either of two developmental stages: (i) stage 2, leaves light green,
143 leaflets separated, lamina unfolded 15 to 30 degrees, and blades not reflexed from the
144 petiole, and (ii) stage 3, leaves light green, leaflets separated, lamina unfolded more than
145 60 degrees, blades reflexed from petiole (Asalf et al. 2014). Leaves were inoculated with
146 conidia harvested from 8- to 10-day old sporulating colonies maintained on colonized
147 leaves in Petri dishes and transferred to the adaxial and abaxial leaf surfaces using a fine
148 artist's paintbrush. The tip of the brush was touched to the sporulating colony and then
149 very lightly touched to and pulled across the adaxial and abaxial surfaces of the leaf to
150 be inoculated. Following inoculation, plants were divided into the following treatment
151 groups: (i) well-watered pre- and post-inoculation (WW), (ii) water stressed pre- and post-
152 inoculation (SS), (iii) well-watered pre-inoculation and water stressed post-inoculation
153 (WS), and (iv) water stressed pre-inoculation and well-watered post-inoculation (SW).
154 Water stress post-inoculation was attained as previously described. Each treatment group

had five replicates of three strawberry plants each, and the experiment was organized in a randomized block design. The experiment was repeated twice with a three-day interval between the inoculations.

Both latency period and severity of leaf colonization were assessed. The duration of the latency period was expressed as the number of days between the date of inoculation and the date that sporulation was first observed on the inoculated plants. Disease severity was visually recorded as the percentage of the inoculated leaf surface macroscopically colonized by the pathogen at two and three weeks after inoculation. Above ground fresh weight, dry weight, number of runners and leaf area of inoculated leaves were also determined three weeks post-inoculation.

The percentage of volumetric soil moisture as a function of electric conductivity in the soil of three replicates of three strawberry plants in each treatment group was monitored prior to watering 1, 3, 7, 10, 12, 15, and 21 days after inoculation using a soil moisture meter (SM150, Delta-T Devices Ltd. Cambridge, United Kingdom)

To assess the viability of the conidial inoculum 21 days after inoculation, five plants (one from each replicate) with powdery mildew colonies from each treatment group were arbitrarily selected. An inoculated leaflet from each plant was gently tapped against a glass microscope slide. The slide was stained with Lactofuchsin, and 100 conidia per sample (leaflet) were examined at 400×. Conidia were considered as germinated if they bore a germ tube equal to or longer than the width of the conidium.

**Germination of conidia harvested from leaves subjected to water stress.** After two weeks in quarantine, six powdery mildew-free ‘Korona’ plug plants were transferred to the greenhouse (16 to 32°C, 35 to 95% RH, and 16 h daylight period). A 15-cm-diameter tray was placed beneath each plant, which was potted into an 11-cm diameter plastic pot containing the growth medium previously described. Three weeks prior to inoculation, the plants were supplied daily with approximately 45 ml of fertilized water as previously specified..

On the day of inoculation, one light green leaf with the leaflets separated and lamina of each leaflet unfolded at an angle of 15 to 30 degrees, and with the leaf blades not yet reflexed from the petiole (*i.e.,* stage 3, Asalf et al. 2014), per plant was tagged. The tagged leaves were inoculated as described previously. Two weeks after inoculation, the plants were divided into two groups, each of which consisted of three plants. The experiment was organized in a randomized block design. One group continued to be watered as described above. Watering ceased completely for the other group. The aim was to obtain a gradient of volumetric soil moisture values ranging from 1 to 50%. The percentage of volumetric soil moisture was monitored for all plants daily using the soil moisture meter previously described. At 0, 24, 48, 72, 96, and 120 h after beginning of water stress treatments, conidia from one inoculated leaflet per plant was deposited on the surface of three water agar Petri dishes (3.5 cm diameter) by gently touching the diseased leaflet to the agar surface. Petri dishes were sealed and incubated for 24 h in a growth chamber (18°C, 16 h light: 8 h dark photoperiod, and 60% RH). A piece of water agar was taken from the center of each Petri dish, mounted on a glass microscope slide, stained with Lactofuchsin, and 100 conidia per sample were examined at 400x× and rated

for germination as before. Morphology of conidiophores and conidia was also observed under a light microscope. The experiment was repeated six times.

**Statistical analysis.** Data of disease severity and germination of *P. aphanis* on the plant were analyzed with analysis of variance (ANOVA) using JMP (SAS Institute 2013). Additionally, data of soil moisture, fresh weight, dry weight, number of runners, and leaf area of inoculated leaves were analyzed with ANOVA. Data were examined for homogeneity of variance and normality with the Shapiro-Wilk test. Watering conditions was considered a fixed effect and experimental repeat was a random effect. Significant differences among treatment means were determined by Tukey's pairwise comparison at $\alpha = 0.05$.

JMP (SAS Institute 2013) was also used to conduct regression analyses on the effect of soil moisture and time on germination of *P. aphanis*. Data were transformed nonlinearly when the residual plot had a nonrandom pattern of data distribution. The transformation method that resulted in the highest coefficient of determination ($R^2$) is presented.

## RESULTS

**Effect of water stress on disease severity *in vivo*.** The soil moisture levels of plants under water stress (SS) was approximately one-third that of plants in the well-watered (WW) treatment. The soil moisture of SW plants rapidly increased as soon as irrigation resumed post-inoculation and was equivalent to the WW plants at 3 days post-inoculation. The soil moisture of the WS plants decreased more slowly and reached the level of the SS plants on Day 7 after inoculation (Table 1). Plant growth was correlated

221 with soil moisture conditions. Water stress either before or after inoculation decreased
222 the fresh and dry weight, number of runners, and the area of the inoculated leaf,
223 compared to plants that were well-watered throughout the experiment (Table 2).
224 Furthermore, water stressed plants developed a leaf curling similar to what may be
225 observed in plants infected by powdery mildew (Fig. 1).

226 The inoculation methods employed yielded a high degree of success. More than
227 90% of inoculated leaflets developed mildew symptoms at 14 days post-inoculation, and
228 all inoculated leaflets bore mildew colonies 21 days post-inoculation, irrespective of pre-
229 or post-inoculation water status. The mean disease incidence 9 days post-inoculation
230 (standard error of the mean, S.E. in parentheses) was 60% (5.26), 62% (3.29), 64%
231 (3.23), and 48% (6.24) for SS, SW, WW, and WS, respectively. Neither the latency period
232 nor the disease incidence values were significantly different among the treatments ($p > 0.05$).
233 Leaf curling symptoms were observed on both non-inoculated and inoculated water
234 stressed plants.

235 The percentage of the leaf surface colonized by *P. aphanis* was significantly
236 greater on the abaxial compared to the adaxial surface by a factor of about 1.5 at 14 days
237 post-inoculation, and by a factor of about 2 by 21 days post-inoculation (Fig. 2, $p = 0.001$).
238 At both 14 and 21 days post-inoculation, all treatments involving water stress significantly
239 but equivalently reduced disease severity on the abaxial leaf surface. Disease severity
240 on the adaxial leaf surfaces was too low and too variable to detect significant treatment
241 effects at either day 14 or 21 after inoculation (Fig. 2, $p = 0.075$). Germination of conidia
242 was significantly different among treatments. There was approximately a four-fold

reduction in percent germination on SS and WS plants compared to WW and SW plants.(Fig. 3, $p = 0.001$).

**Effect of water stress on germination.** Germination of conidia from leaves of strawberry plants was highly correlated with the soil moisture content at the time that the conidia were harvested from plants from 0 to 53% soil saturation. At the lowest levels of soil moisture, percent conidial germination were near 0 and increased linearly to a maximum of approximately 30% germination at a soil moisture content of 53% (Fig. 4, $y = 0.54x + 3.02$, $R^2 = 82.1$, $p < 0.0001$), where y = percent germinated conidia and x = soil moisture content (%). We also observed that conidia and conidiophores were shriveled and desiccated on the leaves removed from water stressed compared to on well-watered plants 6 h after beginning of water stress (Fig. 5).

## DISCUSSION

Our experiments clearly indicated that water stress in strawberry suppressed conidial germination and severity of *P. aphanis*. The rate of germination of conidia was proportional to the soil moisture content of the strawberry plants and water-stressed plants developed less disease than well-watered plants. Our studies relied on soil moisture content to determine the association between water stress and conidial germination. Soil moisture was measured using a soil moisture meter, which is an indirect measure of water stress. Barr and Weatherly (1962) reported that relative water content (RWC), a direct measure, is the most appropriate measure of plant water status. This method, however, is destructive and could not be used for this experiment. Novel, non-destructive direct methodologies, such as thermal imaging or the use of terahertz quantum cascade detectors, could clarify the relationship between water stress and

conidial germination and should be considered for future studies (Born et al. 2014, Lee et al. 2019).

Collectively, the foregoing support the commonly observed and reported unfavorability of plant stress in general, and water stress in particular for a number of powdery mildews (Achuo et al. 2006, Ayres and Woolacott 1980, Caesar and Clerk 1985, Enright and Cipollini 2011, Moyer et al. 2010, Wiese et al. 2004, Woolacott and Ayres 1984). For example, according to Woolacott and Ayres (1984), mildew-susceptible barley cultivars that experienced water stress exhibited a lower number of colonies, lower rates of colony expansion, lower number of spores per colony, and an increase in the latent period. Additionally, Caesar and Clerk (1984) reported that the dimensions of conidia and conidiophores of *Leveillula taurica* were reduced by 25% on water stressed peppers as compared to non-stressed.

The commonly held belief among strawberry growers that severe epidemics of powdery mildew are associated with water stress is difficult to reconcile with the consistently deleterious effects of water stress in the host upon many species within the Erysiphales. However, we believe it is possible that foliar symptoms of leaf curling due to diffuse and inconspicuous infection of the lower leaf surfaces by *P. aphanis* could easily be mistakenly attributed to water stress, which we observed as having a nearly identical leaf curling symptom in strawberry. Inconspicuous and non-sporulating adaxial leaf infections are common in the early stages of epidemic development in this pathosystem, due to leaf folding and obscuring of the adaxial leaf surface during the ontogenically susceptible stages of leaf emergence and expansion (Asalf et al. 2014). The later sporulation of the abaxial colonies, and the spread to fruit and the adaxial leaf surfaces

would add credence to an association of the symptoms incorrectly attributed to water stress with later conspicuously severe levels of powdery mildew.

Deleterious effects on conidial germination were not only observed at levels of water stress that resulted in visible wilting of plants, but also at lower levels of water stress that did not cause wilting. Differential levels of soil moisture across a range generally not associated with wilting (e.g., 20-50% saturation) were well described by a linear model relating the rates of conidial germination to soil moisture content of plants on which the conidia were obtained. Thus, it is possible that germination potential of conidia under field or greenhouse conditions is a dynamic process closely linked to the water relations of the host. Powdery mildews are unique among fungal pathogens in their ability to germinate robustly in the absence of free water. The conidia characteristically bear one or more large water-containing vacuoles that reportedly offset the need for an exogenous water supply. Powdery mildews must absorb water and nutrients from the host plant through the haustoria (Schnathorst 1965, Yarwood 1957). Water stress may make transport of water and nutrients from the host cytoplasm into haustorial cytoplasm more difficult. Further research would be necessary to ascertain if water stress in the host might reduce the quantity of vacuolar water in conidia that develop under water stress in the host.

Perhaps the most significant finding of the present study was not to refute the perception of an association between water stress and more severe development of strawberry powdery mildew. Rather, we quantified the magnitude of the effect of water stress on germination potential of conidia. The magnitude of the impact of mild water stress (*e.g.,* a 50 to 95% reduction in germination) was equivalent to reported impacts of suboptimal or supraoptimal temperature or RH upon germination in *P. aphanis* (Amsalem

312 et al. 2006, Caesar and Clerk 1985, Carroll and Wilcox 2003). However, unlike RH and
313 temperature, host water stress is not presently a component of advisory models for
314 strawberry powdery mildew. Even under conditions of abundant soil moisture, strawberry
315 plants can experience water stress during the warmest parts of the growing seasons in
316 diverse growing regions, in e.g. California, Florida, Spain, Italy, Morocco, and Australia.
317 Furthermore, it is possible that the observed effects of host water stress on conidial
318 germination in *P. aphanis* have parallels in other powdery mildew pathosystems. We are
319 continuing studies to incorporate host water status as an additional component to improve
320 accuracy of an advisory system for strawberry powdery mildew and anticipate that similar
321 modifications could be evaluated for advisory models used in other powdery mildew
322 pathosystems.

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Table 1. Changes in soil moisture levels between days 1 and 21 post-inoculation under four watering regimes: well-watered pre- and post-inoculation (WW), water stressed pre-inoculation and well-watered post-inoculation (SW), water stressed pre- and post-inoculation (SS), and well-watered pre-inoculation and water stressed post-inoculation (WS).

[y] Standard error of the mean.

[z] Means with different uppercase letters within columns are significantly different according to Tukey's pairwise comparison at α = 0.05.

| | Soil moisture (%) | | | | | | |
|---|---|---|---|---|---|---|---|
| Treatment | Day 1 | Day 3 | Day 7 | Day 10 | Day 12 | Day 15 | Day 21 |
| WW | 39.7 (5.2)[y] A[z] | 32.2 (3.5) A | 37.7 (2.3) A | 37.8 (3.8) A | 30.2 (2.2) A | 39.2 (4.0) A | 39.7 (6.0) A |
| SW | 10.7 (1.6) B | 38.2 (2.3) A | 36.6 (2.8) A | 37.9 (3.5) A | 35.4 (3.4) A | 39.5 (1.2) A | 41.0 (4.2) A |
| SS | 9.4 (1.6) B | 9.8 (1.2) B | 12.5 (1.4) B | 10.0 (2.0) B | 9.4 (1.4) B | 10.1 (1.9) B | 8.2 (1.9) B |
| WS | 45.7 (2.9) A | 38.2 (2.3) A | 11.4 (1.4) B | 10.3 (2.4) B | 8.4 (1.5) B | 7.2 (1.0) B | 7.2 (1.6) B |

Table 2. Effects of water stress on fresh and dry weight, number of runners, and leaf area of the inoculated leaves of well-watered pre- and post-inoculation (WW), water stressed pre-inoculation and well-watered post-inoculation (SW), water stressed pre- and post-inoculation (SS), and well-watered pre-inoculation and water stressed post-inoculation (WS) three weeks post-inoculation.

| Treatment | Fresh weight (g) | Dry weight (g) | Number of runners | Leaf area ($mm^2$) |
|---|---|---|---|---|
| WW | 26.1 (1.3)[y] A[z] | 4.4 (0.2) A | 2.2 (0.2) A | 150.7 (6.8) A |
| SW | 22.0 (1.5) B | 3.9 (0.2) A | 1.9 (0.3) A | 129.7 (7.8) AB |

| | | | | |
|---|---|---|---|---|
| SS | 13.0 (0.4) C | 2.7 (0.1) B | 0.8 (0.1) B | 74.8 (5.4) C |
| WS | 14.4 (0.6) C | 3.2 (0.2) B | 0.6 (0.2) B | 104.8 (6.2) B |

[y] Standard error of the mean.
[z] Means with different uppercase letters within columns are significantly different according to Tukey's pairwise comparison at α = 0.05.


Fig. 1. Well-watered plants infected with powdery mildew (A and C) and water-stressed disease free plants (B and D), all of strawberry cv. Korona.

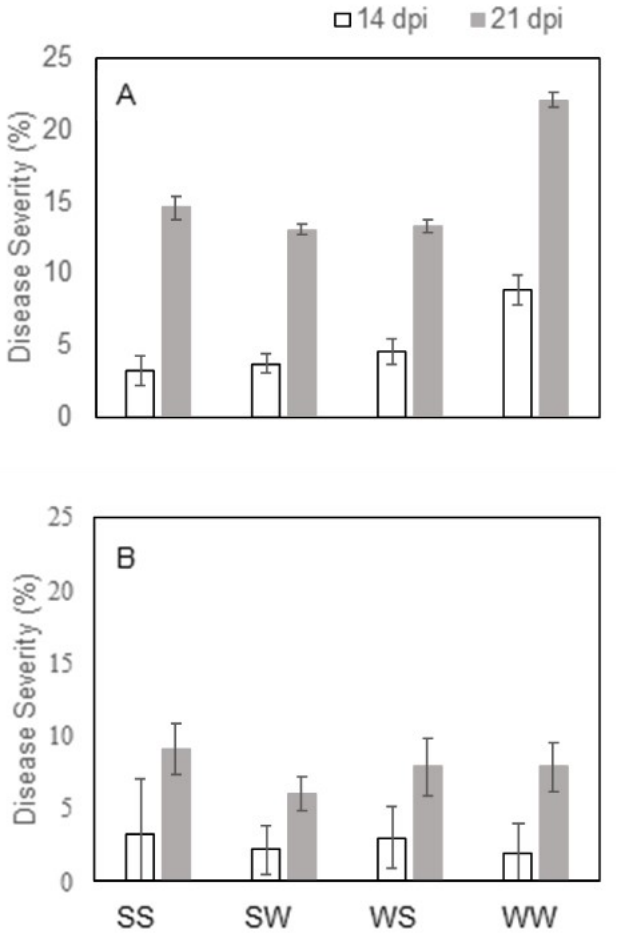
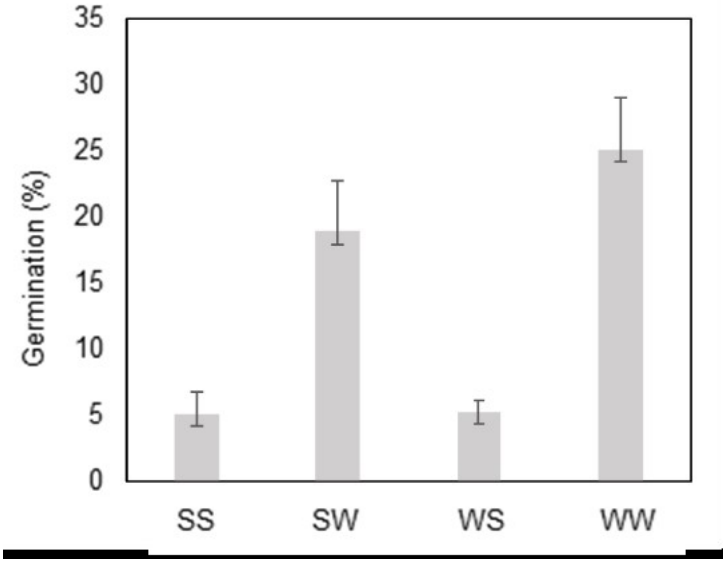


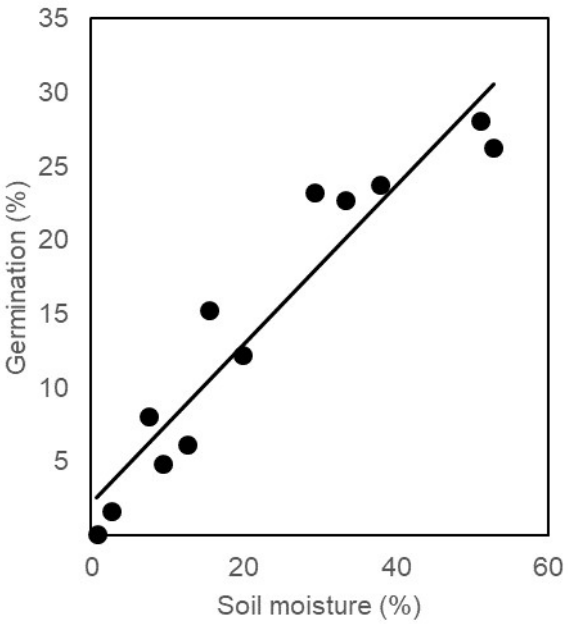

Fig. 2. Disease severity (%) of *Podosphaera aphanis* on the abaxial (A) and adaxial (B) leaf side of plants being water stressed pre- and post-inoculation (SS), water stressed pre-inoculation and well-watered post-inoculation (SW), well-watered pre-inoculation and water stressed post-inoculation (WS), and well-watered pre- and post-inoculation (WW) 14 and 21 days post-inoculation. Vertical bars represent standard error of the mean.




445

446 Fig. 3. Germination (%) 21 days post-inoculation of conidia of *Podosphaera aphanis*
447 from plants being water stressed pre- and post-inoculation (SS), water stressed pre-
448 inoculation and well-watered post-inoculation (SW), well-watered pre-inoculation and
449 water stressed post-inoculation (WS), well-watered pre- and post-inoculation (WW).
450 Vertical bars represent standard error of the mean.

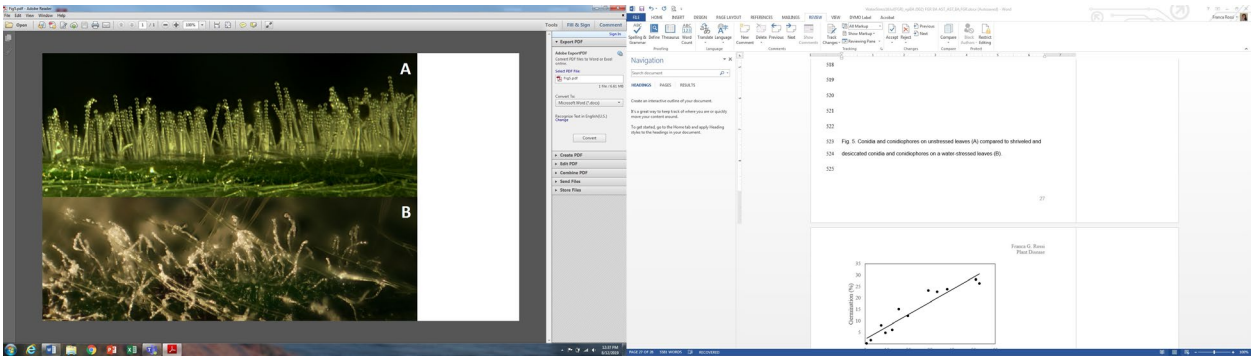
451




452

453 Fig. 4. Effect of soil moisture content on the percentage of conidia that germinated on
454 water agar 24 h after harvest from leaves of potted strawberry plants ($p < 0.0001$); y =
455 percent germinated conidia and x = soil moisture content (%).

456




457

458 Fig. 5. Conidia and conidiophores on detached leaves from well-watered (A) and water-
459 stressed (B) plants 6 h after beginning of water stress.

460