Cell wall-bound phenolic acid and lignin contents in date palm as related to its resistance to *Fusarium oxysporum*

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Abstract

The root cell walls of the resistant cultivars of the date palm were more resistant to the action of the cell wall-degrading enzymes (CWDE) of *Fusarium oxysporum* f. sp. *albedinis* than those of the susceptible cultivars. Date palm roots contain four cell wall-bound phenolics identified as *p*-hydroxybenzoic acid, *p*-coumaric acid, ferulic acid and sinapic acid. The contents of *p*-coumaric acid and ferulic acid in the resistant cultivars (IKL, SLY, BSTN) were about 2 times higher than those in the susceptible cultivars (BFG, JHL, BSK). The contents of *p*-hydroxybenzoic acid and sinapic acid in the resistant cultivars were 8.4 and 4.5 times, respectively, higher than those in the susceptible cultivars. The lignin contents in roots of the resistant cultivars were 1.8 times higher than those of the susceptible cultivars. The cell wall-bound phenols accumulated particularly in resistant cultivars reduced strongly the mycelial growth and the CWDE production *in vitro*.

Additional key words: polygalacturonases, polygalacturonate trans-eliminases, pectinemethyl-esterases, cellulases.

Introduction

The Bayoud disease, caused by *Fusarium oxysporum* f. sp. *albedinis*, constitutes one of the limiting factors of the date palm culture. Several defense mechanisms are involved in the date palm resistance to this pathogen such as the accumulation of the caffeoylshikimic acid (Ziouti *et al.* 1996, El Modafar *et al.* 2000) and the induction of the phytoalexins (El Modafar *et al.* 1999). Our recent data showed that the cell walls of the resistant cultivar roots are more resistant to the action of *F. oxysporum* CWDE than those of the susceptible cultivars (El Modafar and El Boustani 2000). These studies showed the implication of two different mechanisms in the resistance of the cell walls to the extracellular CWDE (El Modafar and El Boustani 2000). In the early stages of cell wall hydrolysis, mechanical properties limited the action of CWDE on the cell walls. In advanced stages, chemical compounds inhibited the biosynthesis of these CWDE. Cell wall-bound phenolic compounds (Eraso and Hartley 1990, Matern and Grimmig 1993, Ikegawa *et al.* 1996) and lignin (Vance 1980, Bell 1981, Asada and Matsumoto 1987, Rioux and Biggs 1994) constitute the factors which intervene in the host cell wall resistance to the action of the CWDE.

The objectives of this work were *1*) to identify and to compare qualitatively cell wall-bound phenolics in date palm roots of three resistant (IKL, SLY, BSTN) and three susceptible (BFG, JHL, BSK) cultivars to *F. oxysporum*, *2*) to compare the constitutive contents of phenols and lignin in these cultivars, and *3*) to test the effect of cell wall-bound phenols on the mycelial growth and the CWDE production by pathogen. The enzyme studied were: pectinemethyl-esterase (PME), polygalacturonase (PG), polygalacturonate trans-eliminase (PGTE) and cellulase.

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Abbreviations: CWDE - cell wall-degrading enzymes, DI_{50} - dose inhibiting 50 % of the mycelial growth or of CWDE production, PG - polygalacturonase, PGTE - polygalacturonate trans-eliminase, PME - pectinemethyl-esterase, CWR - cell wall residue.
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Materials and methods

Plants and cell wall preparation: The study related to the root cell walls of 6 date palm cultivars coming from the palm plantation of Zagora (Southern of Morocco). The roots (3 to 5 mm in diameter) were taken from three susceptible cultivars (BFG, JHL, BSK) and three resistant cultivars (IKL, SLY, BSTN) (Saaidi 1992). For each cultivar, the roots were taken from 7 palm trees. The roots were rinsed, dried between filter paper then crushed in the presence of liquid nitrogen. Soluble compounds of the roots were removed by successive extractions with several solvents: ethanol-hexane-water (2:2:1, v/v), ethanol-water (4:1, v/v), ethanol-water (1:1, v/v) and finally water (El Modafar *et al.* 1999). Final cell wall residue (CWR) obtained after vacuum filtration was freeze-dried.

Extraction, identification and quantification of cell wall-bound phenolics: The cell wall-bound phenolic compounds were released by alkaline hydrolysis according to the technique previously described (Kamisaka *et al.* 1990). CWR (250 mg) was incubated in the presence of 2 M NaOH for 24 h at room temperature under nitrogen atmosphere. The mixture was then acidified to pH 2 with 2 M HCl. After vacuum filtration, the phenols were extracted 3 times by diethyleoxid. After evaporation of diethyloxid, the phenols were resuspended in 1 cm^3 of methanol. The phenolic compounds were characterized by TLC and HPLC techniques as described previously (El Modafar *et al.* 1993, 1996). TLC analysis was performed on the silica gel (HPTLC) and cellulose plates and the eluants applied are benzene-acetic acid-water (6:7:3, v/v, upper phase), butanol-acetic acid-water (4:1:5, v/v, upper phase) and acetic acid-water (1:10, v/v). HPLC analysis was performed on a *Spherisorb Clg* column (250 × 5 mm) and samples were eluted in a solvent consisting of acetonitrile and water pH 2.6 following a gradient of 7 - 27 % acetonitrile. The phenolic compounds were identified as *p*-hydroxybenzoic, *p*-coumaric, ferulic and sinapic acids by comparing their retention time in HPLC, their Rf values in TLC and their fluorescence (254 and 366 nm) to standards (*Sigma-Aldrich Chimie,* St-Quentin Fallavier, France). Phenolic contents were determined by HPLC. Standards were used as references for quantitative analyses.

Extraction and quantification of lignin: Lignin was extracted according to the method of Morisson (1972). The CWR, obtained after extraction of cell wall-bound phenolic acids, were washed 3 times by distilled water then freeze-dried. These CWR (250 mg) were incubated in the presence of 2 cm^3 of the 25 % acetylbromide in glacial acetic acid. After 60 s of incubation at 70 °C, 2 cm^3 of 2 M NaOH were added to the mixture which was then centrifuged at 10 000 *g* for 10 min. The supernatant was transferred into 6-cm^3 volumetric tube containing 0.2 cm^3 of 7.5 M hydroxylamine. Lignin contents were determined spectrophotometrically at 280 nm (Jaegher *et al.* 1985).

Effects of phenolic acids on the CWDE production and fungal growth: The production of PME, PG, PGTE and cellulases and the mycelial growth of *F. oxysporum* were evaluated on liquid medium of Czapek (El Modafar *et al.* 2000) with or without phenolic acids (0 to 3 µmol cm^{-3}): *p*-hydroxybenzoic acid, *p*-coumaric acid, ferulic acid or sinapic acid (*Sigma-Aldrich*, St. Quentin Fallavier, France). The media were then inoculated with 1 cm^3 of a conidial suspension (4 × 10^6 spores cm^{-3}) of strain 133 of *F. oxysporum* f. sp. *albedinis* which is known for its virulence (Sedra and Besri 1994). The conidial suspension was prepared in sterile distilled water from a thallus cultivated on PDA medium (potato dextrose agar) for 5 d at 25 °C. The cultures were then incubated at 25 °C under agitation (2 rps). After 16 d, the mycelial growth and the production of enzymes were determined. The mycelial growth was evaluated in dry mass of mycelium (mg) after dehydration of the fungal biomass at 70 °C for 24 h (El Modafar *et al.* 1993). The mycelial growth was expressed in % compared to the control not containing a phenol and the DI_{50} (dose inhibiting 50 % of the mycelial growth) was determined. The CWDE production was determined in culture filtrate according to the methods previously described (El Modafar *et al.* 2000) and DI_{50} of the CWDE production was determined.

Results

Cell wall-bound phenolics and lignin contents: The cell wall-bound phenolic acids of date palm roots were identified as *p*-hydroxybenzoic, *p*-coumaric, ferulic and sinapic acids. Ferulic acid constituted about 32.4 % in resistant cultivars (IKL, SLY, BSTN) and 46.2 % in susceptible cultivars (BFG, JHL, BSK) of cell wall phenolic compounds. No qualitative difference was observed between resistant and susceptible cultivars. However, the phenolic contents in the resistant cultivars were higher than those in the susceptible cultivars (Table I). The *p*-coumaric acid and ferulic acid in the resistant cultivars were approximately 2 times higher than

those in the susceptible cultivars. The *p*-hydroxybenzoic acid and sinapic acid contents were 8.4 times and 4.5 times, respectively, higher in the resistant cultivars than in susceptible cultivars. The lignin contents in resistant cultivars were 1.8 times higher than those in the susceptible cultivars (Fig. 1).

Table 1. Cell wall-bound phenolic contents [μmol g^{-1}(cell wall d.m.)] in roots of susceptible (BFG, JHL, BSK) and resistant (IKL, SLY, BSTN) date palm cultivars to *F. oxysporum* f. sp. *albedinis*. Means ± SE, $n = 7$.

Cultivars	*p*-Hydroxybenzoic acid	*p*-Coumaric acid	Ferulic acid	Sinapic acid	Total
BFG	0.32 ± 0.14	1.70 ± 0.23	1.61 ± 0.31	0.33 ± 0.17	3.96
JHL	0.30 ± 0.12	0.80 ± 0.15	1.79 ± 0.22	0.35 ± 0.11	3.24
BSK	0.14 ± 0.06	1.75 ± 0.16	1.73 ± 0.20	0.28 ± 0.12	3.90
IKL	2.11 ± 0.48	2.36 ± 0.77	3.02 ± 0.63	2.49 ± 0.43	9.98
SLY	2.19 ± 0.35	3.03 ± 0.48	2.98 ± 0.28	0.60 ± 0.09	8.76
BSTN	1.97 ± 0.31	2.98 ± 0.51	3.06 ± 0.77	1.22 ± 0.18	9.23

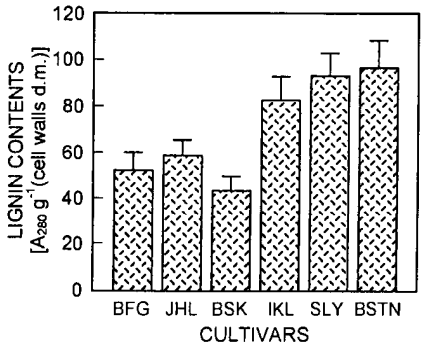

Fig. 1. Lignin contents in date palm roots of suseptible (BFG, JHL, BSK) and resistant (IKL, SLY, BSTN) cultivars to *F. oxysporum* f. sp. *albedinis*. Means ± SE, $n = 7$.

Effect of cell wall-bound phenolics on *F. oxysporum* CWDE: The cell wall-bound phenolics of the date palm roots inhibited the mycelial growth and the CWDE production by *F. oxysporum in vitro* (Fig. 2). In the presence of 2.5 μmol cm^{-3} of sinapic acid, the production of the different pectinolytic enzymes (PME, PG and PGTE) was completely inhibited and that of the cellulases was strongly reduced (about 90 %) (Fig. 2*A*). The production of the cellulases was completely inhibited in the presence of 3 μmol cm^{-3} of sinapic acid (Fig. 2*A*). In the presence of 3 μmol cm^{-3} of ferulic acid, the production of the pectinases was completely inhibited and that of the cellulases was reduced to 74 % (Fig. 2*B*). However, the *p*-coumaric acid and *p*-hydroxybenzoic acid did not induce a total inhibition of the CWDE enzymes with the concentrations tested. Nevertheless, a concentration of 3 μmol cm^{-3} of the *p*-coumaric acid inhibits strongly (83 to 92 %) the production of the pectinases and reduces of 50 % that of the cellulases (Fig. 2*C*). In the presence of 3 μmol cm^{-3} of *p*-hydroxybenzoic acid, the production of the pectinases was inhibited to 35 % and that of the cellulases was inhibited to 30 % (Fig. 2*D*). According to the DI_{50} (Table 2), the different cell wall-bound phenolic acids can be classified according to their decreasing inhibiting effect as follows: sinapic acid > ferulic acid > *p*-coumaric acid > *p*-hydroxybenzoic acid. The different phenolic acids also show an inhibiting effect on the mycelial growth of *F. oxysporum* (Fig. 2). As in the case of the CWDE production, the sinapic acid was the most inhibiting phenolic and the *p*-hydroxybenzoic acid was the lowest inhibiting of the mycelial growth. The *p*-coumaric acid and ferulic acid present intermediate inhibiting effects. In all cases, the mycelial growth appears more susceptible to the effect of different phenolic acids than the CWDE production (Fig. 2, Table 2).

Table 2. DI_{50} [μmol cm^{-3}] of cell wall-bound phenolic acids on the mycelial growth and the cell wall degrading enzymes production of *F. oxysporum* f. sp. *albedinis* ($n = 6$, values followed by a common letter do not differ significantly at $P = 0.05$ according to Duncan's multiple range test).

Phenolic acids	Mycelial growth	PME	PG	PGTE	Cellulases
Sinapic acid	2.00c	0.90a	0.90a	0.80a	1.25ab
Ferulic acid	2.50c	1.05a	1.05a	1.05a	1.50b
p-Coumaric acid	2.95d	1.25ab	1.50b	1.15a	2.50c
p-Hydroxybenzoic acid	> 3	> 3	> 3	> 3	> 3

Discussion

The cell wall roots of the date palm contain four phenolic acids identified as *p*-hydroxybenzoic, *p*-coumaric acid, ferulic and sinapic acids. Ferulic acid represents the major phenolic compound of the date palm cell walls. This abundance of the ferulic acid represent a characteristic of monocotyledons (Harris and Hartley 1976, Hartley and Jones 1977, Hartley and Harris 1981, Shibuya 1984, Kamisaka *et al.* 1990). No qualitative difference was observed between resistant (IKL, SLY, BSTN) and susceptible (BFG, JHL, BSK) cultivars, since all these phenolic acids were present in both cultivars. However, the contents of cell wall-bound phenolics and lignin in the roots of resistant cultivars were higher than those in the susceptible cultivars. This data could explain the differential behaviour of the host cell walls to *F. oxysporum* CWDE (El Modafar and El Boustani 2000). The implication of cell wall-bound phenolics in the resistance of plants to pathogens was reported in

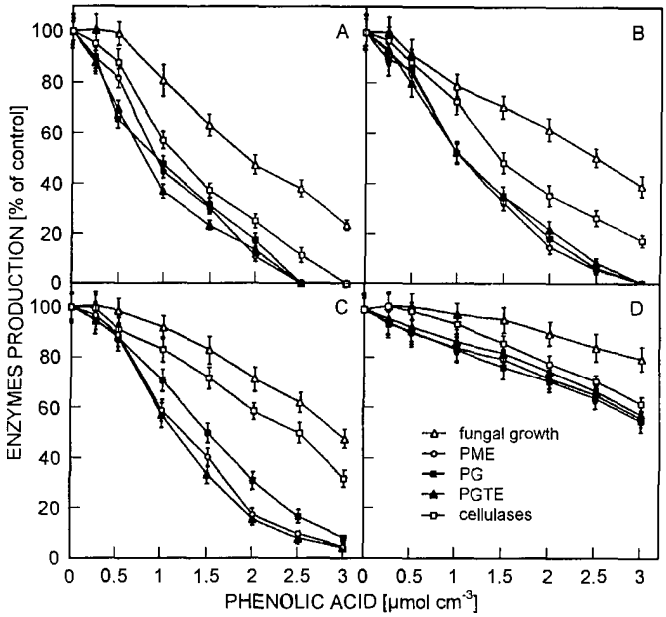

Fig. 2. Effect of phenolic acids of date palm roots on the mycelial growth and the cell wall-degrading enzymes production of *F. oxysporum* f. sp. *albedinis*. Means ± SE, $n = 6$. *A* - sinapic acid, *B* - ferulic acid, *C* - *p*-coumaric acid, *D* - *p*-hydroxybenzoic acid.

several other host-parasite interactions (Friend 1981, Glazener 1982, Bolwell *et al.* 1985, Ampomah and Friend 1988, Southerton and Deverall 1990, Niemann *et al.* 1991, Ikegawa *et al.* 1996). The insolubilization of the phenolic compounds in the cell walls can modify its mechanical properties and decrease its extensibility (Fry 1986, Tan *et al.* 1991, Ikegawa *et al.* 1996) and consequently cell wall would be less biodegradable (Eraso and Hartley 1990, Matern and Grimmig 1993). Therefore, the abundance of phenols in cell walls makes polysaccharides less sensitive to the cell wall-degrading enzymes of pathogens (Matern and Grimmig 1993, Ikegawa *et al.* 1996). In addition, the intervention of lignin in the plant resistance to pathogens was largely demonstrated (Vance 1980, Bell 1981, Asada and Matsumoto 1987, Beckman 1987, Nicholson and Hammerschmidt 1992, Rioux and Biggs 1994). The lignin constitutes a mechanical barrier of defense which protects the other cell wall components (cellulose and pectins) against the action of the extracellular CWDE of the pathogens (Vance 1980, Bell 1981, Beckman 1987).

In addition to this mechanical role, cell wall-bound phenolics (Friend 1981, Eraso and Hartley 1990, Ikegawa *et al.* 1996) and cinnamoyl alcohols of lignin (Vance 1981, Hammerschmidt and Kuc 1982, Southerton and Deverall 1990, Daurade-Le Vagueresse and Bounias 1992) inhibit the activity and the production of CWDE of the pathogens. The cell wall-bound phenolics of the date palm roots inhibit the mycelial growth and the production of CWDE of *F. oxysporum*. This inhibition depends on the concentration, the structure and the nature of phenol substituents in particular the hydroxylation and the methoxylation. Thus, the phenolic acids can be classified according to their decreasing inhibiting effect as follows: sinapic acid (di-methoxylated and mono-hydroxylated) > ferulic acid (mono-methoxylated and mono-hydroxylated) > *p*-coumaric acid (mono-hydroxylated) > *p*-hydroxybenzoic acid (mono-hydroxylated, but more polar than

p-coumaric acid). It appears that the methoxylation increases the inhibition of the mycelial growth and the CWDE production. This property was reported with isoflavonoids (Ravisé and Kirkiacharian 1976, Weidenborner and Zha 1993) and coumarins (Jurd *et al.* 1971, El Modafar *et al.* 1993). The inhibiting effect of phenols on the fungal growth and the CWDE production seems to be related to their lipophily degree and thus on their capacity to penetrate in the fungal cells. The concentrations of phenols accumulated particularly in the resistant cultivar roots can reduce strongly the mycelial growth and the CWDE production *in vitro*. Although the mode of action *in planta* can be different from that shown *in vitro*, the cell wall-bound phenolics of date palm roots can be involved in the host defense by inhibiting the mycelial growth and the CWDE production of *F. oxysporum*.

In conclusion, the root cell walls of date palm resistant cultivars phenolics (*p*-hydroxybenzoic acid, *p*-coumaric acid, ferulic acid and sinapic acid) and lignin contents were higher than those of the susceptible cultivars. This difference could explain the differential behaviour of the cell walls of the susceptible and resistant cultivars to the action of *F. oxysporum* CWDE (El Modafar and El Boustani 2000). The resistance of the cell walls of date palm resistant cultivars to the CWDE seems to depend on the intervention of the cell wall-bound phenolics and the lignin which constitute a mechanical defence. The inhibition of the mycelial growth and the CWDE production by cell wall-bound phenolics constitute a chemical defence.

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