The effect of powdery mildew on barley under simulated Mediterranean drought conditions
by Fatima Zine Elabidine

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Plant Pathology
Montana State University

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Fatima Zine Elabidine

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES -- Continued

LIST OF FIGURES

ABSTRACT

The effect of powdery mildew on barley shoots and roots was investigated. Plants inoculated with powdery mildew exhibited reduced size and number of both primary and secondary roots. The effect of the fungus on dry weight of shoots and both seminal and adventitious roots was statistically significant. The combined effect of powdery mildew and four different soil-water levels also was studied. Diseased plants wilted and died sooner than healthy plants when both were subjected to drought. Dry weight of both shoots and roots was reduced under combined disease and drought stress. Barley seedlings infected with powdery mildew are more likely to be damaged by late season drought, even though symptoms of the disease disappear with the onset of hot, dry weather.

INTRODUCTION

Barley powdery mildew is an important foliar disease, caused by *Erysiphe graminis* f. sp. *hordei*. This disease has been studied intensively in cool and temperate regions in the world. In the Mediterranean area disease symptoms are usually observed on young plants, resulting in serious yield losses. Because powdery mildew symptoms disappear under high temperature and drought conditions in dry Mediterranean areas, the disease was not considered a serious threat to barley production. In these regions where in addition to diseases, barley suffers from harsh environmental conditions, such as high temperatures and drought, the crop performance is often very poor. In the Mediterranean area barley is grown on a large percentage of the arable land and is used as food for both humans and animals. It is used as green grazing, straw roughage, grain or as combinations of all these. Despite the importance of barley in the economy of the farming system in North Africa and the Middle East, it is grown under poor crop management practices and is given less attention than wheat.

Extensive literature is available on the effects of the fungus on above-ground parts of the plant and on the root system. However, little is known of the effect of powdery mildew on barley plants under drought conditions.

The following research was conducted to answer two principal questions:

1. Does barley powdery mildew affect shoot as well as root growth?

2. Can early infection of seedlings by powdery mildew exacerbate later effects of water stress on barley growth and productivity?

The answers to these questions may elucidate our understanding of the interaction between powdery mildew and drought and their effect on barley, and perhaps facilitate the orientation of additional research.

LITERATURE REVIEW

Barley powdery mildew, Erysiphe graminis DC. f. sp. hordei. Em. Marchal is a severe disease that occurs wherever barley (Hordeum vulgare L.) is grown. Although the parasite lives superficially by sending only haustoria into epidermal cells of aerial parts of the plant, it can cause appreciable crop losses (Last, 1962). The disease has been intensively studied in temperate moist climate regions in the world. In northwestern Europe, early infection of spring barley is considered most damaging (Last,1962; Brooks, 1972; Jenkyn, 1974; Griffiths et al., 1975; Jenkyn and Bainbridge, 1978).

Many authors stressed the importance of the disease in Mediterranean Europe (Srivastava and Saari, 1975; Barradas, 1977; Comenge, 1977; Velasco, 1981). Powdery mildew is a devastating disease in Spain (Comenge, 1977; Velasco, 1981). In Portugal and Greece the disease is ranked second in importance to other barley diseases (Barradas, 1977; Skorda, 1977). In North Africa the losses reach 10 to 30%, and the disease is ranked third in importance to other barley diseases (Caddel and Wilcoxson, 1975; Boulif et al., 1981; El-Ahmed et al., 1981; Srivastava, 1981; Kamel, 1981; Kamel et al., 1987). In Egypt the damage from the disease first attracted researcher's attention in 1977 (Abdelhack et al., 1977).

In the Mediterranean regions, barley is cultivated under diverse climatic and edaphic conditions. The crop is sown in October-November and harvested in June depending on temperature and rainfall during the growth cycle. The climate is characterized by mild winters and hot summers. For instance, in Rabat, Morocco the average January and June temperatures are 10°C and 27°C, respectively. Rains occur in fall, winter and spring depending on the region and the rainfall is distributed sporadically. The precipitation is sometimes heavy and it is possible to receive a higher quantity of precipitation than the annual average in only one rain storm (Comenge, 1977). Barley is used as food for both humans and animals in North Africa and is the predominant crop in areas receiving 200-350 mm of annual rainfall (Srivastava and Saari, 1975; Kamel, 1981; Srivastava, 1981). In the other Mediterranean regions, barley is used as livestock feed and/or as a malting crop.

Powdery mildew symptoms are observed early in spring in Morocco (Schluter, 1976). In Tunisia, infections occur during tillering but the symptoms disappear when the plant reaches its adult stage (Ghodbane et al., 1981). In Greece, the infection occurs when the plant is in the 3-5 leaf stage (Skorda, 1981). Many authors have reported the disastrous effect of early infection on barley plants. Schluter (1976) found that the earlier the infection occurs, the higher the losses. Skorda (1981) observed that in Greece early seedling infection has greater potential effect on yield than does infection on flag leaves. Schluter (1976) noticed that an attack during tillering can lead to high losses because the plants remain small through their cycle.

Early development of the disease is favored by high seeding rates and high humidity during winter and early spring (Ghodbane et al., 1981; Skorda, 1981). High seeding rates, combined with high rates of nitrogen fertilization in intensive cultural systems, has lead to a heavy development of the disease (Schluter, 1976; Skorda, 1977 and 1981).

The fungus overseasons as fruiting bodies (cleistothecia) that appear late in spring and early in summer (Schluter, 1976; Moseman, 1981). Under suitable conditions in the fall, cleistothecia open and release ascospores that are able to infect green living tissue (Smedegard-Petersen, 1967; Schluter, 1976). The sources of primary infection are 1) the debris carrying cleistothecia through the hot, dry summer, and 2) infected wild cereals and grasses (Schluter, 1976). Conidia are wind-borne and are responsible for secondary disease spread (Cherewick, 1944; Schluter, 1976). Many authors have reported the effects of the fungus on plant metabolism. E. graminis f.sp. hordei increases the host rate of respiration and decreases its photosynthesis (Allen and Goddard, 1938; Pratt, 1938; Allen, 1942; Rapilly et al., 1971). Moreover, Last (1962) found that the net assimilation rate of infected barley plants was decreased 12 to 68 days after inoculation. Last (1962) and Rapilly et al. (1971) reported that the fungus causes an imbalance between shoots (assimilating system) and roots (absorbing system) by decreasing dry weight of roots per unit of leaf. Dry weight of diseased plants was lower than those of healthy plants (Last, 1962; Paulech, 1966; Brooks, 1972). This imbalance leads to a reduction of the number of tillers, the size and number of spikes, plant height and eventually yield (Last, 1962; Rapilly, 1971; Brooks, 1972; Griffiths et al., 1975). Last's findings indicated that grain size and yield of ears were seriously reduced, especially when infection occurs early in the plant cycle. Jenkyn (1974) obtained increases in grain size when early mildew attack was controlled by seed-applied fungicide (ethirimol). A study on the effects of powdery mildew at different growth stages on grain yield of barley was carried out by Griffiths et al. (1975). The disease was controlled by applications of drazoxolon. The results indicated that early mildew attack (Growth stage 2-6 in Feekes scale, Large 1954) reduced grain size and numbers of grains per tiller.

In a study of the effect of powdery mildew on barley growth, Last (1962) found that the number of shoots per plant was decreased within three weeks of inoculation, and that after this stage the shoot size was affected. He found that plants inoculated at seedling stage grew and yielded less than plants sprayed with lime sulphur. A reduction in shoot number and size was observed by Jenkyn (1974). Early mildew attack reduced tiller number in a study conducted by Griffiths et al. (1975). Graf-Marin (1934) and Last (1962) reported that powdery mildew decreased dry matter production within three weeks of pathogenesis. Last (1962) also found that the total dry matter of mildewed plants was decreased significantly. Tillers of diseased plants are less likely to survive and produce ears (Paulech, 1966 and 1969; Brooks, 1972).

Most studies on powdery mildew have been oriented towards its effect on the leaves, with little attention given to possible effects on roots. However, Last (1962) found that the dry matter reduction caused by powdery mildew was relatively greater on roots than on shoots. In plants inoculated soon after emergence, root growth was decreased by up to 50%, resulting in a small root: shoot ratio (Last, 1962; Jenkyn and Bainbridge, 1978). The effect of powdery mildew on root growth was later confirmed by other authors (Paulech, 1966 and 1969; Brooks, 1972; Vizarova and Minarcic, 1974; Griffiths et al.,1975). Furthermore, Frimmel (1972, 1977) reported that infection at an early stage of plant development reduced the growth of the roots. The reduction of the root system caused by the fungus was explained by Minarcic and Paulech (1975) who found that *E. graminis* caused an excessive inhibition of mitotic cell division in the barley root meristem during pathogenesis. Indeed, four weeks after inoculation, the process had almost fully ceased.

All the studies done on the effect of drought on barley agree that there is an intimate interrelationship between shoots and roots. Water stress affects barley growth and development because it controls the conditions and physiological processes which determine the quality and the quantity of plant growth. The critical periods for soil-water stress for barley are: a) onset of tillering, b) anthesis, which begins shortly after ear emergence (Doorenbos and Pruitt, 1975; Weltzien and Srivastava, 1981).

In a field study conducted in Syrian drylands, Gregory et al. (1984) found that the weight of roots formed a high percentage of the total plant weight: 40% to 50% during early stem elongation and 18% at anthesis. However, Gorny and Patyna (1984) reported that the size of the entire system under lower soil moisture was directly related to the size of the seminal root system, and that the adventitious roots were of minor importance.

Water stress also has an effect on plant nutrition. Mac Key (1980) and Shone and Flood (1983) reported that lack of soil water decreased ion uptake and transport to the shoots.

Drought stress may reduce yield as well (Kramer, 1980). A reduction of the number of grains per ear was observed by

Ayres and Zadocks (1979), depending on the severity and timing of drought. Water stress at tillering and heading stages of the plant reduces seed number (Turner, 1977). After heading, the seed size is reduced (Turner, 1980; Weltzien and Srivastava, 1981). Water stress occurring at the time of floral initiation induces a reduction of grain number per spike. Sustained water stress occurring at anthesis induces embryo abortion and results in a reduction of grain number and grain weight (Townley-Smith and Hurd, 1977; Weltzien and Srivastava, 1981).

Few studies have been conducted on the combined effect of powdery mildew and drought on barley plants. Brooks (1972) and Griffiths et al. (1975) suggested that when drought and mildew occur together they may cause particularly serious yield losses. Ayres and Zadocks (1979) studied the effect of powdery mildew disease on water relations and growth of barley plants in a growth chamber. Plants were grown at three different soil-water levels (dry, wet, medium) and inoculated at different growth stages (26, 64 and 45 days-old). They reported that when infection occurred early in barley plant development, mildew and lack of soil water had additive, harmful effects on plant growth. The inhibition of root and shoot growth caused by mildew, however, was proportionately less when plants were grown in dry soil than in wetter soils. In their study, infection late in the cycle of the plants (ears emerged) had no effect on growth but a small increase in leaf senescence and water consumption.

In most of the studies conducted on the combined effect of powdery mildew and drought stress, barley plants were sown and grown at different soil-water levels. In this investigation the water treatment was applied when the plants were at the growth stage 7-8 in Feekes scale (Large, 1954).

MATERIALS AND METHODS

The barley cultivar Manchuria (CI 2330), susceptible to all known races of *Erysiphe graminis* f.sp. *hordei*, was used throughout the study both to produce inoculum and conduct experiments.

In a preliminary experiment, three different kinds of soil were tested to determine which one was best suited for growing healthy plants and easily washed free of the roots. A mixture of one part soil and three parts sand used in experiment 1, proved to be superior to a soil, sand and peat mixture at a ratio of 1:1:1 or to sand alone used in experiments 2 and 3, respectively.

Plants were grown in plastic pots (9x9 cm). Two seeds were planted per pot and the seedlings were thinned to one per pot after one week. Plants were kept in a growth chamber with a twelve-hour photoperiod. Light was provided by 26 fluorescent light tubes of 95 watts each, and four mercury vapor bulbs (400 watts each), which supplied approximately 2200 lux. Tubes were changed often in order to ensure optimal and constant light conditions during the experiments.

The temperature regime ranged from 23°C in darkness to 28°C during light hours. Average relative humidity was 80%.

Plants were kept under cages of finely woven muslin (50 x 61 x 76 cm). Cages were fitted in metal pans (1.25 x .55 x .025 m each) to avoid cross contamination and plants were watered daily by adding three liters of water directly into the pans. Every week, each plant received 45 ml of the following nutrient solution:

$Ca(NO_3)_2 \cdot 4H_2O$	0.850 g
$NaNO_3$	0.185 g
KH_2PO_4	0.163 g
KNO_3	0.144 g
$MgSO_4$	0.236 g
H_2O	1000 cc.

Each cage was equipped with a clear plastic top (to allow sufficient light penetration), and a muslin sleeve located on one side of the cage. The sleeve was used to avoid cross contamination when cages were opened.

In the first part of the study, the effect of barley powdery mildew on plant roots was studied. A completely randomized design was used with two treatments (inoculated and non-inoculated). Three experiments were conducted consecutively. The replications per treatment were 14, 12 and 13 in the first, second and third experiments respectively. Each replication corresponded to one seedling per pot. Plants were grown as previously described. The inoculation was carried out when plants were ten days old with isolate Bz1 by shaking or brushing conidia from diseased plants over healthy leaves. Thirty days after planting, roots were washed thoroughly under running water. All remaining impurities were removed with a pair of tweezers. A series of three circular copper sieves (USA Standards testing Sieves, ASTME-11 specification No. 6, No. 7, No. 12) were placed under the roots to capture and recover pieces lost during the washing procedure. Shoots and roots were dried separately for 12 hours at 70°C in paper bags in a Fisher isotemp oven. Shoots and roots were weighed with a Mettler balance. A one-way analysis of variance was performed to compare weights of shoots and roots (Lund, 1989).

In the second part of the study, the combined effect of powdery mildew and soil water stress was investigated. Three consecutive experiments were carried out. For each experiment, a 2x4 factorial completely randomized design with four replications was used. The two factors studied were: a) the treatment (inoculated, non-inoculated) and, b) water levels (0 water added = 0 liters, 1/3 of normal water added = 1 liter, 2/3 of normal water added = 2 liters, normal water added = 3 liters). The normal water dose was three liters added to each pan at daily intervals. Each replication contained 32 plants (16 inoculated, 16 non-inoculated). The previously described inoculation technique was carried out when the plants were ten days old. Water treatments were applied when the plants were 60 days old, a growth stage of 7-8 in Feeke's scale (Large, 1945). Plant roots were washed 15 days later in experiments 1 and 3. In the second experiment plant roots were washed 21 days after water treatments were begun. Shoots and roots were dried and weighed as described earlier. Data were analyzed by a multi-variable analysis of variance and covariance (Lund, 1989).

The isolate of Erysiphe graminis f.sp. hordei (Bz1) used in this study was collected in 1985 from naturally infested barley plants in the greenhouse at Montana State University. It was purified by single pustule isolation. The isolate was maintained and increased on Manchuria seedlings. Frequent virulence checks assured its purity throughout the experiment. The virulence spectrum of the isolate was determined by inoculating a set of barley differential cultivars (Table 1). The inoculum was kept available by weekly transfers of conidia from diseased to healthy Manchuria plants. Eight pots containing six Manchuria seedlings each were used. The plants were covered with clear glass lamp chimneys (25 cm tall) with a cotton plug in the top to avoid contamination. When the plants were eight days old, they were inoculated with the isolate Bz1 by shaking or brushing conidia from diseased plants over the healthy leaves. Small artist paint brushes were used. Diseased plants used as the source of inoculum for experiments were shaken 24 hours prior to inoculation, to remove older conidia. Subsequently, inoculations were carried out with newly produced young conidia.

Table 1. Reaction of several barley differential cultivars to inoculation with Bz1 isolate of E. graminis f.sp. hordei.

Cultivar	CI number	Resistance gene[a]	Reaction[b] to Bz1
Black Russian	CI 2202	ML-a2	R
Gopal	CI 1019	ML-a5	R
Long Glumes	CI 6168	ML-a7	R
Monte Cristo	CI 1017	ML-a9	R
Palmella Blue	CI 3609	ML-a+ML-g	S
Peruvian	CI 935	ML-at	S
Sultan	CI 13837	ML-a12	S
Ricardo	CI 6306	ML-a3	R
HLN 70-8		ml-o	R
A 222	CI 11555	ML-a11	S
Iso 1R	CI 16137	ML-a	R
Iso 2R	CI 16139	ML-g	I
Iso 3R	CI 16141	ML-h	R
Iso 4R	CI 16143	ML-k	S
Iso 5R	CI 16145	ML-p	S
Iso 10R	CI 16147	ML-a7	R
Iso 12R	CI 16149	ML-a10	R
Iso 20R	CI 16151	ML-a6+14	R
Iso 24R	CI 16155	ML-a13	R

(a) Genes of resistance of the host to the isolate. ML = dominant, ml = recessive.
(b) R = resistant, S = susceptible.

RESULTS

Effect of Powdery Mildew on Barley Plants

The effect of the fungus on plant roots was substantial. Roots of inoculated plants were visibly smaller and less numerous than those of the non-inoculated controls at washing time. The statistical analysis showed highly significant differences between the dry weight of the roots of diseased plants and the roots of healthy plants in experiments 1 and 2 (Table 2, Appendix A: Tables 7, 8 and 9). However, the fungus had a lesser, but still significant effect on plant roots. The dry weight of roots of infected plants was lower than the dry weight of healthy roots. The inoculated plants exhibited a reduction of almost 50% of root dry weight when compared with the healthy plants (Figure 1).

The effect of powdery mildew on the shoots varied from one experiment to another (Table 2, Appendix B: Tables 10, 11 and 12). Experiment 3 indicated highly significant differences between the dry weight of shoots in the inoculated plants and those in the healthy plants. However, in experiments 1 and 2 the fungus did not have a significant effect on plant shoots (Table 2).

These results indicated that barley powdery mildew adversely affects roots and shoots by decreasing their mass and number.

The effect on roots was more striking than the effect on shoots. This may result in an imbalance between shoots and roots that can reduce the plants ability to yield grain.

Table 2. Effect of powdery mildew on barley shoot and root dry weight.

Experiment	Treatment	Replications	Roots[a]	Shoots[b]
			mg	
# 1	Healthy	14	116.7**	384.7
	Inoculated	14	48.3**	316.6
# 2	Healthy	12	151.5**	380.8
	Inoculated	12	46.25**	310.8
# 3				
	Healthy	13	19.02*	126.7**
	Inoculated	13	10.93*	77.8**

(a) Means of dry weight of roots, in mg.
(b) Means of dry weight of shoots, in mg.
** Means were significantly different at $P < .01$.
* Means were significantly different at $P < .05$.

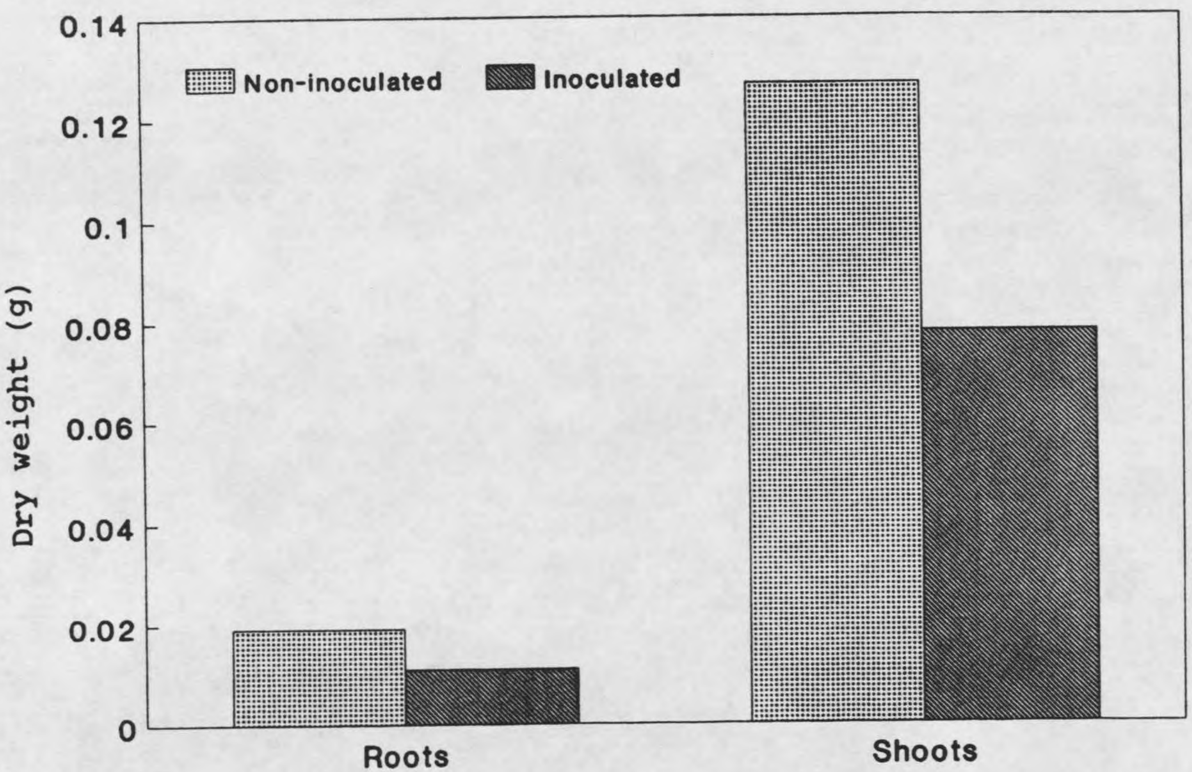

Figure 1. Effect of powdery mildew on barley shoots and roots, experiment 3.

Effect of Powdery Mildew and Water Stress
on Barley Plants

The effect of both drought stress and the fungus on barley plant growth was noticeable when the roots were washed. The inoculated plant shoots and roots were smaller and thinner than those of the healthy plants at each water level. Noticeable differences in plant growth were observed between the four water levels. As the water levels decreased, the size of inoculated and non-inoculated plants decreased.

Furthermore, the interaction between the two factors studied (disease and water stress) was found to be highly significant for both roots and shoots in the three experiments (Appendix C: Tables 13, 14 and 15; Appendix D: Tables 16, 17 and 18, respectively). Both disease and water stress were deleterious to plant shoot and root growth (Tables 3 and 4). The results of the second experiment are illustrated in Figures 2 and 3.

The distribution of dry weight of shoots and roots illustrates the interaction between the fungus and water stress. As water levels decreased, dry weight of both inoculated and healthy plants was reduced (Figures 2 and 3). However, healthy plants exhibited higher dry weights for both shoots and roots at each water level.

Table 3. Dry weight means of barley plant roots placed under inoculum and water stress[a].

Experiment	Replication	Water level (fraction of normal water[b])			
		0	1/3	2/3	3/3
Expt. #1					
Healthy	16	240.9	207.3	526.1	644.6
Inoculated	16	77.4	77.5	109.5	339.9
Expt. #2					
Healthy	16	437.3	440.4	489.6	826.3
Inoculated	16	45.4	90.8	106.8	156.3
Expt. #3					
Healthy	16	97.3	267.3	271.1	358.8
Inoculated	16	36.7	52.8	61.5	117.5

(a) All the means (in mg) were significantly different at $P < .01$.

(b) The normal water level was three liters, added daily.

Table 4. Dry weight means of barley plant shoots under both inoculum and water stress[a].

Experiment	Replications	Water level (fraction of normal water[b])			
		0	1/3	2/3	3/3
Expt. # 1					
Healthy	16	.624	.973	2.722	2.890
Inoculated	16	.364	.459	.623	.643
Expt. # 2					
Healthy	16	2.216	2.506	3.642	5.548
Inoculated	16	.428	1.044	1.081	1.293
Expt. # 3					
Healthy	16	.650	1.052	1.116	1.708
Inoculated	16	.262	.329	.451	.495

(a) All the means (in grams) were significantly different at $P < .01$.

(b) The normal water level was three liters, added daily.

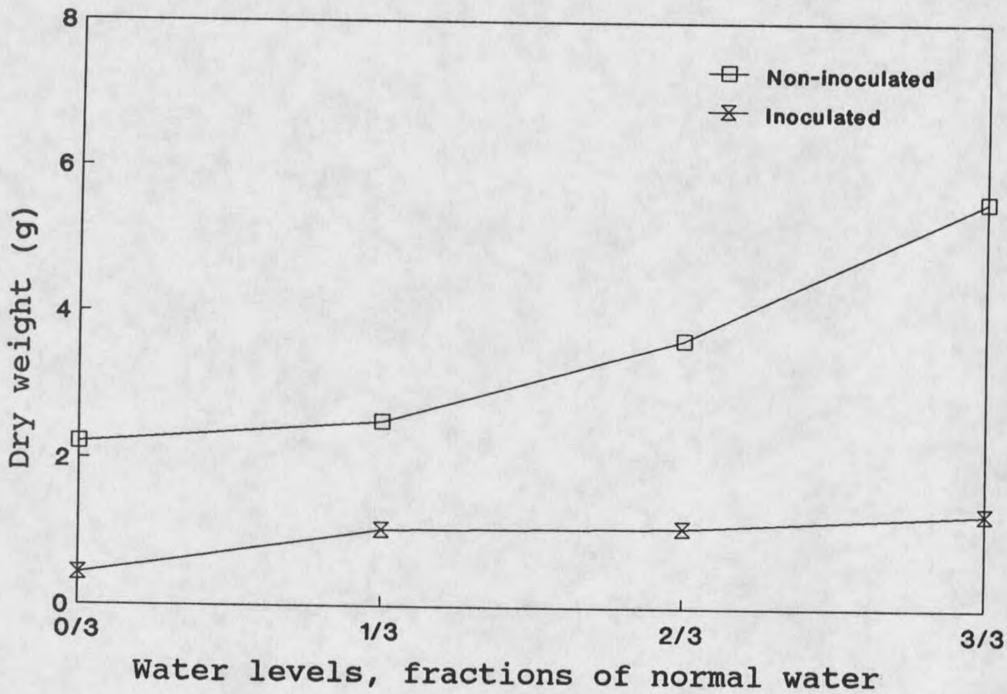

Figure 2. Effect of powdery mildew and water levels on barley shoots, experiment 2.

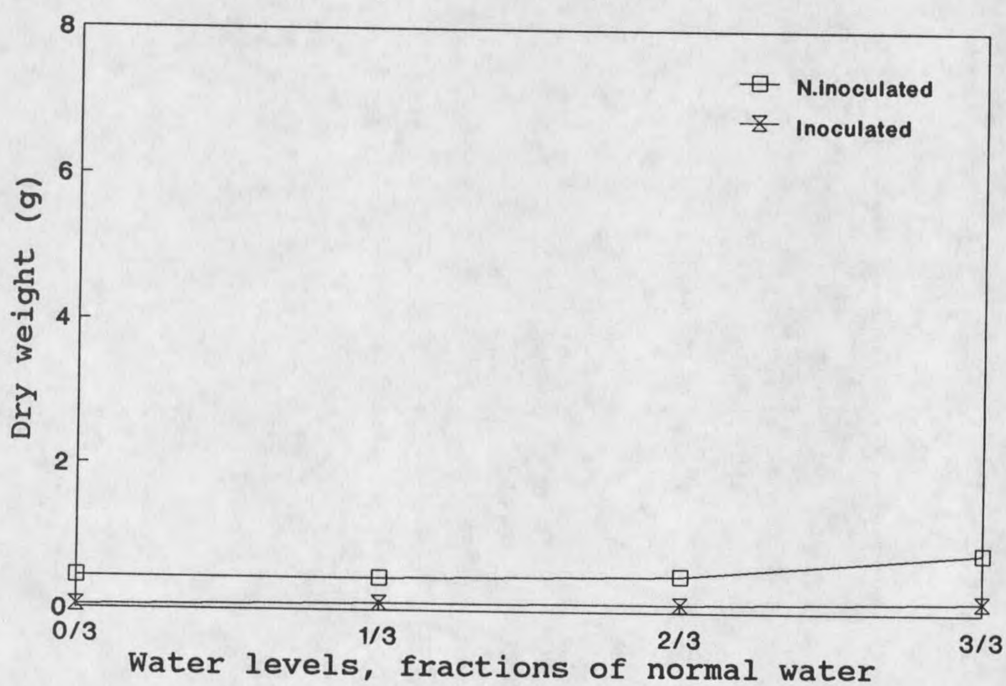

Figure 3. Effect of powdery mildew and water levels on barley roots, experiment 2.

A covariance analysis was performed to determine the relationship between the dry weight of the shoots and the roots under both disease and water stress (Appendix E: Tables 19, 20 and 21). The second and third experiments showed a significant correlation between shoots and roots which indicates the strong interrelationship between the shoots and the roots. The coefficients of correlation between shoots (dependent variable) and the roots (independent variable) were, r = 0.69 and r = 0.54 in the second and the third experiment, respectively. For experiment 2, the distribution of the values of dry weights for shoots and roots, and regression lines for both inoculated and non-inoculated plants are illustrated in Figure 4. The coefficients of regression of shoots on roots were positive for both experiments 2 and 3 (B = 3.669, B = 1.439 respectively), indicating that shoots and roots varied together.

In this investigation the effect of powdery mildew was manifest on roots and shoots. This can be seen in Table 5 and Figure 5, where the results of the second experiment are illustrated.

Water stress induced a decrease in the dry weight of both inoculated and healthy plants (Table 5, Figure 6) corresponding to water level decrease. Analysis of variance showed highly significant results for the three experiments (Appendix D: Tables 16, 17, and 18). Water stress had a

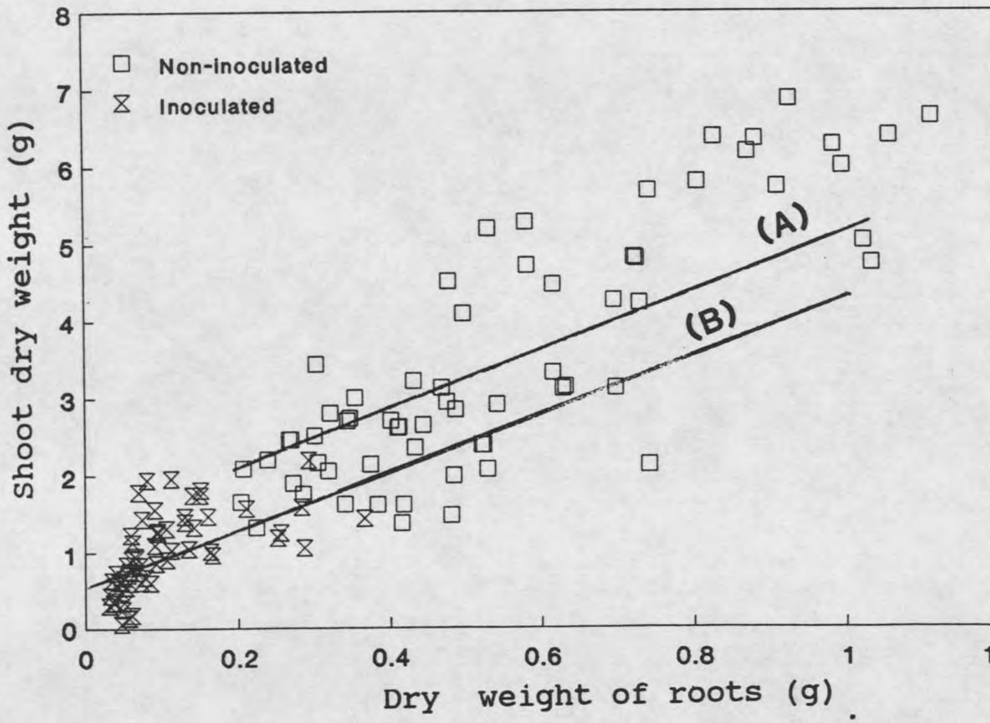

Figure 4. Effect of powdery mildew on barley shoots and roots and the relationship betwwen the two variables. (A) Y + 3.669X + 1.466, (B) Y = 3.669X + .595.

Table 5. Effect of powdery mildew on dry weight means[a] of barley shoot and root, experiment # 2.

Treatment	Replications	Dry weight means	
		Roots	Shoots
		g	g
Healthy	64	.548	3.478
Inoculated	64	.099	.961

(a) means over inoculation levels (in grams).

Table 6. Effect of water levels on barley shoot and root dry weights, means across treatment.

Water level[b] (fraction of normal water)	Replications	Root Dry wt. means	Shoot[c] Dry Wt.
		g	g
Experiment # 1			
0	32	.142	.494
1/	32	.159	.716
2/3	32	.318	1.673
3/3	32	.492	1.766
Experiment # 2			
0	32	.241	1.322
1/3	32	.266	1.775
2/3	32	.298	2.361
3/3	32	.491	3.420
Experiment # 3			
0	32	.067	.456
1/3	32	.160	.690
2/3	32	.166	.784
3/3	32	.238	1.100

(b) The normal water level was three liters per day.
(c) All the means (in grams) were significantly different at $P < .01$.