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REVIEW

Fatty acid unsaturation, mobilization, and regulation in the response of plants to stress

Robert G. Upchurch

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Abstract Stress acclimating plants respond to abiotic and biotic stress by remodeling membrane fluidity and by releasing α-linolenic (18:3) from membrane lipids. The modification of membrane fluidity is mediated by changes in unsaturated fatty acid levels, a function provided in part by the regulated activity of fatty acid desaturases. Adjustment of membrane fluidity maintains an environment suitable for the function of critical integral proteins during stress. α-Linolenic acid, released from membrane lipid by regulated lipase activity, is the precursor molecule for phyto-oxylipin biosynthesis. The modulation of chloroplast oleic acid (18:1) levels is central to the normal expression of defense responses to pathogens in *Arabidopsis*. Oleic (18:1) and linolenic (18:2) acid levels, in part, regulate development, seed colonization, and mycotoxin production by *Aspergillus* spp.

Keywords Abiotic and biotic stresses · Defense response · ω-6 Desaturase · ω-3 Desaturase · Fatty acids · Lipase · Membrane fluidity · Δ-9 Stearoyl acyl carrier protein (ACP) desaturase · Unsaturation

R. G. Upchurch (✉)
Soybean & Nitrogen Fixation Unit, USDA-ARS, Raleigh, NC, USA
e-mail: greg.upchurch@ars.usda.gov

Introduction

Since plants lack mobility they cannot avoid exposure to stresses in their environment, but must adapt to them in other ways. Plants have evolved both constitutive and inducible means to resist stresses. Fatty acids are crucial components of cellular membranes, suberin, and cutin waxes that provide structural barriers to the environment (Beisson et al. 2007). They contribute to inducible stress resistance through the remodeling of membrane fluidity (Iba 2002), the release, through lipase activity, of α-linolenic acid (Grechkin 1998), and as modulators of plant defense gene expression (Kachroo et al. 2001) and seed colonization by fungi (Calvo et al. 1999). The ability to adjust membrane lipid fluidity by changing levels of unsaturated fatty acids is a feature of stress acclimating plants provided mainly by the regulated activity of fatty acid desaturases. Modification of membrane fluidity results in an environment suitable for the function of critical integral proteins, such as the photosynthetic machinery, during stresses. Free linolenic acid is itself a stress signal and the precursor for phyto-oxylipin biosynthesis (Blée 2002). Mounting evidence suggests that chloroplast oleic acid (18:1) levels are critical for normal pathogen defense responses in *Arabidopsis*, including programmed cell death and systemic acquired resistance (SAR; Kachroo et al. 2001). Oleic (18:1) and linoleic (18:2) acid levels, in part, regulate fungal development, seed colonization,

and mycotoxin production by *Aspergillus* spp. (Wilson et al. 2004; Xue et al 2006).

Plants often encounter the abiotic stresses of low or elevated temperature, exposure to salt, drought, and, less commonly, heavy metals, as well as biotic pathogen and insect attack, sometimes simultaneously. Even with the best available land and agricultural practices, the impacts of these stresses can significantly reduce the productivity of food and fiber crops. Thus, the current situation of diminishing farm land worldwide and the potential heightened effects of global climate change on environmental, pathogen and insect stresses provide increased impetus to understand stress resistance in crop plants. More complete knowledge of fatty acid unsaturation, mobilization, and regulation processes may significantly aid the development of effective strategies for managing abiotic and biotic stresses for these plants.

This review focuses on recent advances in our knowledge of fatty acid unsaturation, mobilization, and regulation in the responses of plants to abiotic and biotic interactions. The regulation of fatty acid desaturases and lipases in the remodeling of membrane lipid composition is specifically discussed. The rapidly growing body of knowledge on the phytooxylipins (oxygenated derivatives of α-linolenic acid synthesized in plants in response to biotic and abiotic stresses) has been the subject of regular review. The reader is referred to the following excellent articles for current information about oxylipins and defense signaling and gene regulation (Creelman and Mulpuri 2002; Wasternack 2007), and antimicrobial activity (Prost et al. 2005; Blée 2002).

Fatty acids and abiotic stresses

Low temperature

At low temperatures plant membranes undergo transition from a liquid crystalline to a gel-like phase with reduced fluidity and ion leakage and deactivation of membrane proteins occurs. Observations suggest that saturated phosphatidylglycerol (PG) content in chloroplast membranes may be related to the phase transition temperature and thus related to the low-temperature adaptability of plants (Iba 2002). The temperature of the phase transition in chilling-sensitive plants is higher than the phase transition temperature for chilling-resistant plants which suggests an association with the level of fatty acid saturation of PG in plastid membranes. In chilling resistant plants the amount of PG with saturated fatty acids (16:0, 18:0) is less than 20%, but chilling sensitive plants contain 40% or more saturated PG (Murata et al. 1992; Wolter et al. 1992).

Maintenance of polyunsaturated fatty acid levels in chloroplast lipids has been shown to contribute to low temperature survival and the normal formation of chloroplast membranes under chilling stress (Routaboul et al. 2000; Iba 2002). Both the *Arabidopsis fad5* mutant, which lacks an active chloroplast ω-9 fatty acid desaturase and accumulates high levels of palmitic acid (16:0), and the *fad6* mutant, which lacks an active ω-6 fatty acid desaturase and accumulates high levels of palmitoleic acid (16:1) and oleic acid (18:1), have reduced levels of polyunsaturated fatty acids in the chloroplast galactolipids. Seedlings of these mutants subjected to chilling stress became chlorotic and had half the chlorophyll content of wild-type. In addition, the number of thylakoid membranes in these mutants decreased and their chloroplasts were smaller. The *Arabidopsis fad2* mutant, deficient in an endoplasmic reticulum (ER) localized ω-6 desaturase, had significantly decreased polyunsaturates in the extrachloroplast membrane lipids. Long term culture of these mutant plants at low temperature (6°C) eventually resulted in their withering and death, but not for wild-type plants (Miquel et al 1993). Recent findings suggest that plants capable of cold acclimation accumulate polyunsaturates during cold stress. Cold acclimating potato (*Solanum commersonii*) was found to accumulate linoleic acid (18:2) in the membrane glycerolipids of the leaves, whereas commercial, non-acclimating potato (*Solanum tuberosum*) did not show this trait during cold stress (Vega et al. 2004).

Trienoic fatty acids (TAs), hexadecatrienoic acid (16:3) and linolenic acid (18:3), are the major polyunsaturated fatty acid species in membrane lipids. Increasing TAs in chloroplast membranes has been shown to enhance low temperature tolerance in plants during the early growth stage (Iba 2002). Overexpressing the *Arabidopsis* chloroplast ω-3 desaturase genes *FAD7* or *FAD8* in tobacco increased TAs and decreased dienoic fatty acids (DAs), hexadecadienoic acid (16:2) and linoleic acid (18:2), in leaf tissue (Nishiuchi and Ida 1998). Comparison of wild type with transgenic tobacco showed that chilling tolerance

was achieved in transgenic seedlings, but not in mature plants (Kodama et al 1995). When the levels of TAs in tobacco phospholipids, the main constituent of extrachloroplastic membranes, were increased by overexpressing an ER localized ω-3 fatty acid desaturase *FAD3* gene, no significant differences were detected between wild type and transgenic tobacco for resistance to chilling and freezing (Hamada et al. 1998).

Elevated temperature

In contrast, decreasing the amount of TAs in chloroplast membranes has been shown to strongly enhance high-temperature tolerance in plants. Cosuppression by gene silencing of the chloroplast ω-3 desaturases in transgenic tobacco resulted in very low levels of TAs and increased levels of DAs in the chloroplast membranes. When compared to control plants, these transgenic plants demonstrated resistance to high temperature (36°C) that was not transient. Moreover, thermal denaturation of photosynthetic machinery proteins was observed in the chloroplast membranes of wild-type plants exposed to high temperature but not in transgenic plants with decreased TAs (Iba 2002). The effects of elevated temperature on the fatty acid composition of storage lipids have been examined extensively in developing seeds. For example, the changes in soybean seed glycerolipid composition observed at high temperatures (Wilson 2004; Rajcan et al. 2005; Hou et al. 2006) were an increase in 18:1 and a decrease in polyunsaturated fatty acids (18:2 + 18:3), a pattern similar to the one for plant leaves acclimating to rising temperatures.

Salt and drought

The hydrophobic lipid interior of the membrane acts as a barrier to the passage of many ions and large molecules. Moreover, membrane integrity and the functionality of integral membrane proteins (for example the photosynthetic machinery proteins) are maintained by membrane structure and fluidity. Non-tolerant plants subjected to salt stress commonly show decreased levels of 18:3 in their membranes which suggests that the decrease in 18:3 reflects damage caused by this stress. Experiments with transgenic tobacco cells and plants demonstrated that overexpression of ω-3 desaturases, which increases 18:3, increases tolerance to salt and drought stress (Zhang et al. 2005). This suggests that tolerance of plants to salt and drought is, to large degree, dependent on the inherent level of fatty acid unsaturation and/or the ability to maintain or adjust fatty acid unsaturation (Berberich et al. 1998; Mikami and Murata 2003). Further support for the importance of fatty acid unsaturation in salt stress is provided by transgenic research with *Cyanobacteria* and *Saccharomyces cerevisiae*. *Cyanobacteria* may be considered analogous to plant chloroplasts. Mutants of the *Synechocystis* which lack ω-6 and ω-3 desaturase activities ($desA^{-}/desD^{-}$) contain monounsaturated but not polyunsaturated fatty acids. Tolerance to and recovery of the photosynthetic machinery of these mutants from salt stress was much reduced compared to the wild-type which contained polyunsaturated fatty acids (Allakhverdiev et al. 1999). The introduction of two sunflower (*Helianthus annuus*) ω-6 desaturases (*FAD2-1*, *FAD2-3*) into yeast, which can only synthesize monounsaturates, resulted in the production of dienoic fatty acids, an increased unsaturation index and fluidity, increased tolerance to NaCl, and increased tolerance to freezing (Rodríguez-Vargas et al. 2007).

Water-deficit stress causes degradative processes such as the inhibition of lipid biosynthesis (Monteiro de Paula et al. 1993), and stimulation of lipolytic and peroxidative activities (Matos et al. 2001; Ferrri-Iliou et al. 1994) that are associated with decreased membrane lipid content. Analysis of the fatty acid composition of leaf lipids in drought-stressed rape (*Brassica napus*) plants shows decreased 18:3 mainly in the chloroplast monogalactosyldiacylglycerol (MGDG) and decreased 18:2 in phospholipid fractions (Dakhma et al. 1995). On the other hand, *Arabidopsis thaliana*, another *Brassica* species, shows remarkable tolerance to drought stress. The most streaking features of this tolerance are the capacities to maintain polar lipid content and stable lipid composition, and increase the digalactosyldiacylglycerol (DGDG):MGDG ratio, and fatty acid unsaturation (Gigon et al 2004).

Heavy metals

Exposure of plants to heavy metals produces a rapid inhibition of the growth of above and below ground parts, the onset of senescence, and decreased

photosynthetic activity. Of the many described effects of heavy metal exposure, direct effects include the release of protein and lipid components necessary for photosynthesis from thylakoid membranes, and metal replacement of Mg^{2+} in chlorophyll (Maksymiec 2007). Highly reactive oxygen species (ROS) are also produced during heavy metal exposure. For example, the highly reactive hydroxyl radical (·OH) is generated in situ under both abiotic and biotic stress conditions (Mithöfer et al. 2004). The ·OH molecule can be produced in the presence of redox active metals (Cu^{+}, Fe^{2+}) by the Fenton reaction from H_2O_2, itself a stress induced ROS. ROS may also accumulate in the presence of non-transition heavy metals (Cd^{2+}, Hg^{2+}) by a proposed mechanism involving metal inhibition of antioxidative enzymes, especially glutathione reductase. Among the plant genes that are activated by heavy metal stress are several encoding enzymes with fatty acid peroxidase activities including, α-dioxygenases, peroxidases and lipoxygenases which are also induced by pathogen stress (Mithöfer et al. 2004; Koeduka et al. 2005; Maksymiec 2007). As a consequence of heavy metal-induced accumulation of ROS and induced enzymatic peroxidase activities, polyunsaturated fatty acids (18:2, 18:3) in plant membrane lipids may undergo peroxidation resulting in damage and loss of membrane integrity. Not surprisingly, heavy metal sensitivity to both Cu^{+} (redox active) and Cd^{2+} (redox inactive) increase with increasing fatty acid unsaturation in plasma membranes. In yeast cells containing increased levels of 18:2 and 18:3, both Cu^{+}- and Cd^{2+}-induced lipid peroxidation and declining membrane integrity are rapid (Howlett and Avery 1997).

The cellular responses that occur when plants are exposed to heavy metals include changes in the amounts of various lipids and lipid fatty acid composition. Pepper (*Capsicum annuum*) seedlings cultured in solution with cadmium have lower MGDG, a decreased MGDG:DGDG ratio, and enhanced accumulation of phospholipids (phosphatidylcholine, PC; phosphatidylethanolamine, PE; and PG in leaves, but in the roots PC and both MGDG and DGDG decreased. Fatty acid composition of the leaves changed with exposure, but no major composition changes were detected in the roots. Lipid unsaturation in leaves (18:2 + 18:3) was decreased (Jemal et al. 2000). Tomato seedlings grown in heavy metal contaminated soil showed alterations in the fatty acid composition of chloroplast lipids but not the fatty acid composition of the roots (Verdoni et al. 2001). The percentage of 18:3 decreased significantly and 18:1 and 18:2 fatty acid levels greatly increased in primary leaves. The target of the heavy metal induced changes did not appear to be inhibition of the integral, extraplastidal ω-3 desaturase since the percentage of 18:3 in roots and in the phospholipid fraction of leaves did not decrease. Although the mechanisms by which membrane extraplastidal 18:3 decreased and 18:1 and 18:2 increased are unknown, it was suggested that metal inhibition of lysophosphatidylcholine acyltransferase may result in decreased import of lipids from the ER to the chloroplasts resulting in these effects. Maize (*Zea mays*) seedlings exposed to Cu^{+} have decreased unsaturation of total fatty acids in the roots, however compositional changes in polar fatty acids showed a general trend of increased unsaturation. These responses suggest that the 18-C fatty acid classes may have specific roles in maintaining membrane function such that plant growth can occur under copper stress. Copper stress was also associated with a decrease in total root phospholipid levels, and a decrease in the MGDG/DGDG ratio which may alter membrane permeability and fluidity. In shoots, unsaturation increased in PC and MGDG, but decreased in phosphatidylinositol (PI) and PG. The decreased abundance of several lipids (PI, PG, MGDG, DGDG) in shoots may have been responsible for altered photosynthetic membranes (Chaffai et al. 2007).

Fatty acid desaturases respond to abiotic stress

Abiotic stress-induced changes in the fatty acid composition of plant membrane lipids mainly occur through the regulated activities of fatty acid desaturases. A large body of research suggests that temperature regulates fatty acid desaturase expression at both the transcriptional and post-transcriptional levels. The first example suggesting that cold acclimation involves a response of a Δ-9 stearoyl acyl carrier protein desaturase (*SAD*) was reported for cold acclimating potato (Vega et al. 2004). Transcript accumulation of *SAD* and 18:2 levels increased in the leaves of cold acclimating *S. commersoni* potato leaves, but showed no such increases in a cultivated,

nonacclimating species. Enzymatic activities of both ω-6 and ω-3 desaturases significantly increased in soybean (*Glycine max*) cell suspensions when the cultures were incubated at low temperatures (Cheesbrough 1989). A post-transcriptional control mechanism is likely for the temperature-dependent regulation of the *Arabidopsis FAD2*-encoded ω-6 desaturase. *FAD2* was shown to be required for normal *Arabidopsis* growth at low temperature (Miquel et al. 1993), but no changes in *FAD2* transcript levels were observed when plants were transferred from 22 to 6°C (Okuley et al. 1994). Post-transcriptional regulation was demonstrated for the temperature regulation of isoforms of the soybean seed specific ω-6 desaturase gene, Gm*FAD2-1* (Tang et al. 2005). Heterologous expression in yeast revealed that FAD2-1A was less stable and had a higher protein turnover rate than FAD2-1B in cultures maintained at elevated growth temperatures. In addition, a specific serine residue was identified in both FAD2-1 sequences that, when phosphorylated at elevated temperature, might down-regulate enzyme activity. Subsequent research has shown that in addition to this kind of regulation, Gm*FAD2-1A* and *-1B* transcript accumulation is also down-regulated and associated with decreased levels of 18:2 in seed lipid during seed development at warm temperature (Byfield and Upchurch 2007a).

In maize, the transcript accumulation of a plastid localized ω-3 desaturase gene increases in response to growth at low temperature, suggesting regulation at the gene transcription level (Berberich et al.1998). In contrast, an ER associated ω-3 desaturase of wheat showed increased enzyme accumulation with increased 18:3 in roots at low growth temperatures, but in the absence of significant changes in transcript abundance (Horiguchi et al. 2000). This suggested that low temperature regulates the wheat ER ω-3 enzyme at the translational or post-translational level. In *Arabidopsis*, the expression of the ER-localized ω-3 desaturase *FAD3* responds to the synergistic and antagonistic interaction of plant hormones and the tissue specificity of expression is modified during plant development (Matsuda et al. 2001). Transcript accumulation of one of the two chloroplast ω-3 desaturases in *Arabidopsis*, *FAD8*, changed dramatically in response to growth at elevated temperature, but expression of the other, *FAD7* did not change with temperature (Gibson et al. 1994; McConn et al. 1994), but was found to be light-responsive (Nishiuchi and Iba 1998). The introduction of chimeric genes created from *FAD7* or *FAD 8* into a *fad7fad8* double mutant deficient in ω-3 desaturase activity has clarified the temperature dependency of *FAD7* encoded enzyme expression. Analysis of the transgenic plants showed that the temperature-dependent expression of *FAD7* was due not to the 5′-flanking region (promoter and untranslated region), but to the inherent exon/intron structure of *FAD7* (Iba 2002). Thus it is unlikely that *FAD7* gene expression is simply regulated at the transcriptional level. *Arabidopsis* FAD7 enzyme was later reported to be specifically destabilized by higher temperatures suggesting regulation by a post-translational mechanism (Matsuda et al. 2005). On the other hand, two ω-3 desaturase genes controlling 18:3 levels in flax seed have been identified (Vrinten et al. 2005) and the transcript accumulation of both genes (Lu*FAD3A* and Lu*FAD3B*) and 18:3 increased at a cold growth temperature. Significantly increased 18:3 levels in seed lipid was also associated with increased transcript accumulation of three soybean seed microsomal ω-3 desaturase genes (Gm*FAD3A*, Gm*FAD3B*, Gm*FAD3C*) in seeds that developed in a cool (20°C) compared to a warm (30°C) environment (Byfield and Upchurch 2007b).

Fatty acids and biotic stress

Pathogens

Recent studies suggest that free oleic acid (18:1) levels in the chloroplast regulate the defense response of plants to pathogens including programmed cell death and SAR. Stearoyl-ACP desaturases (SADs) are cytoplasmic enzymes that catalyze the conversion of stearic acid (18:0) to oleic acid (18:1), a key step regulating the cellular polyunsaturated fatty acid content. The *Arabidopsis* suppressor of SA insensitivity mutation (*ssi2*) defines a defective *SAD*, *FAB2* (Kachroo et al. 2001), which confers high 18:0 and reduced 18:1 levels, constitutive activation of the salicyclic acid (SA)-dependent pathway and repression of the jasmonic acid (JA)-dependent pathway (Kachroo et al. 2003b). Among the phenotypes of *ssi2* mutants are dwarfing, constitutive expression of pathogenicity related (PR) genes, accumulation of high levels of SA, spontaneous cell death,

susceptibility to the necrotroph *Botrytis cinerea*, and enhanced resistance to *Pseudomonas syringae*, *Peronospora parasitica*, and cucumber mosaic virus (Nandi et al. 2005). The *suppressors of (stearoyl) fatty acid desaturase deficiency* (*sfd*) class of mutants (for example the loss-of-function mutation in the plastidial glycerol-3-phosphate acyltransferase, *act1*), rescue all *ssi2* mutant phenotypes and have elevated levels of 18:1 and restored defense signaling (Nandi et al. 2003; Kachroo et al. 2004). This suggests that 18:1 levels, regulated by glycerolipid metabolism, modulate defense gene expression in *Arabidopsis* (Kachroo et al. 2003a; Chandra-Shekara et al. 2007). Interestingly, all *sfdssi2* mutants contain reduced levels of 16:3, a TA specifically acylated in chloroplast galactolipids, but are unaltered in 18:3 content. This suggests that reduced 16:3 may promote the *ssi2* conferred pathogen resistance phenotypes (Yaeno et al. 2004).

The release of 18:3 from plant membrane lipids by stress activated lipases is thought to provide the substrate for lipoxygenase and subsequent octadecanoid (oxylipin) pathway synthesis of JA and methyl jasmonate (Padham et al. 2007; Wasternack 2007). JA and methyl jasmonate participate in the signal regulation of a number of plant processes including wound and pathogen defense responses. Efforts have been successful to identify and characterize fatty acid-deesterifying lipases that are activated by pathogen attack and/or environmental stress. Results suggest that both A1 and A2 phospholipases (Grechkin 1998; Padham et al. 2007) are involved in 18:3 mobilization form membrane lipids. The *Arabidopsis* mutant *defective in anther dehiscence 1* (*dad1*) shows defects in anther dehiscence, pollen maturation, and flower opening that are rescued by exogenous application of 18:3 or JA, consistent with reduced JA in *dad1* flower buds. Characterization of the *DAD1* has shown it to encode a novel chloroplast A1 phospholipase that catalyzes the release of 18:3 from phospholipids (Ishiguro et al. 2001). Another phospholipase from *Arabidopsis* that is UV-B inducible (Lo et al. 2004) has properties that also suggest involvement in the initiation of octadecanoid synthesis. Both phospholipase A1 and A2 activities are induced in tomato leaves by wounding, treatment with the wound signal systemin, and treatment with oligosaccharide elicitors which suggests involvement in the lipid-mediated signaling responses to herbivory and pathogen attack (Narváez-Vásquez et al. 1999). Evidence suggests that some members of the patatin multigene family of vacuolar proteins may also function as lipolytic acyl hydrolases that can deesterify unsaturated fatty acids in membrane lipids to provide the initial substrate for octadecanoid synthesis (Dhondt et al. 2000; Holk et al. 2002). Deesterification of chloroplast galactolipids has been shown to be induced by drought stress, chilling, and senescence (Kaniuga et al. 1999; Matos et al. 2000). A chloroplast acyl hydrolase with galactolipase activity has been identified that can deesterify plastid galactolipids. The gene *Vupat1*, cloned from cowpea (*Vigna unguiculata*), encodes a patatin-like protein with galacto-acyl hydrolase activity (Matos et al. 2001). *Vupat1* expression increases during drought stress and may be involved in chloroplast membrane degradation during water stress.

Plant–pathogen interactions

Plant derived fatty acids have been shown to regulate the colonization of by seeds pathogens by controlling fungal pathogen development and mycotoxin synthesis. *Aspergillus* spp. are commonly encountered seed-colonizing fungi that complete their disease cycles through the development of asexual spores, and the formation of cleistothecia and sclerotia. The development of all three structures in *A. nidulans*, *A. flavus*, and *A. parasiticus* is affected by 18:2 and light (Calvo et al. 1999). *A. nidulans* metabolizes 18:2 into a series of sporogenic molecules, called psi factors. In *A. nidulans* the ratio of asexual spores (conidia) to sexual spores (ascospores) is affected by 18:2, 18:1 and endogenous psi factors derived from them (Calvo et al. 2001). Linoleic acid and hydroperoxylinoleic (oxylipin) derivatives from seeds increase asexual spore production in *A. flavus*, *A. parasiticus*, and *A. nidulans*. This suggests that the sporogenic effect of seed fatty acids may involve interference with and/or mimicking of psi factors (Calvo et al. 2002). Support for the role of 18:2 acid as a signal for conidiation in *A. parasiticus* is provided by experiments with an *A. parasiticus* ω-6 (Δ-12) desaturase mutant unable to convert 18:1 to 18:2 resulting in impaired polyunsaturated fatty acid biosynthesis. The desaturase mutant displayed delayed spore germination, a two-fold reduction in

growth, a reduced level of conidiation and complete loss of sclerotial development compared to the wild type (Wilson et al. 2004). These results are similar to those reported earlier for the Δ*odeA* deletion mutant of *A. nidulans* which also lacks an ω-6 desaturase. In this mutant, polyunsaturated fatty acids (18:2 and 18:3) are also depleted and 18:1 increased as per cent of total fatty acid content. The *odeA* strain has reduced conidial production and mycelial growth, and these effects are most apparent in cultures grown in the dark. In the dark the *odeA* strain showed delayed ascospore production but produced more ascospores over time than the wild type, suggesting a role for oleic acid derived psi factors as well in influencing the asexual to sexual spore ratio. Fatty acid composition and spore development were also affected by *veA*, a gene shown previously to control light driven conidial and ascospore development. These results suggest an interaction between the *veA* and *odeA* alleles for fatty acid metabolism and spore development in *A. nidulans* (Calvo et al. 2001).

Experiments have shown that 18:2 supports aflatoxin production by *A. flavus* and *A. parasiticus* in culture, whereas down stream 18:3-derived intermediates hydroperoxylinoleic acid derivatives and other oxylipins (Tsitsigiannis and Keller 2007) inhibit or stimulate aflatoxin production (Calvo et al. 2002). To determine whether seed concentrations of 18:2 were directly associated with aflatoxin contamination levels in field-grown peanuts, seeds of genotypes with a range of 18:2 content were inoculated with *Aspergillus flavus* and assayed for aflatoxin content. Low-18:2 peanut lines consistently contained more aflatoxin while normal- to high-18:2 lines contained variable amounts (Xue et al. 2005). Interestingly, when the levels of aflatoxin production were measured in normal- and high-18:1 backcross-derived peanuts, the high-18:1 peanuts averaged nearly twice as much aflatoxin as normal lines. The increase in 18:1 associated with the high 18:1 trait of peanut was achieved by a corresponding reduction in the level of 18:2, the fatty acid reported to support aflatoxin production in fungal culture (Xue et al. 2003).

Fatty acid desaturases respond to biotic stress

As has been discussed, the *Arabidopsis* chloroplast ω-3 fatty acid desaturases *FAD7* and *FAD8* are significantly up-regulated by cold temperature and salt stress. *FAD7* and *FAD8* are also induced by wounding and pathogen attack resulting in a marked accumulation of TAs and JA (Nishiuchi and Iba 1998). Recent studies have shown that TAs derived from the chloroplast play an important role in the early events leading to pathogen resistance (Yaeno et al. 2004). *Arabidopsis fad7fad8* double mutants lack chloroplast ω-3 desaturase activity which prevents the accumulation of TAs in the chloroplast membrane. In these mutants, the production of ROS associated with the NADPH oxidase-catalyzed oxidative burst, an early event in pathogen defense signaling, are greatly reduced. This suggests that TAs, especially chloroplast derived 18:3, are effective activators of NADPH oxidase. In the *fad7fad8* mutants, this major source of mobilizable 18:3 is greatly diminished, and the other *Arabidopsis* microsomal encoded ω-3 desaturase, *FAD3*, does not compensate this loss. The *fad7fad8* mutants display attenuated cell death in leaves inoculated with *Pseudomonas syringae* pv. *tomato* and reduced resistance to avirulent pathogens. The tomato *Spr2* (suppressor of prosystemin-mediated response 2) gene has been shown to encode a chloroplast ω-3 fatty acid desaturase (Le*FAD7*) most likely functionally analogous to the *Arabidopsis FAD7* that desaturates both 16:2 and 18:2. Mutation of this gene, which is responsible for most of the TA content in tomato leaves, results in 18:3 content of less than 10% found in the wild-type and a corresponding increase in dienoic fatty acids. *Spr2* mutants are impaired in JA accumulation, production of the transmissible wound signal, and have decreased defense against attack by tobacco hornworm larvae (Li et al. 2003). These results strongly suggest that wound and anti-herbivore defense responses are dependent on chloroplast 18:3, the precursor of JA produced by LeFAD7 activity.

The response of fatty acid desaturases to pathogen stress may be quite rapid. Expression profiling of soybean inoculated with the bacterial pathogen *Pseudomonas syringae* has shown that an ω-3 fatty acid desaturase was one of 94 chloroplast-associated genes specific to the resistance response that was significantly regulated 8 hours post-inoculation (Zou et al. 2005). In parsley (*Petroselinum crispum*) a plastid localized ω-3 desaturase gene was rapidly and transiently induced at the site of oligopeptide elicitor treatment in leaves (Kirst et al. 1997a). Treatment of cultured parsley leaf cells with the same elicitor

(derived from the pathogenic oomycete, *Phytophthora sojae*) also produced a rapid and transient transcriptional activation of a microsomal ω-6 gene (Kirst et al. 1997b). Large accumulations of polyunsaturated fatty acids (16:2,18:2,18:3) were detected in the elicitor treated plants and cells.

Fatty acid desaturases are regulated at both the transcriptional and post-translational levels in response to pathogen stress. Inoculation of avocado fruits (*Persea americana*) with spores of the fungal pathogen *Colletotrichum gloeosporioides* resulted in transcriptional activation of a Δ-9 stearoyl ACP desaturase (*SAD*), increased levels of 18:2, and the accumulation of antifungal diene compounds (Madi et al. 2003). Fruits with increased *SAD* expression were more resistant to the pathogen. In *Arabidopsis*, as discussed, the *suppressor of SA insensitivity* mutation (*ssi2*/*fab2*) defines a defective SAD, the activity of which is critical for normal defense responses to pathogens. Six other, similar *Arabidopsis* SAD isoforms have been characterized, but the native expression of none of the six can compensate for the *ssi2* loss-of-function mutation. However, the low levels of 18:1 detected in the *fab2* mutant background do show that four of the six isoforms have activity (though greatly reduced), and thus contribute to the 18:1 pool. Transcript levels of the SAD isoforms are reduced in plants containing high 18:1. Overexpression of *S-ACP-DES1*, one of the six low activity isoforms, in *ssi2* plants resulted in restoration of 18:1 levels and rescued all *ssi2*-associated phenotypes. Thus, in *Arabidopsis*, 18:1 levels are regulated at both *SAD* transcriptional and post-translational levels (Kachroo et al. 2007). Transgenic expression of the yeast *SAD* in eggplant (*Solanum melongena*) and in other solanaceous plants (Xing and Chin 2000; Chin et al. 2001) increased cytosolic levels of 16:1, 18:1, and 16:3 fatty acids in their leaves. Expression of this *SAD* transgene in eggplant conferred resistance to *Verticillium dahliae*. Other *SAD* transgenic solanaceous species, showed resistance to *Erisyphe graminis*, *Phytophthora capsicci*, *Pseudomonas syringae*, and tobacco mosaic virus.

Future prospects

Molecular genetic and transgenic approaches with *Arabidopsis* in particular have rapidly expanded our knowledge of the inducible mechanisms that plants possess to resist abiotic and biotic stresses. Applying this knowledge to develop resistance to stress in crop plants and enhance their productivity has had some limited successes (Xing and Chin 2000; Chin et al. 2001). However, current crop improvement efforts rely on molecular breeding or transgenic approaches to capture, express, overexpress, or silence single candidate genes. For agricultural crops, durable stress resistance will likely require the directed regulation of multiple genes. Moreover crop plants, in their environment, are simultaneously subjected to multiple stresses (Iba 2002). Progress in identifying critical stress resistance-related genes is forthcoming, though gene expression profiling results show the responses to even a single stress to be complex (Schenk et al. 2003; DeVos et al. 2005; Zou et al. 2005). The experimental modeling of simultaneous multiple stresses would be expected to produce even more challenging and complex patterns to decipher. Therefore, the development of effective strategies that will enable crop plants to resist a wide range of stresses remains a challenge for the future.

On the other hand, there are common aspects to the responses of plants to both abiotic and biotic stresses. In stress tolerant plants the degree of membrane lipid unsaturation, principally 18:3 content, increases in response to low temperature, salt, and pathogen stresses, but decreases in response to elevated temperature and heavy metal stresses. Thus, the ability to simply direct membrane unsaturation in a single direction in the plant cannot provide tolerance or resistance to all stresses, especially since pathogen stress in addition involves the release of 18:3 from membrane lipids by lipase activity. However, since membrane fatty acid composition is, to a great extent, determined by the activities of complexly regulated integral fatty acid desaturases and lipases, continued efforts are warranted to find ways to finely regulate their expression in organelles and tissues during plant development.

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