Ferulic Acid: An Allelochemical Troublemaker

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ABSTRACT

Ferulic acid, a cinnamic acid derivative, is a well-known allelochemical that is widely distributed in plants. Stress on plant roots by ferulic acid affects several physiological and biochemical aspects, such as water utilization, foliar expansion, root elongation, photosynthesis, cell respiration, membrane integrity and nutrient uptake, among others. Moreover, ferulic acid may be esterified with cell wall polysaccharides, rigidifying the cell walls and restricting cell growth. This review describes general aspects of allelopathy and focuses on the role of ferulic acid as an allelochemical and its supposed mode of action in plants.

Keywords: allelopathy, cell wall cross-linkage, lignification, phenylpropanoid

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Invited Review

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cells. However, clear insight into the primary allelochemical action on plant physiology has not been obtained. Several modes of action for allelochemicals are involved in the inhibition and modification of plant growth and development (Fig. 1). There are several factors that may influence the effects of an allelochemical. Temperature, photoperiod, mineral composition of the soil and interactions with other allelopathic compounds may affect the chemical stability, availability and toxicity of an allelochemical (Inderjit 1996). It is thus rather difficult to examine how each factor influences the response of plants. Another issue is that experiments with allelochemicals have been carried out under the restricted conditions of a laboratory, which controls temperature, light, nutrient solution and pH, among others. This is a relevant problem since laboratory conditions cannot be directly compared to natural conditions (Seigler 1996). However, many researchers are finding success in their comparative studies, especially when the concentrations of allelochemicals are similar in both systems (Sène et al. 2000).

**Ferulic acid: Yesterday and today**

Phenolic compounds contain aromatic substances formed via the shikimic acid pathway or the malonic acid pathway, including benzoic and cinnamic acid derivatives. These two pathways supply 60% and 40%, respectively, of carbon for the biosynthesis of phenolic compounds (Gross 1981). Linked to the shikimic acid pathway, the phenylpropanoid pathway starts with deamination of phenylalanine, by phenylalanine ammonia-lyase (PAL) or tyrosine ammonia-lyase (TAL) to form cinnamic acid, its first metabolite. Cinnamate is converted to monolignols by the subsequent actions of different enzymes (Fig. 2).

![Fig. 1 Action model for allelochemicals in plants.](image)

Ferulic acid (FA) is a cinnamic acid derivative that was initially isolated as a yellow precipitate by alcoholic extraction from the commercial resin of *Ferula foetida* (Umbeliferae, Apiaceae) by Hlasiwetz and Barth (1866). They then determined its chemical composition as C_{10}H_{10}O_{4} and named it *Ferulasäure* or ferulic acid [3,4-(hydroxy-3-methoxyphenyl)-2-propenoic acid]. Over the next 60 years, no additional information was reported on this compound. Then between 1925 and 1988, it was chemically synthesized (Dutt 1925), its cis and trans isomers were separated (Comte et al. 1957), and stereochemistry was ascertained by NMR spectroscopy (Kelley et al. 1976) and unequivocally confirmed by X-ray crystallographic analysis (Nethaji et al. 1988). FA is a strong dibasic acid in which the first proton dissociation generates the carboxylate anion, while the second produces a phenolate anion. The anion has a high degree of resonance stabilization, which increases its acidity in comparison with similar phenolic acids (Graf 1992).

Several reports have evaluated its occurrence, soil levels, metabolism in plants and microorganisms, industrial applications, its physiological role during lignification, and its role as an allelochemical. In soils, FA has been detected at level up to 10 mM (Macias 1995). Widely present in the plant kingdom, it has also been studied for its properties as an anti-oxidant, food conservant (Graf 1992; Walters et al. 1997), co-adjuvant, anti-inflammatory, analgesic (de Campos et al. 1998) and anti-carcinogenic (Dobhal et al. 1999). Moreover, FA may be found as feruloyl-CoA in the phenylpropanoid pathway and as a component of cross-linked polymers in the cell wall (Smart and O’Brien 1979; Sánchez et al. 1996). As a metabolite of monolignols synthesis, FA is ester-linked to primary cell wall oligosaccharides,
typically to arabinose residue from glucuronoarabinoxylans. Smith and Harris (2000) reported that FA may be ester-linked in monocotyledons (Arecales, Commelinales, Poales, Zingiberales, etc). In dicots, FA may be present in Caryophyllales (Hartley and Harris 1981), Solanales (Keller et al. 1996), Brassicaceae (Chen et al. 1998), and Apiales (Parr et al. 1997). In soils, FA has been considered to be a strong allelochemical with several effects on plants, such as reduction in water utilization, inhibition of foliar expansion and root elongation, reduction in the rates of photosynthesis and inhibition of nutrient uptake (Siqueira et al. 1991; Einhellig 1995). Einhellig (2004) suggested that simple phenolic acids such as ferulic acid, coumarins and tannins appear to have similar modes of action that affect the growth of plants and microbes through multiple physiological effects that confer on them a general toxicity. More recently, Reigosa and Pazos-Malvido (2007) reported the potential phytotoxic effects of different allelochemicals on germination and root growth of Arabidopsis thaliana. The authors observed that eleven of the 21 molecules showed significant inhibitory effects on germination, and 17 inhibited root growth. Although different physiological effects are known, its primary mode of action has not been conclusively established. **Allelochemical-soil-microorganism interactions: A big hindrance**

With the elucidation of certain mechanisms by which allelochemicals cause their effects, researchers have been forced to realize that it is rare for a single allelochemical to exist alone under field conditions in concentrations large enough to have significant effects (Einhellig 1995). As described
earlier, an interfering factor in allelopathy is the interaction between the allelochemical and another chemical compound in the soil. Mixtures of non-inhibitory concentrations of individual phenolic acids may inhibit plant growth in an additive (equal to the sum of the effects of each allelochemical tested separately), synergistic (greater than the sum of the effects of each allelochemical) or antagonistic (lower than the sum of the effects of each allelochemical) manner (Rasmussen and Einhellig 1975). Lehman and Blum (1990) demonstrated that, in nutrient solutions, the leaf expansion and dry weight were reduced by single and multiple treatments of FA, vanilliac acid (VA) and p-coumaric acid (p-CA). The effects of the mixture of allelochemicals were additive (for 0.5 mM FA plus 0.5 mM p-CA mixture) and antagonistic (for 0.5 mM FA plus 0.5 mM VA mixture). Using soil systems, Blum et al. (1985) and Gerg and Blum (1991) reported that the effects of FA plus VA, FA plus p-hydroxybenzoic (p-HBA) and p-CA plus p-HBA acid mixtures on leaf area expansion revealed additive effects. Similar additive (FA plus VA) effects on lettuce root growth were observed by Sampietro et al. (2006). Conducting split-root experiments, Lehman et al. (1994) verified that the simultaneous effects of FA and p-CA on leaf expansion were additive. The inhibition of leaf expansion was directly related to the concentrations of the acid(s) and the proportion of roots treated with the acid(s). Soybean roots cultivated in nutrient solution containing FA or VA (0.5 mM; 1.0 mM and equimolar mixtures) for 48 h were affected (Suzuki et al. 2003). Acting by themselves, both compounds (at 0.5 or 1.0 mM) decreased root length, and fresh and dry weights, and increased soluble and cell wall-bound peroxidase activities. At 1.0 mM, FA increased (but VA decreased) the phenylalanine ammonia-lyase (PAL) activity. Acting simultaneously, the effects of the allelochemical interaction were lower than the sum of the effects of each compound tested separately, an example of antagonism.

Another complex issue involves soil interactions. Reversible sorption of phenolic acids by soils provides short-term protection to FA and other phenolic acids from microbial degradation, affecting the intensity and the duration of this intensity (Blum 1998). Introduction of microorganisms into the soil indicates rapid utilization of allelochemicals. Differential soil fixation, microbial production of benzoic acids (VA, p-HBA) from cinnamic acids (FA and p-CA, respectively) and further differential utilization of cinnamic and benzoic acids by microorganisms reveal that these conditions may influence the magnitude and duration of the phytotoxicity of the individual allelochemical. Furthermore, the rhizosphere and bulk-soil bacteria may affect the access of allelochemicals toward the root. Phenolic acid-utilizing bacteria are induced/selected by less than 0.1 μmol g⁻¹ of phenolic acid. For a 0.6 μmol g⁻¹ soil, equimolar phenolic acid mixture composed of p-CA, FA, p-HBA and VA, modeling indicated that a 500% increase of phenolic acid in the rhizosphere, utilizing bacteria, would decrease the inhibition of cucumber leaf expansion by about 5%. In some cases, there is an inverse relationship between the size of the microbial rhizosphere population and the intensity of the allelochemicals’ effects (Blum et al. 2000).

**Uptake of FA: More complexity**

One of the aims of investigating allelopathic interactions has been to develop means of predicting plant effects after their uptake. In this context, the uptake of FA (as radiotracer U-14C-fumaric acid) from solutions (0.1 to 1.0 mM, pH 4.0 to 7.0) was monitored in intact and excised cucumber roots by Shann and Blum (1987). Results revealed that FA uptake was directly proportional to its concentration and inversely to the pH of the nutrient solution. The effects were more evident in relation to the concentration of FA than its net uptake (Lehman and Blum 1999). After uptake, the intensity of the effects depended on the constant presence of the allelochemical surrounding the seedling roots. If removed from the nutrient solution, effects may be reversed. Moreover, the proportion of the root system in direct contact with FA directly affects the allelopathic responses, such as root growth, water utilization and nutrient uptake (Klein and Blum 1990). In fact, Lehman and Blum (1999) demonstrated that the inhibition of net phosphorous uptake was related to the direct contact of the root system with FA rather than to its uptake.

A significant interaction has been verified between environmental temperatures and FA treatments. At 0.4 mM, FA reduced the dry weight of soybean seedlings grown at 34°C, while its effects were lower at 23°C. It may be plausible that temperature stress enhances allelochemical inhibition, indicating that interactions with the environment should be taken into account in understanding allelopathy (Einhellig and Eckrich 1984). Similarly, excudation of some benzoic and cinnamic acid derivatives by cucumber roots also increased with the temperature and/or photoperiod (Pramanik et al. 2000). FA caused more damage in root growth, water utilization, and leaf transpiration than other cinnamic and benzoic acids derivatives (Rasmussen and Einhellig 1977; Blum and Dalton 1985; Gerg and Blum 1991). In general, the main effects were associated with an increase in number of secondary roots and a reduction of the root/stem ratio (Blum and Rebeck 1989; Vaughan and Ord 1990).

**EFFECTS OF FA ON METABOLISM: SEEKING ANSWERS**

There are several proposed modes of action for allelochemicals. As pointed out by Einhellig (1995), “the phytotoxicity of many allelochemicals may be from a generalized cellular disruption rather than a specific mechanism”. Due to the diversity of compounds, a common allelochemical does not exist, nor is there a single mode of action for all allelochemicals. Therefore, the mode of action remains an open question. Some FA effects on plant metabolism will be related below.

**Effects on carbon partition, carbohydrates and lipids**

It has been verified that FA reduces the conversion of glucose to soluble amino acids, proteins and organic acids (Danks et al. 1975), and facilitates the incorporation of phenylalanine in proteins (van Sumere et al. 1971). A plausible explanation is that carbohydrate partitioning in plants drives toward growth and synthesis of secondary metabolites, during differentiation or under stress (Matsuki 1996). Under FA stress, glucose may be released into the cytosol and, further, used in the shikimic and phenylpropanoid pathways, reducing the carbon flux in the primary metabolism. In addition, FA decreases CO₂ reduction by photosynthesis (Yu et al. 2003), which may be related to changes in chlorophyll content (Einhellig and Rasmussen 1979; Blum and Rebeck 1989), in glucose metabolism (Ferrarese et al. 2000). This might be associated with the conspicuous reduction in the starch stores of cap cells shown by ultrastructural assays (dos Santos et al. 2007).

Utilization of energy necessary for cells to grow and multiply in response to FA has been affected in plants. FA reduced lipid mobilization followed by the accumulation of unsaturated fatty acids in canola (Brassica napus) seeds during germination (Baleroni et al. 2000). It also increased the contents of saturated and unsaturated fatty acids of the polar and non-polar lipid fractions and xyllose, fructose and sucrose in soybean root (Ferrarese et al. 2001), as seen in **Table 1**. Consequently, cellular structure changes appear to be, at least partially, associated with alterations in lipid and carbohydrate metabolism (Hio 1988; Ohlrogge and Browse 1995; Surjus and Durand 1996; Harwood 1997). Another fact is that malondialdehyde content, a product of lipid peroxidation, was strongly enhanced (152%) in cucumber roots by 0.5 mM FA. Moreover, the membrane injury, which indicates the integrity of the membrane, increased by 10% under FA action. It is well known that unsaturated fatty
Table 1 Changes in some physiological and biochemical indicators in plants submitted to the FA treatment.

<table>
<thead>
<tr>
<th>Function</th>
<th>Indicator</th>
<th>Change</th>
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<tbody>
<tr>
<td>Energy carbohydrate</td>
<td>Glucose</td>
<td>(-)</td>
</tr>
<tr>
<td></td>
<td>Fructose</td>
<td>(+)</td>
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<td></td>
<td>Sucrose</td>
<td>(+)</td>
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<tr>
<td>Structural carbohydrate</td>
<td>Rhamnose</td>
<td>(-)</td>
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<tr>
<td></td>
<td>Xylose</td>
<td>(+)</td>
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Lipid metabolism

| Fatty acids               | Palmitic acid      | (+)          |
|                          | Stearic acid       | (+)          |
|                          | Behenic acid       | (+)          |
|                          | Oleic acid         | (+)          |
|                          | Linoleic acid      | (+)          |
|                          | Linolenic acid     | (+)          |

Lipid peroxidation

| Malondialdehyde          | (+)                |

Enzyme activities

| PAL                      | (+)                |
|                         | CAD/SAD            | (-)          |
|                         | POD                | (-)          |
|                         | ICL                | (+)          |
|                         | ATPases            | (-)          |
|                         | β-GT               | (+)          |
|                         | β-GL               | (+)          |

Symbols: (-), decreased; (+), increased; (=): unchanged.

CO2 fixation: (-), decreased; (+), increased; (=): unchanged.

Table 1 Changes in some physiological and biochemical indicators in plants submitted to the FA treatment.

Peroxidases

Some researchers have reported alterations in POD activity under FA action. For example, in cucumber root treated with FA (0.5 or 1.0 mM), the soluble and bound form of POD increased significantly (Shann and Blum 1987; Politycka 1996; Politycka et al. 2004). Application of 1.0 mM FA also caused a significant increase in both soluble and bound POD in maize roots and correlated with a pronounced decrease in root growth (Devi and Prasad 1996). At 1.0 mM, FA also increased POD activity in soybean roots (dos Santos et al. 2004). Increase of soluble POD activity was accompanied by a decrease in root growth. Based on these results, the researchers above attributed FA effects to the production of free radicals. It is well known that soluble POD catalyzes the oxidation of diverse phenolic substrates and is often regarded as an antioxidant enzyme that protects cells from the destructive influence of oxygen radicals. However, if the cells ability to scavenger oxygen radicals is exceeded, phenolic acid oxidation by soluble POD leads to the production of quinones, which increase depolymerization of the cell membrane and changes in lipid composition (Politycka 1996, 1998; Ferrarese et al. 2001; Doblinski et al. 2003). Moreover, cell wall-bound POD is associated with cell wall stiffening and growth-restriction (Passardi et al. 2005). POD is able to convert phenolic compounds, such as ferulic, p-coumaric and caffeic acids, into free radicals, which spontaneously polymerize. This essential role for POD in the stiffening of cell walls through the formation of biphynyl bridges between wall polymers and, thus, the reduction of the cell wall extensibility have been proposed by some researchers (Fry et al. 1992; Sánchez et al. 1996; dos Santos et al. 2004).

Effects on mitochondrial respiration

Several allelochemicals, such as sorgoleone, juglone, quercetin, umbelliferon, gramine and cineole, have been found to perturb respiratory metabolism. In general, the production of ATP in mitochondria was inhibited by a variety of flavonoids (Einhellig 1995). Sert et al. (1998) demonstrated that POD activity in soybean roots after 24 to 72 h of FA treatment. In addition, Politycka (1999) reported that an increase in the POD activity induced by the action of FA and associated with reduced root growth of cucumber depended on ethylene synthesis. Application of an ethylene synthesis inhibitor (aminooxyacetic acid, AOA) cancelled out the effect of FA on POD activity (Politycka and Mielcarz 2007). According to these authors, ethylene participates in the retardation of cucumber root growth by FA.
a high allelochemical concentration.

CELL WALL, FA AND LIGNIFICATION: PERFECT LINKS

Integrated with the cytoplasm, the cell wall performs a role of exoskeleton, conferring to the cell its form, mechanical resistance, pathogen protection, adherence to vicinal cells, and restriction of water and saccharides as cellulose, hemicelluloses and pectins constituting its basic structure. Lignin is an important component of secondarily thickened plant cell walls. The biosynthesis of lignins proceeds through a long sequence of reactions that involve the cytosolic shikimate pathway. It supplies phenylalanine and tyrosine. Subsequently, the general phenylpropanoid pathway converts phenylalanine (or, in lesser extent, tyrosine) into \( p \)-hydroxycinnamoyl-CoA esters. The lignin-specific pathway starts with \( p \)-hydroxycinnamoyl-CoA esters and converts them into free cinnamic acids and monolignols (Fig. 2, Boerjan et al. 2003). FA and other cinnamic acids may covalently cross-link cell wall polymers (Fry 1986; Ramakrishna et al. 1998), hardening the cell wall. This process is important in stopping elongation (Fry 1986; Iiyama et al. 1990) and blocking access of pathogens (Asahbani et al. 1993) into the cytoplasm. Apoplastic peroxidases (ionic and covalently bound to the cell wall) are thought to catalyze the oxidation of both hydroxycinnamitate cross-linkage and monolignol polymerization, which may be regulated by the supply of \( \text{H}_2\text{O}_2 \) and ascorbic acid (Côrdoa-Pedregosa et al. 1996; Mehlhorn et al. 1996; Sánchez et al. 1996; Vianello et al. 1997).

As reported earlier (Ferrarese et al. 2001), a decrease in rhamnose and an increase in xylose contents were verified in soybean roots treated with FA. Rhamnose is a component of pectin and is related to the number of pectin gel ramifications and to reinforcement of the cell wall. It is thus possible that exogenous FA, esterified to polysaccharides, decreases free rhamnose content by reducing pectin hydrolysis. On the other hand, the increased content of xylose suggests an activation of cell wall hydrolases and esterases, which release oligosaccharides (Grant Reid 1997). In brief, FA might directly affect the structure of the cell wall. During treatment, root cells may accumulate FA in the apoplast (Akin et al. 1992) and peroxidases may catalyze the link of FA in the polysaccharides, lignin (Chakraborty et al. 1993; Politycka 1996; Wallace and Fry 1999) and other FA. Dehydrodiferulic acid may form diester, ester-ether or diester-ether cross-linkages between cell wall polymers, which may reinforce the cell wall against cellulases, pectinases (Akin et al. 1992; Wojtaszek 1997), laccase (Sterjads et al. 1993) produced by pathogens, and involved in the cessation of cell elongation. In addition to free FA, FA-oligosaccharides also show biological activity as inhibitors of cell growth (Ishi 1997) and are involved in signal transduction between plants and microorganism (Peters and Verma 1990).

Exogenously applied FA incorporates into the lignin residues (Shann and Blum 1987), inducing lignification and related enzymes associated with the reduced root growth of treated plants (Devi and Prasad 1996; Politycka 1999; dos Santos et al. 2004). Shann and Blum (1987) verified an increase in lignin contents associated with a decrease in root growth. In maize (\textit{Zea mays}) roots, FA increased the activity of cell wall-bound POD correlated to a significant increase in lignin content and a reduction in root growth (Devi and Prasad 1996). Politycka (1999) also verified that cucumber (\textit{Cucumis sativus}) seedlings treated with FA stimulated lignin production, coupled to a decrease in root growth.

IS THE CELL WALL AN ACTION SITE OF FA?

Recent data obtained by dos Santos (2007) revealed that FA affects soybean root growth due to the incorporation of FA into the phenylpropanoid pathway. Using phenylpropanoid enzyme inhibitors, the authors concluded that 4CL catalyzes the conversion of exogenously applied FA into feruloyl-CoA (Fig. 2). The feruloyl-CoA formed is then converted into coniferal- and sinapaldehydes, which must circumvent the inhibited CAD reaction by polymerizing toward lignin in the aldehyde state. Based on this fact, and linking the information available in the literature for FA, these authors suggested a mode of action for FA (Fig. 3) considering an elegant model for plant response throughout biotic stress proposed by Wojtaszek et al. (1997).

In the model, the contact of exogenous FA with the root cell inactivates sulphhydryl groups of carrier proteins, causing an ionic disturbance and affecting nutrient uptake by the cell membrane (Baziramakenga et al. 1995). In the Wojtaszek’s model, the pathogen infection generates a cascade of signaling events – including Ca\(^{2+}\) influx and proton efflux – that activates the NADPH-oxidase complex (generating \( \text{H}_2\text{O}_2 \)) and pH-sensitive cell wall POD (producing \( \text{H}_2\text{O}_2 \)), which produces an oxidative burst. To date, there are no data on signaling events caused by FA stress. However, the general disturbance caused by FA must be enough to increase the Ca\(^{2+}\) influx since its concentration is kept lower inside the cytoplasm by the action of ATPases. Short-time experiments revealed that the absence of Ca\(^{2+}\) in nutrient solution reduces FA effects on soybean roots (unpublished data). In addition, Converso and Fernandez (1996) found evidence that Ca\(^{2+}\) modulates POD isozymes.

The reduced linoleic acid content after FA treatment (Ferrarese et al. 2001) may also be related to signaling events. Linoleic acid is a precursor to oxylipins, such as traumatic, jasmonic acid, etc. (van der Selt et al. 2000), which are involved in the plant defense signaling mechanisms (Trawatha et al. 1995). The oxylipins pathway starts with the oxidation of linolenic acid by lipoxygenases, which are activated under stress/disease circumstances such as an increase of \( \text{H}_2\text{O}_2 \) (Fornaroli et al. 1999). On the other hand, jasmonic acid may inhibit plant growth and may be associated with the inhibition of root growth caused by FA (Cree man et al. 1992). Jasmonic acid is also related to the expression of specific POD isozymes during stress (Allison and Schulz 2004).

The control of pH in \( \text{H}_2\text{O}_2 \) production has been demonstrated. In beans, \( \text{H}_2\text{O}_2 \) is generated from \( \text{O}_2 \) by a pH-sensitive cell wall POD that requires a reducer group (Wojtaszek 1997). FA oxidation by POD might produce \( \text{H}_2\text{O}_2 \) and the resulting phenoxy radical may undergo dimerization. These dimers are, eventually, esterified to hemicelluloses, linking the cell wall polymers, stiffening the cell wall and decreasing the root growth (Zimmerman et al. 1994; Bolwell et al. 1995; Vianello et al. 1997; Bleu et al. 2001; Bolwell et al. 2002; Stobiecki 2002). Furthermore, an increase in \( \text{H}_2\text{O}_2 \) contents enhances activities of cell wall POD and lignification (Whetten et al. 1998; dos Santos et al. 2004; Politycka et al. 2004). As cited earlier, FA cross-linkages are the initial steps of lignification (Boerjan et al. 2003).

Experiments using inhibitors of this pathway revealed that FA might be channeled into the phenylpropanoid pathway and, later on, may increase the lignin production (dos Santos 2007). In addition, the FA-oxidizing enzyme ‘fructanase’ (Politycka 1996; Doblinski et al. 2003) has been related to an oxidative burst (Baziramakenga et al. 1995; Devi and Prasad 1996). When the oxygen radicals exceed the scavenger capacity of the cells, phenolic acid oxidation by PODs will lead to accumulation of quinones (Appel 1993; Politycka 1998). These compounds may act as proton carriers, intensifying depolarization of the root cell membrane. In addition, FA cross-linkages, lignin lipid peroxidation and changes in the membrane permeability may cause reduced root growth (Lee et al. 1982; Devi and Prasad 1996).

FERULIC ACID TOMORROW: WHAT HAPPENS NEXT?

Available data related to the effects of FA on plants indicate plausible action sites during FA stress, especially the putative starting effects on sulphhydryl groups of carrier proteins.
and the irreversible reduction of cell wall extensibility. Root responses to the FA action include activation of POD, cross-links between cell wall polymers and reduction in cell wall extensibility. Moreover, exogenous FA activates cell wall POD, increases apoplastic H$_2$O$_2$ content, and may be incorporated into the metabolic pathway that leads to lignin production.

Fig. 3 Proposed mode of action for ferulic acid on lignification of soybean roots. PAL, phenylalanine ammonia-lyase; C4H, cinnamate 4-hydroxylase; 4CL, 4-coumarate-CoA ligase; HCT, hydroxycinnamoyl-CoA:quinone/hydroxycinnamoyltransferase; C3H, p-coumarate 3-hydroxylase; CCoAOMT, caffeoyl-CoA O-methyltransferase; CCR, cinnamyl-CoA reductase; F5H, ferulate 5-hydroxylase; COMT, caffeic acid/5-hydroxy ferulic acid O-methyltransferase; CAD, cinnamyl alcohol dehydrogenase; peroxidase (POD); ferulic acid (FA); piperonylic acid (PIP); 3,4-(methyleneoxy) cinnamic acid (MDCA). (1), Chen et al. (2006); (2), dos Santos et al. (2004); (3), Shann and Blum (1987); (4), Baziramakenga et al. (1995); (5), Wojtaszek (1997); (6), Boerjan et al. (2003).
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