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HYPOXIA AND DEVELOPMENT

Air conditional

Hypoxia has long been studied in relation to anaerobic metabolism. It has now been shown to control development, acting as a cue to maintain the seedling's protective apical hook and a trigger of developmental decisions both before and after the plantlet emerges from the soil into the light.

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Sub-ambient levels of cellular oxygen (hypoxia) are typically associated with flooding stress and anaerobic metabolism in plants[1]. As they report in *Current Biology*, Abbas *et al.*[2] now demonstrate that hypoxia serves as an ecological component of underground seedling development, informing a hypocotyl about its position during skotomorphogenesis (seedling development in darkness) and slowing the transition to photomorphogenesis until the well-aerated and illuminated soil surface is reached.

When seeds of eudicots germinate in the darkness of the soil, they undergo a developmental programme that optimizes elongation growth in a manner that protects the apical stem cell niche and minimizes photo-oxidative damage when the cotyledons finally reach the light. Once in the light, development segues into photomorphogenesis, characterized by the conversion of cotyledon etioplasts to photosynthetic chloroplasts and accompanied by reduced elongation of the hypocotyl[3]. Skotomorphogenesis is promoted by the gaseous phytohormone ethylene and inhibited by light. Gibberellic acid and auxin also regulate seedling development in darkness or when covered by soil[4,5]. Abbas *et al.*[2] add a new regulator to this list. They demonstrate that sub-ambient oxygen conditions (<12% O_2), characteristic of water-saturated soils, promote the maintenance of the apical curvature of the seedling hypocotyl and dampen transcription of essential chlorophyll biosynthetic enzymes (Fig. 1). Both are adaptive mechanisms that protect the shoot meristem as the hypocotyl pushes upwards through the soil and limit photo-oxidative damage of the cotyledons and first leaves as they reach the light, respectively[3,6]

Abbas and co-workers[2] show that the apical hook gradually opens in seedlings grown in complete darkness under well-aerated conditions, but to progressively smaller degrees as external O_2 levels fall below 12%. Hypoxia limits hook opening in darkness by stabilizing group VII ethylene response factor (ERF-VII) transcription factors, which are degraded via the N-end rule pathway of proteolysis when O_2 and NO levels are sufficient[7–9]. Hypoxia-impaired hook opening could be ecologically relevant, as the associated low energy status might slow seedling growth, extending the time in the soil and therefore requiring protection of the apical stem cell niche for a longer period. As seedlings elongate in the soil, the resistance from the soil matrix promotes ethylene production and consequently triggers the triple response: inhibited hypocotyl and root elongation, radial swelling of the hypocotyl and exaggeration of the apical hook[3]. The similarity between delayed hook opening under hypoxia[2] and the ethylene-driven maintenance of the apical hook in soil[3] suggests a common downstream pathway supported by the observations that hypoxia can promote ethylene production[10] and sensitize some tissues to ethylene[11].

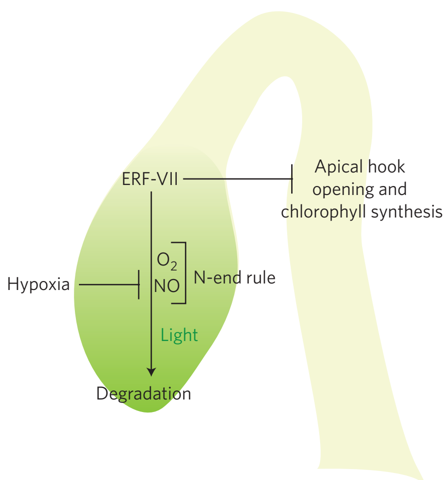

Figure 1 | The effect of sub-ambient oxygen levels during early development. Hypoxia prevents apical hook opening and chlorophyll biosynthesis through stabilization of ERF-VII transcription factors. Light is proposed as a regulator of ERF-VII stability, through a process other than the N-end rule.

Abbas *et al.*[2] also document the hypoxia-induced prolongation of seedling survival after an extended dark period followed by a transition to light. This was associated with ERF-VII-dependent downregulation of chlorophyll biosynthesis and consequently with a reduction in photo-oxidative damage. It is beneficial for the biosynthesis of chlorophyll to coincide with the emergence of the seedling above the soil, as precocious development of the photosynthetic machinery can lead to lethal photo-oxidative damage on exposure to the light[3]. If hypoxia indeed slows growth in darkness, chlorophyll biosynthesis may also be slackened, providing insurance against excessive photo-oxidative damage on illumination.

The delayed apical hook opening and the inhibited biosynthesis of chlorophyll during hypoxia both point to an unprecedented role of local oxygen concentration in the plastic regulation of seedling development during growth in darkness and the transition to light. Remarkably, the inhibition of chlorophyll biosynthesis by hypoxia overrides the well-characterized repression of this process mediated by the phytochrome interacting factors (PIFs) under well-aerated (normoxic) conditions[12].

Sufficient availability of O_2 and NO triggers the breakdown of ERF-VIIs[13]. Abbas *et al.*[2] find that ERF-VII stability is also affected by light, but through a mechanism not requiring the conserved N-terminal motif of these proteins. This light-dependent degradation of ERF-VIIs is faster under normoxia than hypoxia. As ERF-VII accumulation is strongly linked to flooding tolerance, the possibility of an alternative mode for regulation of ERF-VII levels raises many questions. Moreover, flooded shoots are exposed to a variety of light levels, owing to variation in flooding depth and turbidity. It will be fascinating to study the impact of these variable light levels on ERF-VII stability and thus on flood-adaptive responses.

Elucidation of the relationship between O_2 as an environmental positional cue and seedling-produced ethylene and NO during skotomorphogenesis and photomorphogenesis would be a challenging avenue for future studies. The suggestion by Abbas *et al.*[2] that ERF-VIIs integrate responses to these three gases is appealing. Connecting these mobile signals to the roles of PIFs in light signalling[12] would form a nexus of abiotic (light, oxygen) and cell-derived signals that tune the transition between germination and seedling establishment.

This is not the first time that oxygen status has been implicated in developmental plasticity. A previous study[14] found that low levels of oxygen in the lobes of developing maize anthers promote maintenance of premeiotic cells that ultimately form pollen, in-keeping with knowledge that hypoxia sustains pluripotency of stem cells in mammals[15]. Thus, in addition to triggering changes in metabolism and growth to survive flooding, local oxygen levels inform developmental decisions, either within developing organs or the microenvironment of germinating seeds. ❐

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