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Arbuscular mycorrhiza increased the activity of a biotrophic leaf pathogen – is a compensation possible?

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Abstract Arbuscular mycorrhizal barley-plants were more susceptible to the obligate biotrophic shoot pathogen *Erysiphe graminis* f. sp. *hordei*. In experiments under greenhouse and open-air conditions on leaves of mycorrhizal plants, the sporulation rate of the mildew fungus was more than twice that on control plants. However, mycorrhizal plants suffered less than non-mycorrhizal plants in terms of grain number, ear yield and thousand-grain weight. Disease-yield-relationship analysis showed that the symbiosis neutralised the positive correlation between disease severity and yield loss (up to 25% infected leaf area tested). After mildew infection, nitrogen in ears of non-mycorrhizal barley was higher because of an impaired starch accumulation during grain filling. In mycorrhizal plants, leaf disease did not impair either the quantity or quality of grain yield. This improved compensation in mycorrhizal plants was related to maintained photosynthetic capacity and a delay in pathogen-induced senescence. Thus filling of long-term storage pools (fructans in internodes) and consequently reallocation of these reserves during grain filling was improved. The results suggest that higher availability of energy and material during grain formation, together with longer physiological activity, were the basis of yield maintenance and, therefore, expression of mycorrhiza-induced tolerance towards the pathogen.

Keywords Arbuscular mycorrhiza · *Erysiphe graminis* · Sink-source relationship · Tolerance · Yield

Introduction

Plant producers are showing increasing interest in the role of mycorrhizal fungi as bioprotectors, biostimulators or biofertilisers (Azcon-Aguilar and Barea 1997). It is known that plants benefit from fungal presence in roots when exposed to a broad range of abiotic stresses like high salinity, drought or heavy metal concentration in soil. Arbuscular mycorrhizal (AM)-fungi in combination with micropropagation techniques reduce mortality rates during transfer of in vitro plantlets to ex vitro conditions (Azcon-Aguilar and Barea 1997). Mycorrhiza inoculation can be effective even against soil-borne pathogens, which are difficult to control by chemical and physical treatments (Azcon-Aguilar and Barea 1996, 1997; Cordier et al. 1997). In contrast, formation of the symbiosis mostly leads to higher susceptibility to shoot pathogens (Lindermann 1994; Dugassa et al. 1996), viruses (Dehne 1982), and aphids (Gange and West 1994). This mycorrhizal side-effect of promoting shoot pathogens is worth investigating in more detail since individual plants may be able to compensate negative influences but species or cultivars may show high variability.

The experiments presented here were aimed at a closer insight into compensatory effects within the source–sink system of AMF–plant pathogen. Several yield parameters were analysed in pot experiments under greenhouse and open-air conditions. To ensure that effects were based on compensation and not on classical mycorrhizal growth promotion, a plant/AM system was used that showed no difference in growth between mycorrhizal and non-mycorrhizal plants after sufficient fertilisation. To elucidate the physiological background of this compensation, photosynthesis (CO_2 assimilation), development of senescence and allocation of carbohydrates in the plant were quantified. Competition between the different sinks (pathogen, AM, stem and ear of the plant) was measured at different developmental stages and in different sink and source tissues of the plant.

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Materials and methods

Plant material, pathogen and AM fungus inoculation

The experiments were carried out with the plant–AMF–pathogen system *Hordeum vulgare* L. cultivar Aura, *Glomus etunicatum*

(isolate 139, collection of the Institute) and *Erysiphe graminis* DC. f. sp. *hordei* Em. Marchal.

Three barley plants were grown in a 5-l pot containing a mixture of sterilised compost and expanded clay as AMF inoculum carrier (Dehne and Backhaus 1986) at the ratio of 95:5 (v/v). The same amounts of AMF-free expanded clay were added to the substrate for non-AM plants. Experiments were conducted twice in a greenhouse under a 16-h day length with supplementary light and twice in a vegetation hall (cage with concrete surface and wire netting) under open-air conditions. Plants were fertilised weekly with 500 ml of a 0.3% Wuxal top N solution (Schering, N/P/K: 12/4/6). *Erysiphe graminis* was cultured on barley cultivar Aura and used for inoculation of the experimental plants by ventilation. During the experimental period, infected control plants were sprayed four times with the fungicide Corbel (BASF) to inhibit the infection. This fungicide did not affect CO_2 assimilation of the plant or the frequency of mycorrhizal infection.

The infection density of powdery mildew on barley was determined by estimation of the surface area (%) covered with powdery mildew for both surfaces of all leaves three to four times at different stages of plant development (open-air: EC 25, EC 31, EC 39, EC 71; greenhouse: EC 51, EC 65, EC 85, where EC is the Eucarpia Code established by the European Association of Plant Breeders). Pathogen activity was estimated in terms of sporulation rate. Two weeks after inoculation of *E. graminis*, the old conidia were removed from plants. Infected leaves were excised and incubated in test tubes containing 0.5 ml of 0.1% Tween-20 at 20°C and 8,000 lux light intensity for 48 h. The conidia produced in this time were harvested by thorough shaking, counted under the microscope and expressed as number of spores per unit mildewed leaf area.

Approximate values of mycorrhizal colonisation frequency (%) were estimated by counting the proportion of 40 root pieces (1 cm) with mycorrhizal structures.

CO_2 assimilation

CO_2 assimilation rates of leaves were assessed in a mini-cuvette system (Walz, Mess- und Regeltechnik, Effeltrich, Germany) under controlled conditions (20°C, 65% relative humidity) by infrared gas analysers operating with ambient air (flow rate 1,300 ml min^{-1}) in differential mode.

Analysis of carbohydrates

Leaf and internode sections were harvested into liquid nitrogen at three to five times during plant development. Extracts were prepared by grinding the frozen tissue using mortar and pestle under liquid nitrogen, boiling in 3 ml aqueous 80% ethanol (v/v) and extracting twice with 5 ml distilled water (80°C, 30 min), each followed by centrifugation at 3,000 *g* (10 min). After adjusting the volume to 10 ml, extracts were stored at –20°C until determination of carbohydrate content.

The content of starch was determined as described by MacRae (1971). The pellet containing the starch was dissolved in double-distilled water and incubated in a water bath (100°C, 3 h). The suspension was then incubated (40 h, 60°C) with 15 ml amyloglucosidase solution (1 U/ml) in acetate buffer (0.2 N, pH 4.8) and assayed using 2 ml anthrone/H_2SO_4 reagent as described by Heisterüber et al. (1994). Glucose, fructose and sucrose were determined in a microplate assay using an enzyme-coupled colorimetric reaction as described by Hendrix (1993).

Fructan content was estimated by assaying for total fructosyl residues and subcontracting free fructose and sucrosyl-fructose, determined as above. The total fructosyl residue content was determined colorimetrically as described by Heisterüber et al. (1994). Aliquots of extract (400 µl) were mixed with 2 ml of resorcinol/HCl reagent. After incubation in a boiling water bath (15 min), the absorbance was measured at 470 nm. Solutions of fructose in double-distilled water were used as standards.

Determination of chlorophyll

Leaf blades were homogenised with mortar and pestle in liquid nitrogen and extracted three to four times in 5 ml acetone, each followed by centrifugation (3,000 *g*, 4°C, 10 min). The supernatants were adjusted to 20 ml with 80% acetone. Chlorophyll content was calculated from the absorption at 647 and 664 nm.

Statistical analysis

A completely randomised design was used in the open-air experiments and a randomised block design in the greenhouse. Each experiment was repeated at least twice and replicated as indicated in the tables. The analysis of variance in each experiment was performed using Systat (Systat Inc.). Tukey's test was used for comparing differences between treatments.

Results

Activity of the pathogen and yield parameters

The frequency of the mycorrhizal infection was 95% under open-air and 70% under greenhouse conditions from 6 weeks (open-air) and 10 weeks (greenhouse) after sowing to harvest (EC 92), respectively. Application of the fungicide did not influence the mycorrhizal infection frequency.

Erysiphe graminis produced nearly threefold more conidia on leaves of mycorrhizal than non-mycorrhizal plants (Table 1), whereas there was no difference in infected leaf area. This higher pathogen activity on AM plants was independent of the growth conditions (greenhouse or open-air). However, the mildew fungus infected a greater leaf area and produced more conidia in the greenhouse than in the open-air condition, irrespective of the mycorrhizal infection.

Powdery mildew significantly reduced the grain number per ear, an early determined yield parameter (Table 2). Yield parameters determined later during grain filling, such as yield per ear and thousand-grain weight (TGW), were also reduced by the mildew. However, the pathogen produced no yield-losses in mycorrhizal plants (except a 5% reduction in TGW in open-air conditions). There was no AM-mediated increase in yield parameters in non-mildewed plants. Interestingly, AM induced late tillering during grain formation (Table 2, immature tillers). These tillers were too young to contribute to yield.

Table 1 Sporulation of *Erysiphe graminis* on mycorrhizal (*AM*) and non-mycorrhizal barley under open-air (n=10) or greenhouse conditions (n=12; EC 71; mean±SD). Values in parentheses show sporulation relative to non-mycorrhizal plants. Within each parameter, means followed by the same letter are not significantly different ($P \leq 0.05$)

Treatment	Number of spores per unit mildewed leaf area	
	Open-air	Greenhouse
Mildewed	184±130 (100)a	470±210 (100)a
Mildewed/AM	543±281 (296)b	1323±358 (282)b

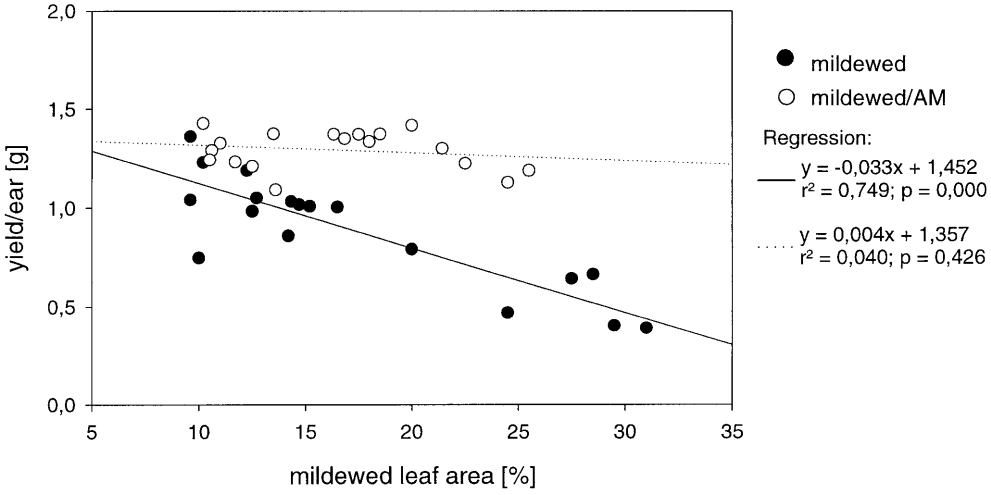

Fig. 1 Yield per ear of mycorrhizal and non-mycorrhizal barley affected by the mildewed leaf area at EC 85 under greenhouse conditions (main tiller; *n*=18)

Table 2 Yield components of mycorrhizal and non-mycorrhizal barley as affected by powdery mildew under open-air (*n*=32) and greenhouse conditions (*n*=18; EC 92; mean±SD). Values relative to healthy controls (fungicide) are shown in parentheses. Within each parameter, means followed by the same letter are not significantly different (*P*≤0.05) (*dw* dry weight in grams, *TGW* thousand-grain weight in grams)

Conditions	Treatment	Grain number/ear	Ear number	Immature tiller number	Yield/ear (dw)	TGW (dw)
Open-air	Mildewed	25.1±1.9 (94)a	6.53±2.18 (100)a	4.78±3.40 (119)ab	1.42±0.15 (88)a	56.6±3.0 (94)a
	Mildewed/AM	26.3±1.4 (99)b	5.97±1.21 (91)a	7.16±3.34 (178)b	1.51±0.09 (94)b	57.5±2.0 (95)a
	Fungicide	26.6±1.5 (100)b	6.53±1.64 (100)a	4.03±3.08 (100)a	1.61±0.08 (100)c	60.4±1.9 (100)b
	Fungicide/AM	26.3±1.3 (99)b	6.63±1.45 (101)a	6.13±4.82 (152)ab	1.58±0.10 (98)bc	60.1±1.8 (100)b
Greenhouse	Mildewed	22.1±6.5 (76)a	7.1±2.1 (84)a	13.0±4.5 (103)ab	0.88±0.27 (72)a	40.5±2.0 (96)a
	Mildewed/AM	29.9±1.9 (103)b	10.8±2.1 (128)b	12.9±3.2 (103)ab	1.30±0.07 (105)b	43.5±2.8 (103)ab
	Fungicide	29.0±1.3 (100)b	8.4±0.9 (100)ab	12.6±2.1 (100)a	1.23±0.13 (100)b	42.3±3.4 (100)ab
	Fungicide/AM	30.7±1.9 (106)b	10.4±1.4 (123)b	16.1±7.2 (128)b	1.28±0.12 (104)b	41.7±2.3 (99)a

Table 3 Ratio between generative and vegetative parts (ear/straw) of mycorrhizal and non-mycorrhizal barley (yield index) as affected by powdery mildew under open-air (*n*=32) and greenhouse conditions (*n*=20; EC 92; mean±SD; main tiller). Values relative to healthy controls (fungicide) are shown in parentheses. Within each parameter, means followed by the same letter are not significantly different (*P*≤0.05)

Treatment	Open-air	Greenhouse
Mildewed	1.24±0.20 (111)b	0.99±0.17 (87)a
Mildewed/AM	1.31±0.09 (117)b	1.20±0.21 (106)b
Fungicide	1.12±0.08 (100)a	1.13±0.09 (100)ab
Fungicide/AM	1.22±0.06 (109)b	1.20±0.10 (107)b

On the basis of single main tillers, it was possible to establish a yield-loss-relationship (Fig. 1). Non-mycorrhizal barley showed a positive correlation between infection density of the powdery mildew fungus (% mildewed leaf area) and yield loss. AM eliminated this correlation and the yield of mycorrhizal barley was independent of the infection density of the pathogen up to a mildewed leaf area of 25% (tested range).

The yield index, defined as the ratio of generative/vegetative (ear/straw) plant parts, is presented in Table 3. Mycorrhizal symbiosis and the stress of the moderate pathogen infection tested increased the yield index by reducing straw weight.

Physiological background

Mildew not only reduced yield but also altered the quality of grains (Table 4). Ears showed a decreased starch/nitrogen ratio due to impaired starch accumulation after mildew infection. In mycorrhizal plants, the starch concentration in grains was not reduced, in spite of the pathogen.

One important source of carbohydrates for yield is the current photosynthesis during grain filling (Fig. 2). Mildew led to a reduction (–44%) in net CO_2-assimilation rate (CO_2 consumption) in diseased leaves (10% mildewed leaf area) of 6-week-old barley plants. At the same time, the dissimilation rate (CO_2 release) was nearly doubled. Mycorrhizal plants without mildew showed an increased net assimilation (+34%). When they were additionally infected by mildew, assimilation was also reduced by the disease. However, the level reached was that of the non-infected, non-mycorrhizal control plants. The rates of dissimilation of pathogen-infected mycorrhizal and non-mycorrhizal plants did not differ. In the upper and always healthy leaves, assimilation showed a trend similar to the lower ones but rates were not significantly different. Dissimilation of these leaves was the same in all treatments.

Reallocation from storage pools as well as photosynthesis supplied grain filling. Barley stores fructan in veg-

Table 4 Grain quality of mycorrhizal and non-mycorrhizal barley plants as affected by powdery mildew under open-air (n=5) and greenhouse conditions (n=6; main tiller; EC 92; mean±SD). Within each parameter means followed by the same letter are not significantly different ($P \leq 0.05$) Values relative to healthy controls (fungicide) are shown in parentheses. (*dw* dry weight)

Treatment	Open-air		Greenhouse	
	Starch content (mg/g dw)	Starch/nitrogen	Starch content (mg/g dw)	Starch/nitrogen
Mildewed	431±31 (85)a	21.7±2.2 (78)a	463±76 (75)a	14.5±4.2 (71)a
Mildewed/AM	569±25 (112)c	31.6±1.3 (114)b	583±28 (95)b	20.7±3.5 (101)b
Fungicide	507±28 (100)b	27.7±2.6 (100)b	614±37 (100)b	20.5±2.3 (100)b
Fungicide/AM	577±34 (114)c	29.2±1.9 (105)b	574±43 (93)b	19.5±2.5b (95)a

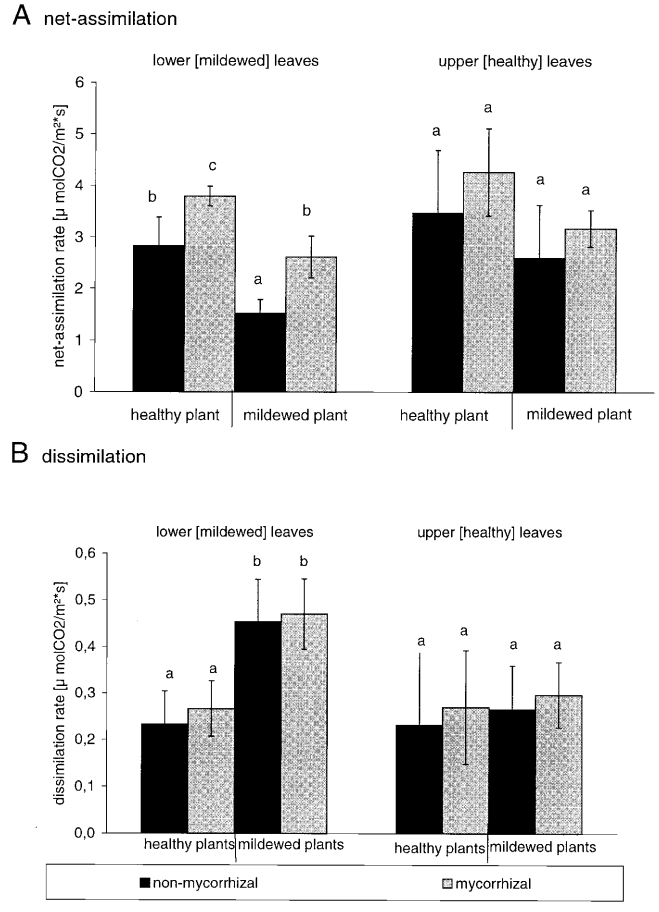

Fig. 2 CO_2 net-assimilation and dissimilation rates of mycorrhizal and non-mycorrhizal barley as affected by powdery mildew on lower mildewed leaves (10% mildewed leaf area) and upper healthy leaves (<1%) of the same plant (6 weeks after sowing; n=5; mean ±SD) Within each parameter, means followed by the same letter are not significantly different (P<0.05)

etative tissues (Gaunt and Wright 1992) and this accumulated from the onset of flowering (EC 61) and reallocation started with milky ripeness (EC 71, Fig. 3). Mildew hindered the storage of fructan in internodes. Mycorrhizal plants were able to accumulate higher amounts despite the higher pathogen activity (sporulation, Table 1).

The duration as well as the rate of starch deposition in the developing grain is particularly important for yield formation and this process terminates with senescence. Development of senescence was quantified as a decrease in chlorophyll content (Fig. 4). Chlorophyll content decreased earlier in flag leaves of plants with mildewed lower leaves than control plants. Mycorrhizal plants showed no pathogen-induced decline in chlorophyll content and resembled healthy plants in this parameter.

Discussion

Increased leaf pathogen activity on mycorrhizal plants is well documented (Schönbeck and Dehne 1979; Lindermann 1994; Dugassa et al. 1996). Results presented here using mycorrhizal barley confirm previous findings of a higher sporulation rate of powdery mildew (flax, Dugassa et al. 1996). Dehne (1982) postulated that this systemic influence of AMF is attributable to enhanced nutrition, plant growth and physiological activity of mycorrhizal plants. With increased concentrations of assimilates, such plants can serve as better nutrient sources for plant parasitic organisms. Another possible factor is a systemic change in the defence system of the plant induced by formation of an AM symbiosis. A correlation between mildew resistance and reduced development of AM fungi in roots has been documented in Begonia by Feldmann and Boyle (1998).

In barley, different yield components are built up during the early and late stages of plant development. Environmental factors such as a pathogen infection, and in particular the time of attack, strongly influence accumulation and decay of these yield components (Carver and Griffiths 1982; Chiariello and Gulmon 1991). In our experiments, the deleterious effect of mildew on both early- and late-determined yield components was less marked in mycorrhizal than in non-mycorrhizal plants. This has also been shown by Dugassa et al. (1996) using mildewed flax plants in terms of fresh weight production. In contrast to their findings, the mycorrhizal effect on the yield of mildewed barley was a result of compensatory mechanisms and not of a mildew-independent stimulation of growth caused by AM.

During ear development, two types of source contribute photosynthates for grain filling: (1) current photosynthesis transferring carbohydrates directly to the grain and (2) reallocation of sugars from reserve pools (Schnyder 1993). Both sources were reduced by powdery mildew

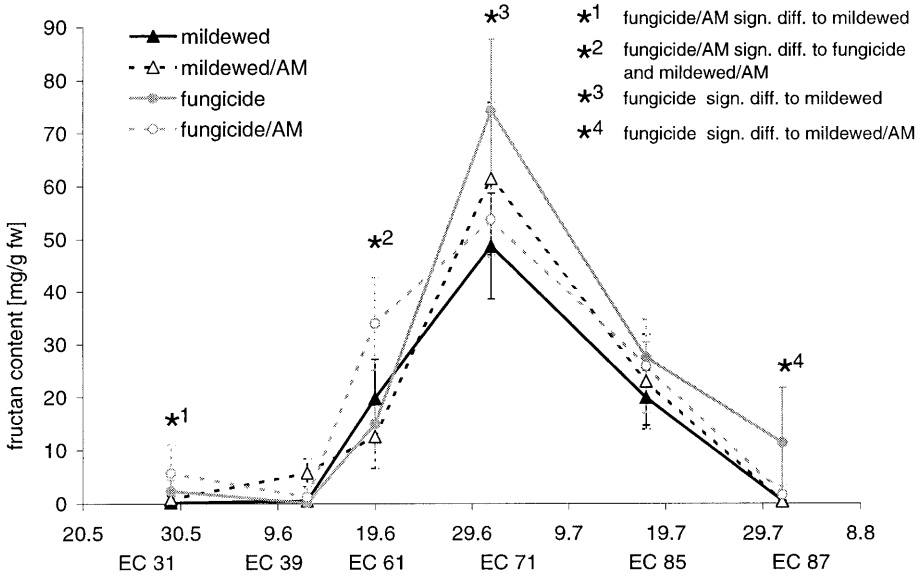

Fig. 3 Fructan content of mycorrhizal and non-mycorrhizal barley affected by powdery mildew (main tiller; *n*=5; mean ±SD; *P*≤0.05) (*fw* fresh weight)

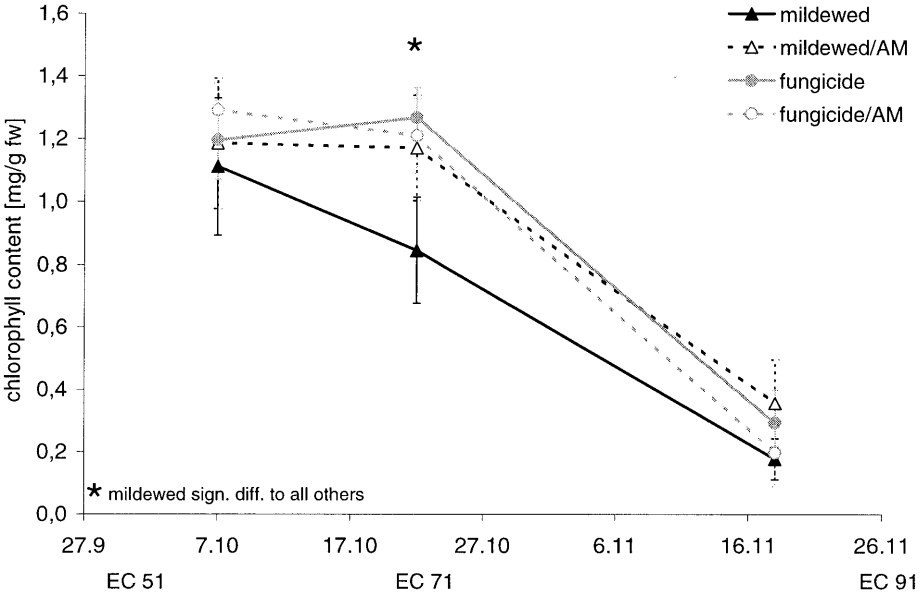

Fig. 4 Chlorophyll content of the flag leaf of mycorrhizal and non-mycorrhizal barley as affected by powdery mildew (main tiller; *n*=5; mean ±SD; *P*≤0.05) (*fw* fresh weight)

on barley. Towards the end of grain filling, when the leaves are more or less senescent, the stem is the major source of assimilates (Gaunt and Wright 1992). After anthesis in our experiments, the upper internodes were particularly important sources of stored assimilates that could be reused for grain filling (Bonnett and Incoll 1993). Analyses of the culms before anthesis and harvest supported the view of Carver and Griffiths (1982). They attributed the smaller grain weight of plants which had been attacked by mildew early to a deficiency in carbohydrate storage in culms during or after anthesis and, consequently, to reduced reallocation to the developing grain. In agreement with these findings, the impaired starch accumulation in the ears of mildewed barley caused a higher nitrogen concentration.

In mycorrhizal plants, the pathogen was not able to induce such a change in grain quality. Sink-source relationships between the pathogen and the host were changed to the advantage of the mycorrhizal plant in that the supply of assimilates during grain filling was less impaired. This suggests that a better filling of long-term storage pools in mycorrhizal plants, efficient utilisation of these during grain filling and unimpaired photosynthesis are factors determining compensation of pathogen attack. Systemic effects of mycorrhiza on assimilate partitioning in shoots of barley plants had been reported by Müller et al. (1999) as represented by an altered gradient of fructan content in the youngest and oldest leaves of AM plants.

Since AM fungi, like biotrophic pathogens, are a sink for the carbon resources of the host, mycorrhizal plants require improved production of assimilates. The stimulatory effect of AM on photosynthesis of barley is in agreement with the findings of Drüge and Schönbeck

(1992) and Smith and Read (1997). Wright et al. (1998) suggested that it is the AM fungus, acting as a sink for assimilates, that facilitates stimulation of the rate of CO_2 assimilation by the plant partner. In contrast, Black et al. (2000) suggested that the increase in photosynthetic rate in leaves of AM-infected cucumber was due to an increased P status rather than a consequence of a mycorrhizal sink for assimilates.

Changes in the phytohormone balance may play a role in the delay of senescence in mycorrhizal barley (West 1995). Dugassa et al. (1996) concluded that an enhanced cytokinin concentration might be relevant for improving photosynthesis and growth of mycorrhizal flax. A delaying effect of AM on senescence has also been observed in roots of herbaceous plants (Lingua et al. 1999; Gavito et al. 2001).

Contrary to AM fungi, the biotrophic pathogen reduced photosynthesis and induced senescence of the barley plants. Wright et al. (1995) described the same effects with mildewed wheat. Both the rate and duration of grain growth are important for a good yield and both can be reduced by mildew or rust diseases (McGrath and Pennypacker 1991). To compensate these negative impacts, plants need the improved management of their storage pools provided by the AM-symbiosis. There is evidence from our results that AM enables the mildewed host plant to maintain productivity by eliminating the relation between disease intensity and damage, as far as medium infection densities are concerned. The mechanisms underlying this AM effect may be multiple. Although phytohormones are likely to be important, it was not possible to perform analyses in this direction during our experiments.

In conclusion, compensation of yield loss threatening mildewed plants is possible if the plants develop a symbiosis with an efficient mycorrhizal fungus. The role of AM fungi naturally occurring in the field might be neglected but important in agriculture from this point of view. They can stabilise yield under pathogen attack and probably under a broad spectrum of other stresses (i.e. drought, salinity and heavy metals). This implies the need for maintenance of AM associations by agricultural practices. Thus, it will be necessary to test new barley cultivars, including genetically engineered plants, for their ability to form and benefit from mycorrhizal symbioses, since mutation of genes involved in barley resistance/susceptibility to powdery mildew can also differentially mediate AM formation (Ruiz-Lozano et al. 1999).

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