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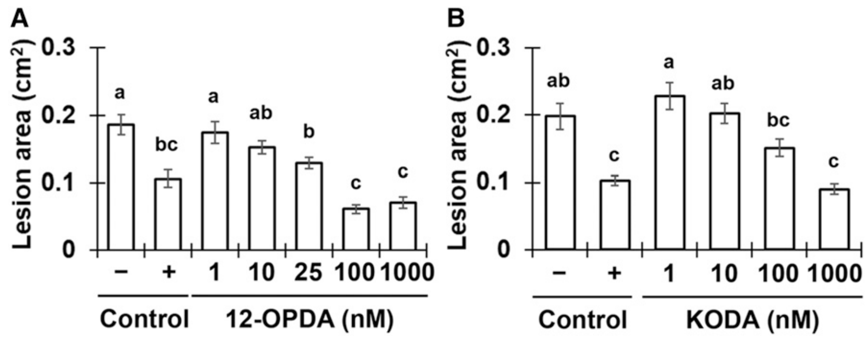
IN BRIEF

Xylem-Mobile Oxylipins Are Critical Regulators of Induced Systemic Resistance in Maize[OPEN]

In addition to promoting plant growth and development, the colonization of roots by beneficial microorganisms often provides aboveground tissues with enhanced resistance to pathogen attack. This form of resistance, referred to as induced systemic resistance (ISR), relies on the long-distance movement of root-derived signals that travel through the vasculature to access and prime defenses in aerial plant organs (Pieterse et al., 2014).

The growth-promoting fungus *Trichoderma virens* is a potent activator of ISR in several angiosperms. In the monocot maize (*Zea mays*), the ability to manifest ISR relies on secreted fungal proteins that modulate host oxylipin biosynthesis (Djonović et al., 2007; Constantino et al., 2013). In particular, the 9-lipoxygenase *LOX3* has emerged as a negative regulator of ISR, such that *lox3* mutants exhibit constitutive resistance to foliar pathogens and xylem sap collected from these plants is sufficient to induce ISR in wild-type receiver plants (Constantino et al., 2013).

To further explore oxylipin-based ISR signaling, **Wang et al., 2020** took an analytical approach that leveraged fungal and maize germplasm with contrasting capacities to manifest ISR. First, the authors investigated the role of the 13-lipoxygenase *LOX10* during fungal colonization in maize roots. Wild-type *T. virens* and *T. virens* Δ*sir1* mutants (*Tv*-Δ*sir1*) with enhanced ISR activity both induced *LOX10* expression in maize roots, unlike ISR-deficient *T. virens* Δ*sm1* (*Tv*-Δ*sm1*). To better define the role of *LOX10* during ISR, the authors assessed *lox10* mutants for *T. virens*-induced ISR to fungal infection in distant leaves. Surprisingly, *lox10* mutants colonized by *T. virens* displayed "systemic-induced susceptibility" to *Colletotrichum graminicola* (hemibiotroph) and *Cochliobolus heterostrophus* (necrotroph) compared with untreated plants. Xylem sap-swapping experiments further underscored the importance of oxylipins for ISR, as fluids collected from *T. virens*-treated *lox10* produced systemic-induced susceptibility in wild-type receiver plants while sap collected from untreated *lox3* mutants (constitutive ISR) or *T. virens*-treated wild-type plants increased ISR in untreated wild-type receiver plants.



The Oxylipins 12-OPDA and KODA are Potent Inducers of ISR.

Wild-type maize receiver plants display dose-dependent resistance to *C. graminicola* infection when transfused with xylem sap supplemented with increasing concentrations of 12-OPDA (A) or KODA (B). In each case, the level of resistance is compared against untreated controls (−) or *T. virens*-treated control plants (+) displaying ISR. Letters indicate statistically significant differences (ANOVA, Tukey's HSD $P < 0.05$) between samples. (*Adapted from Wang et al. [2019], Figure 7.*)

The contrasting ISR phenotypes of *Tv*-Δ*sm1*/*Tv*-Δ*sir1* and maize lipoxygenase mutants facilitated comparative analytical studies aimed at identifying oxylipin ISR signals in xylem sap. To this end, the authors identified two xylem-mobile oxylipins that were strongly associated with ISR; the jasmonic acid (JA) precursor 12-oxo-phytodienoic acid (12-OPDA) and an α-ketol of octadecadienoic acid (KODA). Importantly, both 12-OPDA and KODA provided enhanced resistance to *C. graminicola* in a dose-dependent manner when transfused with xylem sap collected from untreated maize (see figure). Moreover, 12-OPDA restored ISR activity in plants colonized by *Tv*-Δ*sm1* and in *lox10* mutants, supporting the idea that 12-OPDA is a critical signal for long-distance ISR signaling in maize.

Since 12-OPDA is a precursor of the defense hormone JA, the authors investigated the relevance of bioactive jasmonic acid-isoleucine (JA-Ile) during ISR in maize. Phenotypic analysis of the JA-deficient *opr7 opr8* double mutant demonstrated that JA itself was dispensable for ISR. Moreover, increasing doses of JA-Ile led to enhanced susceptibility when transfused with maize xylem sap. Collectively, the data suggested that the accumulation of 12-OPDA rather than JA-Ile is required for the establishment of *T. virens*-induced ISR in maize. In support of this idea, transcriptome analysis of maize plants undergoing ISR revealed that 12-OPDA and KODA biosynthesis genes were induced upon *T. virens* colonization, whereas JA-related genes were ultimately repressed. Together, the data illustrate a directed effort to accumulate the mobile-oxylipin signals 12-OPDA and KODA during ISR. Further efforts to understand the contribution of these oxylipins to ISR in maize and other

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angiosperms will provide fundamental insight into long-distance immune signaling activated by beneficial interactions with rhizosphere microbes.

Philip Carella
Sainsbury Laboratory
University of Cambridge
Cambridge, United Kingdom
philip.carella@slcu.cam.ac.uk
ORCID ID: 0000-0002-5467-7290

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