Abscisic Acid (ABA)
ABSCISIC ACID (ABA) controls many plant processes including stress responses, development and reproduction.

ABSCISIC ACID (ABA) controls many plant processes including stress responses, development and reproduction.
Lecture Outline

• ABA biosynthesis, homeostasis and transport
• ABA receptors
• Downstream signaling
• Whole-plant responses
• Guard cell responses
• Root developmental responses
• Vegetative desiccation responses
• Seed desiccation and dormancy
• Biotic stress responses
Biosynthesis, homeostasis and transport

Jan Zeevaart (1930-2009) was a major contributor to our understanding of ABA synthesis and homeostasis.

ABA levels increase during stress but decrease when stress is relieved.

ABA is synthesized in the plastid and cytoplasm and is derived from zeaxanthin, a plant pigment.

Zeaxanthin is abundant in green tissues but can be limiting for ABA synthesis in roots.

Zeaxanthin epoxidase (ZEP) converts zeaxanthin to violaxanthin

ZEP mutants are ABA deficient and lose water rapidly

All-trans-violaxanthin rearranges to form 9-cis-epoxycarotenoids

NCED cleaves 9-cis-epoxycarotenoids to produce xanthoxin
The first NCED gene was identified from the maize *vp14* mutant

Leaves from *vp14* plants lose water more rapidly than wild-type leaves because of reduced levels of ABA

The VP14 protein has NCED activity in vitro

Thin-layer chromatography showing cleavage of 9-cis-epoxycarotenoids by VP14

NCEDs are part of a large family, but only some are involved in ABA synthesis.

NCED genes are induced by drought stress and during seed maturation

Increased NCED correlates with increased ABA synthesis

Tobacco plants transformed with an inducible Phaseolus vulgaris NCED gene show increased ABA levels, enhanced drought tolerance and increased seed dormancy.

Collectively these studies show that NCED expression is highly correlated with ABA levels and a key regulatory event in ABA synthesis.

Conversion of xanthoxin to ABA requires two enzymes


ABA levels are also controlled by inactivation pathways.

Rehydration Developmental signals

[ABA]

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Rehydration of vegetative tissues causes ABA levels to drop

Xanthium strumarium

Rehydration of vegetative tissues causes ABA levels to drop

Leaf detached to initiation drying at time ZERO

Rehydration by immersion in water

ABA accumulates

ABA converted to phaseic acid

Rehydration

Phaseic Acid

ABA

ABA is deactivated by ABA-8′-hydroxylase, encoded by CYP707A

Low humidity  High humidity

CYP707A genes are upregulated upon transfer to high humidity

Drought tolerance by chemical inhibition of 8′-hydroxylase action

Inhibitors of P450 enzymes can slow the degradation of ABA by ABA 8′-hydroxylase

Uniconazole inhibits P450 enzymes, but non-specifically.

P450 inhibitors are often non-specific. Uniconazole inhibits ABA inactivation AND gibberellin (GA) synthesis, causing growth reduction.

Chemical modification of uniconazole leads to a more specific inhibitor

The modified compound is specific for 8’-hydroxylase and confers drought tolerance without growth inhibition.

Seed germination also requires ABA inactivation by 8′-hydroxylase

Loss-of-function of one CYP707A gene copy reduces germination, and loss-of two copies nearly abolishes it.

ABA can be reversibly inactivated by glucosylation

ABA glucosyltransferase

β-glucosidase

ABA

ABA-glucosyl ester

ABA-glucosyl ester (ABA-GE) is an inactive storage and transfer form


ABA-glucosyl ester (ABA-GE) is an inactive storage and transfer form
Mutants that cannot recover ABA from ABA-GE are ABA deficient

Conversely, mutants that cannot conjugate glucose to ABA have an ABA-excess phenotype

Plants deficient for UDP glucosyltransferase UGT71C5 have less glucosyl ester and more free ABA. and are more resistant to drought stress than wild type plants.

ABA accumulation and homeostasis are tightly controlled

NCED
9-cis-exopoxycarotenoids → xanthoxin → [ABA]

Rehydration Developmental signals
Water stress Developmental signals

8'-Hydroxy ABA → (-) Phaseic acid
ABA movement – between organs and cells

ABA translocation and root hydraulic signals may be involved in signaling from root to shoot.

Well-watered plant with open stomata and high transpiration rate

Water-stressed plant with closed stomata and low transpiration rate
Partial rootzone drying is a method to reduce water use.

Well-watered plant with open stomata and high transpiration rate.

Exposing part of the root system to dry conditions reduces stomatal aperture and water use without inducing detrimental drought stress effects.
After water stress ABA accumulates in the veins and then guard cells

A reporter construct made of an ABA-inducible promoter fused to luciferase was used to image ABA levels

ABA is a weak acid and exists in charged and uncharged forms.

As a weak acid, abscisic acid is a charged anion (ABA\(^-\)) in the cytoplasm (pH 7).

In the more acidic cell wall (pH 5.5) some is uncharged (ABAH). This presumably enhances the movement of ABA into but not out of cells.
Transporters enhance ABA movement across membranes

AtABCG25 is expressed in veins and encodes an ABA exporter

AtABCG25 is transcriptionally induced by ABA

Water loss from detached leaves is reduced in *AtABCG25* overexpressing plants

AtABCG40 is an ABA transporter expressed in guard cells

Guard cells in loss-of-function abcg40 mutants are less sensitive to ABA, rendering the mutants more susceptible to drought stress.

Other putative ABA transporters have been identified

ABA exporter

ABA importer

Transporter of ABA-GE

EcS = extracellular space
Cpl = cytoplasm
Vac = vacuole

ABA exporter

ABA importer

ABA importer

Biosynthesis, homeostasis and transport - summary

• In most but not all tissues NCED is rate limiting for ABA synthesis

• ABA synthesis increases with drought stress and during seed maturation

• ABA can be degraded to phaseic acid or reversibly conjugated to ABA-GE

• ABA can be transported within the plant, from root to shoot and from vascular tissues to guard cells
Perception and Signaling

ABA RESPONSES

ABA

PYR1

PYR/RCAR receptors

Phosphatase

PP2C Protein phosphatases (including ABI1)

Protein kinases (including SnRK2s and CDPKs)

The core signaling pathway

ABA

P

P
The PYR/RCAR ABA receptors made Science magazines Top 10 list

The PYR/RCAR ABA receptors are necessary for ABA responses

Wild-type plants fail to germinate on ABA-containing medium

The ABA-insensitive mutant abi1 germinates on ABA-containing medium

Pyrobactin-insensitive mutants are ABA-insensitive and so germinate on ABA-containing medium

There are many genes encoding PYR/RCARs

The 14 PYR/RCARs in Arabidopsis

<table>
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<tr>
<th>Common Name</th>
<th>Species</th>
<th>Number of genes</th>
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<tbody>
<tr>
<td>Soybean</td>
<td>Glycine max</td>
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<tr>
<td>Corn</td>
<td>Zea mays</td>
<td>20</td>
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<tr>
<td>Western poplar</td>
<td>Populus trichocarpa</td>
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<tr>
<td>Rice</td>
<td>Oryza sativa</td>
<td>11</td>
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<td>Grape</td>
<td>Vitis vinifera</td>
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</tr>
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<td>Sorghum</td>
<td>Sorghum bicolor</td>
<td>8</td>
</tr>
<tr>
<td>Barrel medic (a model legume)</td>
<td>Medicago truncatula</td>
<td>6</td>
</tr>
<tr>
<td>Arabidopsis</td>
<td>Arabidopsis thaliana</td>
<td>14</td>
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</table>

Different PYR/RCARs affect ABA responses slightly differently

<table>
<thead>
<tr>
<th>Gene</th>
<th>Expression Pattern</th>
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</thead>
<tbody>
<tr>
<td>PYR1</td>
<td></td>
</tr>
<tr>
<td>PYL1</td>
<td></td>
</tr>
<tr>
<td>PYL2</td>
<td></td>
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<td>PYL5</td>
<td></td>
</tr>
<tr>
<td>PYL8</td>
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The genes have different expression patterns

But there’s some functional redundancy – ABA insensitivity increases as more genes are knocked-out


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ABA sensitivity can be regulated by receptor proteolysis

The ABA receptors are targets of selective proteolysis by ubiquitination. ABA stabilizes the receptors by limiting their polyubiquitination.

Low ABA levels enable ABA receptor proteolysis, effectively shutting down ABA responses when ABA levels drop.

ABA sensitivity can be regulated by membrane anchoring of receptors.

CAR proteins have a domain that physically interacts with PYR/PYL proteins and a Ca-dependent lipid binding C2 domain that anchors them to the membrane. Overexpression of CAR1 leads to enhanced ABA inhibition of shoot growth. Triple car mutants are less sensitive to growth inhibition by ABA. Thus, CAR proteins enhance ABA sensitivity.


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PYR/RCAR receptors bind ABA in a complex with ABI1 or other PP2Cs

The PYR/ABI1 interaction forms the basis of an ABA visualization system

FRET = Fluorescence Resonance Energy Transfer

ABA lowers FRET efficiency, which can be measured by light emission ratios

No ABA, energy transferred between chromophores
+ ABA, no energy transferred between chromophores

This reduction in the emission of fluorescence is seen here in guard cells as a shift towards blue in the emission ratio scale following treatment with 10 µM ABA over time.

The Arabidopsis *abi1-1* mutant has ABA-insensitive germination

abi1-1 mutants are ABA-insensitive in all their responses

- Germination is not inhibited on ABA
- Root growth is not inhibited on ABA
- Guard cells are not ABA-responsive
- ABI1 encodes a PP2C protein phosphatase

The *abi1* mutation stabilizes the inhibitory effect of ABI1

**WILD TYPE**

- **PYR1**
- **ABI1**
- Kinase

**WILD TYPE + ABA**

- **PYR1**
- **ABI1**
- Kinase

**abi1-1 + ABA**

- **PYR1**
- **abi1-1**
- Kinase

**NO ABA RESPONSES**

**ABA RESPONSES**

**NO ABA RESPONSES**
Arabidopsis has 76 PP2Cs. Only clade A participates in ABA signaling.

Six of the clade A proteins (indicated) have a confirmed role in ABA signaling.

PP2Cs interfere with the action of SnRK2 protein kinases

In the absence of ABA, SnRK2 protein kinase activity is inhibited by PP2C phosphatases.
In the absence of ABA, PP2Cs and SnRKs physically interact

This interaction is stabilized in the dominant abi1 mutant

Yeast two-hybrid assay – when two proteins interact, the yeast cells grow

ABA / PYR1 binding sequesters PP2C and permits SnRK2 activity.

PYR1, ABA and PP2C form a complex that inactivates PP2C.

This permits SnRK2 activation. Phosphorylation targets include SnRK2s, ion channels and transcription factors.
PP2C binds ABA + receptor & SnRK kinase similarly

A PP2C tyrosine indicated by interacts with both SnRK2 and PYL+ABA. A serine (S) on both SnRK2 and PYL interacts with PP2S

When PYL+ABA binds PP2C, SnRK2 is released and autophosphorylates (S-P_
SnRK2 turnover & stability is subject to additional regulatory controls

- Enhanced binding / sustained switch “off” of ABA responses
- Enhanced proteolysis, dampens ABA responses

Environmental, developmental information and signals

Casein kinase 2 (CK2)
SnRK2s are protein kinases that promote ABA responses

The CPDK-SnRK superfamily of protein kinases

The SnRK2 subfamily

ABA RESPONSES

SnRK2

Ion channel

P

P

P

TF

SnRK2s were first characterized in wheat and *Vicia faba*

PKABA1, an ABA-inducible SnRK2 protein kinase from wheat, accumulates in developing seeds. A dominant negative form of AAPK interferes with guard cell response to ABA.

A protein kinase activity of the SnRK2 AAPK is enhanced by ABA.

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A SnRK2 mutant, ost1, was identified by thermal imaging

Wild type

ost1-1

ost1-2

Loss-of-function ost1 mutants have reduced stomatal closure response. OST1 is expressed in guard cells and vascular tissues

Wild type

ost1-1

ost1-2

Thermal imaging can be used to monitor guard cell responses

Mutants impaired in ABA synthesis (aba2-13) or signaling (ost1-4) show reduced stomatal closure in response to a decrease in humidity, and so are cooler than wild-type plants.

Francis Darwin recognized stomatal effects on leaf temperature (1904)

The temperature of the leaf might be used... as an index of the condition of the stomata

Francis Darwin
1848 - 1925

ON A SELF-RECORDING METHOD APPLIED TO THE MOVEMENTS OF STOMATA.

Francis Darwin.
(with fifteen figures)

In my paper on stomata\(^2\) it was incidentally shown that the temperature of a leaf varies, other things being equal, with the condition of the stomata. Thus if there are two leaves, in one of which (O) the stomata are open, while in the other (C) they are closed, it is found that O is cooler than C. It is evident that this must be so because the evaporation from O is greater than that from C; in fact, one corresponds to the wet bulb, and the other to the dry bulb of a psychrometer. In the experiments above referred to the leaves employed were those of Tropaeolum, C being a leaf in which the stomata were closed by separating it from the plant, and thus allowing it to wither; while O was a leaf still attached to the plant, with normally open stomata. As the stomata of O closed in the evening, its temperature approached more and more to that of C, and to that of the dry bulb thermometer, while the temperature of an aquatic leaf (of a species in which the stomata are open at night) remained cooler than the dry bulb thermometer.

These experiments suggested that the changes in the temperature of a leaf might be used, with certain precautions, as an index of the condition of the stomata. It was hoped that by the use of this method it would be possible to check and control


Botanical Gazette
FEBRUARY, 1904
SnRK2.2, SnRK2.3, and SnRK2.6 are all involved in ABA response

The triple mutant is ABA insensitive in its germination response

The triple mutant guard cells are nearly completely insensitive to ABA

Calcium-dependent protein kinases (CDPKs) participate in ABA signaling

There are 34 CDPKs in Arabidopsis. A few have been confirmed to transduce the ABA signal

Drought tolerance is correlated with activity of some CDPKs

ABA signaling contributed to evolution of drought tolerance in land plants

Transcription factors are major targets of CDPKs and SnRK2s

Some TFs were identified genetically

Some TFs were identified biochemically
Viviparous-1 and ABI3 genes encode seed-specific transcription factors

These transcription factors are highly expressed in seeds, and bind to the RY DNA element (CATGCA(TG)) that is enriched in the promoters of seed-expressed genes


Several ABA-regulated TFs are basic region–Leucine Zipper (bZIP) type
The bZIP transcription factors were identified biochemically

Early studies of seed-specific and ABA-responsive genes identified a conserved DNA promoter sequence called the ABA-responsive element (ABRE)
The bZIP transcription factors were identified biochemically

Proteins that bind to the ABRE were identified by gel mobility shift assays and DNase footprinting.

These ABRE-binding proteins are called ABFs or AREBS.


The bZIP transcription factors were also identified genetically.


The Arabidopsis AREB/ABF/bZIP subfamily has nine members.

Overexpression of ABF3 or ABF4 confers ABA hypersensitivity

Overexpression of the ABF3 or ABF4 transcription factors confers drought tolerance

Overexpression of the ABF3 or ABF4 transcription factors causes hypersensitive germination

ABA-induced transcription can be reconstituted in vitro

Using protoplasts as an assay system, expression of a TF (ABF2) and SnRK2 is sufficient for ABA-induced gene expression. Also adding PYR1 and ABI1 works too.

ABI4 is a transcription factor involved in different ABA responses

A major output of ABA signaling is changes in transcription patterns. Many of the transcriptionally upregulated genes have functions in osmoprotection.
Other potential ABA receptors have been described

G-protein coupled receptors (GPCRs)

In the absence of ABA, WRKY transcription factors that are weakly bound by Mg-chelatase subunit H (CHLH) move to the nucleus and repress ABA-responsive genes. In the presence of ABA, WRKY transcription factors are tightly bound at the plastid membrane and can no longer repress nuclear genes.

[The name CHLH derives from the fact that it supports chlorophyll (CHL synthesis by delivering Mg)]

ABA signaling - review

ABA RESPONSES

PYR1

PYR/RCAR receptors

PP2C Protein phosphatases (including ABI1)

Kinase

Protein kinases (including SnRK2s and CDPKs)

ABA
ABA’s roles in the control of guard cell turgor

Turgid guard cells
= open stomata
= gas exchange
+ transpiration

Flaccid guard cells
= closed stomata
= decreased gas exchange
+ decreased transpiration

ABA concentration and stomatal sensitivity change developmentally

As leaves develop and mature, the ABA concentration declines and older leaves export ABA to younger ones. At the same time, the sensitivity of stomata to ABA increases throughout leaf development.

Guard cells responding to ABA

Image courtesy Yizhou Wang, University of Glasgow
Guard cells responding to ABA
Osmotic movement of water controls guard cell turgor

Stomatal movements are mediated by cell turgor, which is controlled by the transport of ions across membranes.
Ion channels and pumps control the movement of guard cells.

Ion channels are found on the vacuolar and plasma membranes and include inward and outward transporting K⁺ channels, anion (A⁻) channels and Ca²⁺ channels.
ABA triggers the movement of ions out of the cell

ABA causes ion channels in the vacuolar and plasma membranes to open, releasing ions from the cell, and inactivates a proton-ATPase (red)
ABA

INNER WALL

Water follows by osmosis
ABA

The cell volume shrinks, closing the stomatal pore
When ABA is no longer present..

ABA

The proton pump is reactivated, generating a proton gradient and hyperpolarizing the membrane

Potassium ions and anions are taken up again

K⁺ + H⁺ → K⁺ + H⁺

When ABA is no longer present..
ABA

Water follows by osmosis
The volume of the cell increases and the stomatal pore opens
Guard cells respond to ABA with a rapid increase in cytosolic Ca\(^{2+}\)

Calcium is a second messenger that coordinates some of ABA’s actions

ABA stimulates an increase in \([\text{Ca}^{2+}]_{\text{cyt}}\) by activating calcium channels at the plasma and internal membranes.
Membrane voltage and ABA interact to facilitate $[\text{Ca}^{2+}]_{\text{cyt}}$ increases

Membrane hyperpolarization triggers a wave of $\text{Ca}^{2+}$ inwards from the cell periphery.

ABA changes the membrane voltage threshold at which $[\text{Ca}^{2+}]_{\text{cyt}}$ increases

Increased $[\text{Ca}^{2+}]_{\text{cyt}}$ helps coordinate the action of many ion channels

ABA

Ca$^{2+}$

Calcium activates ion channels, probably through calcium-dependent protein kinases (CDPKs)
Calcium dependent protein kinases contribute to guard cell movement

ABA-induced stomatal closure is impaired in \textit{cpk} mutants

Anion channel currents are impaired in \textit{cpk} mutants

Anion channel activity is reduced in \textit{cpk3-1 cpk6-1} mutants as compared to wild-type plants

Membrane depolarization and increased pH promote the outward movement of K⁺.

ABA

ABA

The movement of anions out of the cell increases the pH and depolarizes the membrane, which activates the pH- and voltage-sensitive potassium channels.
Reactive oxygen and nitric oxide contribute to the increase in $[\text{Ca}^{2+}]_{\text{cyt}}$

Protein kinases and phosphatases are critical for guard cell responses

An inactive form of SnRK2 (labeled with GFP) was introduced into the right cell of a pair of guard cells. The left cell responded to ABA and lost turgor; the right cell did not

The open stomata caused by abi1 can be rescued by a phosphatase inhibitor

ABA control of guard cell turgor - summary

Guard cell turgor is regulated by a complex network of interacting second messengers, pH, membrane potential, protein phosphorylation, ion channel activity – and more!!
ABA in whole-plant processes

- Root growth
- Vegetative dehydration responses and osmoprotectants
- Fruit ripening
- Seed development
- Biotic stress responses
- Drought-tolerant plants

Days post-anthesis

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<th>Days</th>
<th>Wild-type</th>
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<td>45</td>
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</table>
Water stress and ABA promote root growth at the expense of shoot growth

Increasing water stress

ABA promotes root elongation and suppresses branching

Drought stress suppresses lateral root growth while primary root elongation is maintained.

Lateral roots resume growth upon rewatering.
ABA selectively represses lateral root elongation under salt stress

Salt stress induces a prolonged quiescent stage in lateral roots, delaying their outgrowth

ABA synthesis in the endodermis suppresses lateral root outgrowth – perhaps this prevents them from emerging from the primary root into salt-contaminated soil?

ABA is necessary for primary root growth under water stress

Under drought stress, root growth of the maize ABA-deficient vp5 mutant of severely compromised

Fluridone (FLU) an ABA synthesis inhibitor interferes with root elongation under drought stress

A few organisms can tolerate extreme desiccation

Artemia brine shrimp embryos can survive extreme desiccation. They have been sold as pets that “come to life” when put into water.

Studying how Artemia survive desiccation is helping us learn how to make human cells desiccation tolerant.
Some plants can tolerate extreme desiccation

A few plants, such as these “resurrection plants” can stay alive even when 90% of their water content is lost.

Studies of desiccation tolerant plants contributes to our understanding of cellular desiccation responses.

See also TTPB28: How plants manage water deficit and why it matters.

ABA induces genes that protect cells from desiccation damage

Osmoprotectants (sugars, proline, glycine betaine)

Chaperone functions (HSPs, LEAs)

Oxidative stress defense – peroxidase, superoxide dismutase

Movement of water and ions (aquaporins, ion channels)
ABA interacts with ROS in local and systemic stress responses

Reactive oxygen species (ROS) and calcium propagate stress signals. Stomata respond to many cues and integrate local and systemic signals.

ABA plays a role in fruit development and ripening

In many fruits, a peak of ABA synthesis, which often precedes the peak in ethylene synthesis, occurs during ripening or the onset of ripening.

Although ripening of all fruits depends on ethylene and ABA, ABA plays a more dominant role in non-climacteric fruits such as grape and citrus.
ABA regulates fruit ripening in tomato

The zinc-finger transcription factor ZFP2 in tomato represses ABA biosynthesis genes to fine-tune ABA levels during fruit ripening.

Days post-anthesis

Wild type

SlZFP2 over-expression

Days post-anthesis

Wild type

SlZFP2 down-regulation

A lower ABA concentration leads to delayed fruit ripening.

An increased ABA concentration leads to more rapid ripening.

ABA controls seed maturation, dormancy and desiccation

Seed dormancy and desiccation tolerance is correlated with high levels of ABA synthesis and accumulation.

Germination involves catabolism of ABA and synthesis of GA.

Embryonic patterning

Reserve accumulation

Desiccation tolerance

Reserve mobilization

Cell expansion
ABA interacts with ethylene and nitric oxide in seed dormancy and germination

Ethylene synthesis → ABA → ABA inactivation → ABI3 → seed dormancy

NO → Ethylene synthesis

ABA → Ethylene

germination
Seed-specific transcription factors coordinate seed development

Transcription factors work synergistically to control seed development, dormancy and desiccation tolerance.

**Physical interactions between TFs help confer specificity**

Seeds of ABA synthesis or signaling mutants are not desiccation tolerant and germinate prematurely.

ABA-induced stomatal closure can exclude some pathogens

Some pathogens override the plant’s response and reopen stomata

The role of ABA in biotic defence is pathogen-dependent

ABA enhances some biotic defense responses and interferes with others.

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ABA has both positive and negative effects on disease resistance

ABA

Defense response

This pathogen is more virulent in ABA mutants, meaning ABA enhances resistance. *Pythium irregulare* is a necrotrophic pathogen.

This pathogen induces ABA synthesis which makes the plant less resistant. *Pseudomonas syringae* is a biotrophic pathogen.


Plant defenses can interfere with ABA responses

Expression of *RD29*, an ABA-inducible gene, is diminished in the presence of a pathogen

ABA accumulation can tip the balance between stress responses

Abiotic stress

Biotic stress
When ABA levels are low, the defense responses can dominate.

Abiotic stress

Biotic stress
ABA response are also regulated by other hormones

Brassinosteroids inhibit ABA responses epigenetically during early seedling development via ABI3 and ABI5

Auxin activates ABI3 expression via degradation of AXR2/3

Cytokinins promote the proteosomal degradation of ABI5, and antagonise the inhibition of germination by ABA

Gibberellins promote seed germination

Seed germination at high temperature

- Auxin activates ABI3 expression via degradation of AXR2/3
- Cytokinins promote the proteosomal degradation of ABI5, and antagonise the inhibition of germination by ABA
- Gibberellins promote seed germination
- Seed germination at high temperature
We face a profound water crisis that will limit agricultural productivity

Climate change, deforestation, population growth are combining to create a “perfect storm” of water scarcity

Projection of percent of time spent under drought conditions in 2050, relative to 2000

Intensive research to develop drought-tolerant plants is underway.

How does ABA contribute to root development, water uptake, rate of transpiration and cellular desiccation responses?
Towards drought-tolerant plants

Many approaches are being investigated to breed drought-tolerant plants:

• Modification of ABA synthesis and inactivation to reduce transpiration

• Increased ABA sensitivity of guard cells to reduce transpiration

• Increase root growth for better water uptake

• Drought-inducible expression of desiccation tolerance genes

See also TTPB28: How plants manage water deficit and why it matters
ABA - summary

The hormone ABA and its signaling pathway were instrumental in the evolution of land plants.

ABA participates in physiological, developmental and defense responses throughout the plant body.

Studying ABA is important for the development of drought-tolerant crops.
Conclusions and future directions - Synthesis and Transport

What controls the expression of ABA biosynthesis genes?

How are ABA deactivation and conjugation / deconjugation regulated?

How do ABA transporters contribute to ABA movement?

What are the relative contributions of locally synthesized and transported ABA in root and shoot responses?

Conclusions and future directions – Signaling

What is the role of each of the PYR/RCARs as well as other ABA receptors?

What other factors activate SnRK2s? Are their additional upstream kinases?

What are other targets for SnRK2 phosphorylation?

How are Ca\(^{2+}\) signals and CDPK activities integrated into the signaling network?

What are other targets for SnRK2 phosphorylation?

How do the ABA-induced TFs coordinate their actions?

How do ROS and NO integrate with other signals?
Conclusions and future directions – Whole Plant Responses

ABA RESPONSES

How do guard cells integrate multiple signaling pathways?

What controls ion channel activities?

Why does expression of stress-responsive genes lead to reduced growth rates and yields?

Can we breed plants that are drought-tolerant and pathogen resistant?

How do seeds integrate ABA and other signals?

Oxidative stress detoxification

Osmoprotectants

Chaperone functions

Water and ion movement