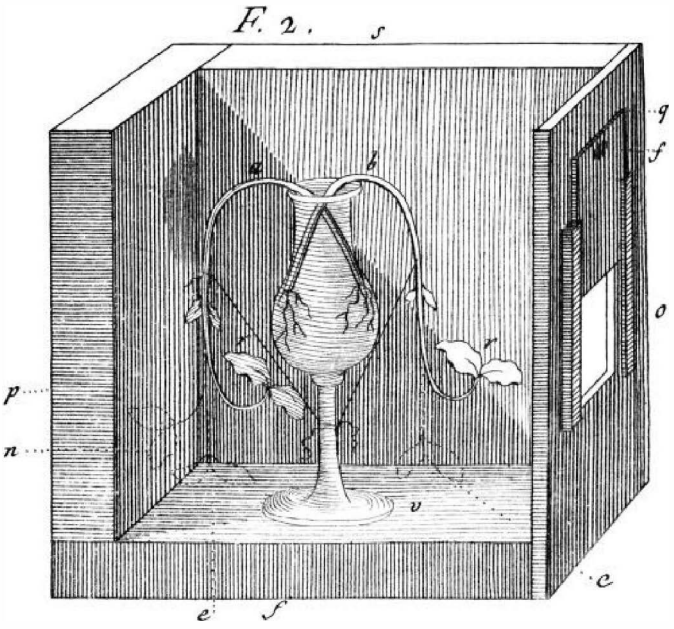
Transduction de signaux par les hormones: historique

Source: Whippo, C. W. & Hangarter, R. P. Phototropism: Bending towards Enlightenment. *The Plant Cell* **18**, 1110–1119 (2006)

Two etiolated bean seedlings (a and b) oppositely placed in a vase (v) of water were tied downward (e). With the shutter (f) closed, each seedling reoriented upward toward the nearest wall (seedling a toward wall q and seedling b toward wall p). When the shutter was raised, both seedlings reoriented toward the opening (o). Reprinted from Bonnet (1779).

Charles Darwin (1809-1882) further explored the inductive nature and mechanistic connection between phototropism and gravitropism. He proposed that the back and forth circumnutation associated with plant growth could be directed by a stimulus such as light or gravity (Darwin, 1880). Although Darwin's circumnutation theory of tropism served to propose a common mechanism underlying gravitropism and phototropism, the most significant discovery from his studies of plant movements was his demonstration that the site of photoperception at the shoot tip and the location of curvature are separable. From his observations, Darwin was able to propose that a transmissible substance produced in the tip is responsible for inducing curvature in lower regions of the plant (Darwin, 1880). This insightful discovery eventually lead to the discovery of the first plant hormone, auxin.

Darwin's ideas were initially dismissed by other plant physiologists (reviewed in Heslop-Harrison, 1980). Nevertheless, evidence in favor of Darwin's transmissible substance began to accumulate when Rothert (1894) also showed that light sensitivity is greatest near the tip of maize coleoptiles. Subsequent results of Fitting (1907), Boysen-Jensen (1911), and Paal (1918) provided more direct evidence that a transmissible substance produced in the tip participates in the response. This research culminated in a model put forth independently by Cholodny (1927) and Went (1926, 1928), which proposed that light-mediated lateral redistribution of a plant growth hormone to the shaded side of the seedling causes the differential growth associated with phototropic curvature. This growth substance was shortly identified from human urine by Kogl and Haagen-Smit (1931), who named the hormone auxin, derived from the Greek verb auxein, meaning "to grow."



Transduction de signaux par les hormones

Source: Jensen, P. J., Hangarter, R. P. & Estelle, M. Auxin Transport Is Required for Hypocotyl Elongation in Light-Grown but Not Dark-Grown Arabidopsis. *Plant Physiology* **116**, 455–462 (1998)

The development of a plant is influenced by a variety of environmental cues. Differences in light quantity and quality can lead to dramatically different growth forms. Light signals are perceived by a number of different photoreceptors, including the phytochromes and the blue light receptors. Developmental processes under the control of the phytochromes include stem elongation, hypocotyl hook unfolding, leaf expansion, seed germination, and flower initiation (for review, see von Arnim and Deng, 1996). Blue light receptors have been shown to be involved in phototropism, regulation of stem elongation, stomatal opening, and the initiation of chloroplast development (for review, see Senger and Schmidt, 1994).

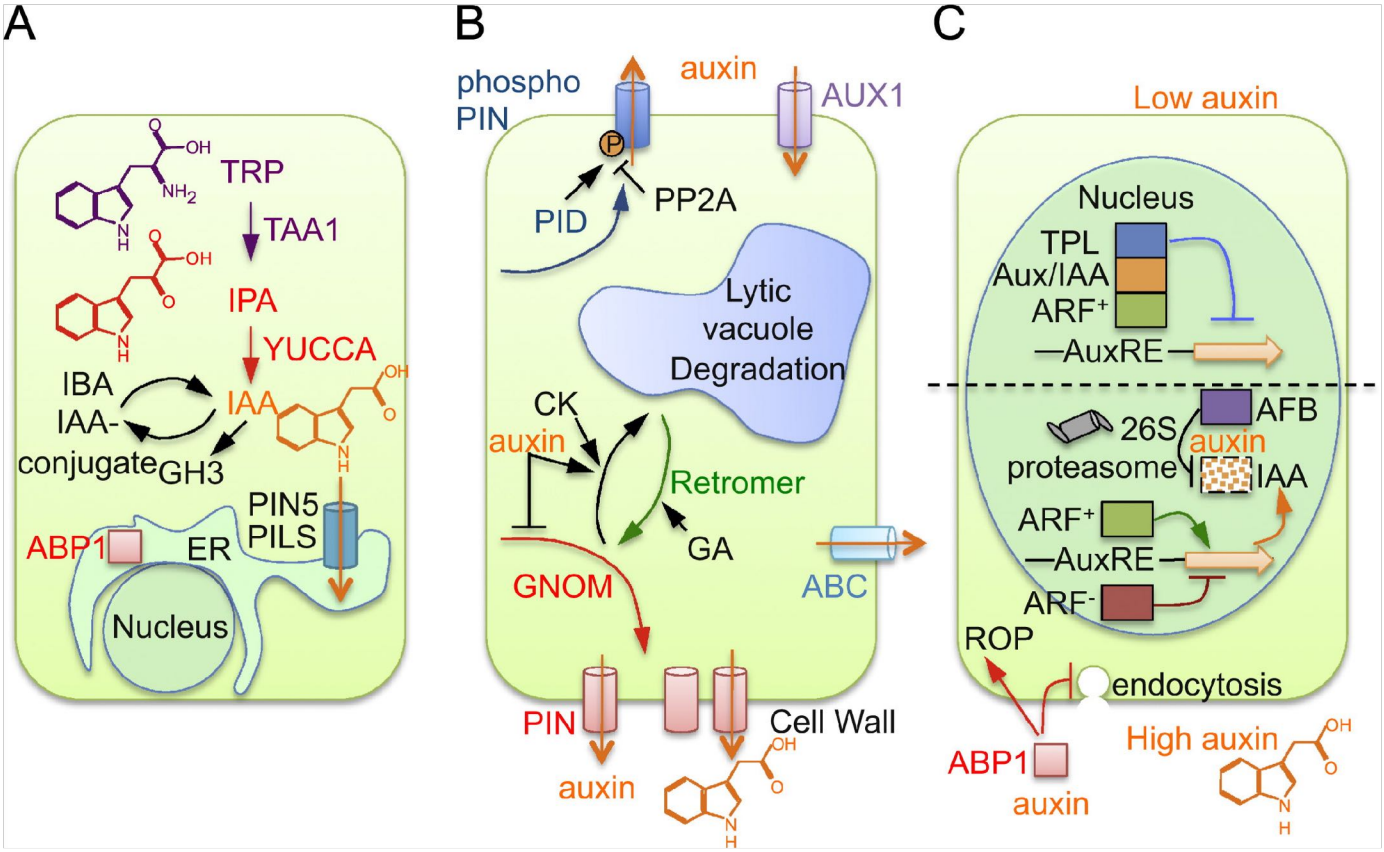
Many of the developmental processes that occur as a result of light signals are dependent, at least in part, on the action of phytohormones. For example, light has been shown to alter the levels of IAA (Bandurski et al., 1977; Jones et al., 1991; Behringer and Davies, 1992), GAs (Ross et al., 1992; Foster and Morgan, 1995), ABA (Weatherwax et al., 1996), cytokinins (Qamuruddin and Tillberg, 1989; Kraepiel et al., 1995), and ethylene (Kathiresan et al., 1996, and refs. therein). Behringer and Davies (1992) proposed that phytochrome regulation of stem elongation is partly the result of changes in IAA levels. Phytochrome-deficient mutants of Arabidopsis thaliana require GAs to express the elongated phenotype of these plants (Peng and Harberd, 1997). Light regulation of BR levels or sensitivity clearly plays a central role in light-regulated development, because Arabidopsis mutants with defects in BR biosynthesis and response are severe dwarfs in both light and dark conditions (Clouse et al., 1996; Kauschmann et al., 1996; Li et al., 1996; Szerkes et al., 1996).

The phytohormone auxin is involved in diverse developmental processes, many of which depend on regulated auxin transport (Went and Thimann, 1937). For example, apical dominance is maintained by auxin produced in the apical meristem and transported basipetally to the target tissues, where it inhibits growth of lateral branches. In the case of tropic responses, lateral redistribution of auxin gives rise to differential growth rates, resulting in curvature of the growing organ. In addition, a gradient in auxin concentration from tip to base is believed to be responsible for differential elongation rates in different regions of shoots (Went and Thimann, 1937; Sanchez-Bravo et al., 1992).

The formation and maintenance of auxin gradients is thought to occur through the action of a specific polar auxin-transport system that requires active efflux of auxin through an auxin-anion uniport (Sabater and Rubery, 1987). Auxin efflux is inhibited by synthetic phytotropins such as NPA (Morgan, 1964; Katekar and Giesler, 1980; Jacobs and Rubery, 1988). The exact nature of this inhibition is not known, but NPA and other auxin-transport inhibitors bind to a single plasma-membrane protein (Lembi et al., 1971; Muday et al., 1993; Bernasconi et al., 1996). The endogenous auxin IAA does not compete with NPA for this binding site (Lomax et al., 1995). In the tir3 mutant of Arabidopsis, reduced NPA binding is associated with defects in auxin-regulated growth processes, suggesting that the NPA-binding site is important for auxin transport (Ruegger et al., 1997).

Auxine: généralités et transporteurs (1/2)

Source: Finet, C. & Jaillais, Y. AUXOLOGY: When auxin meets plant evo-devo. *Developmental Biology* **369**, 19–31 (2012)



Schematic representation of auxin signaling: (A) biosynthesis and homeostasis, (B) polar auxin transport and (C) perception. GA, gibberellin; CK, cytokinin; auxRE, Auxin Response Element.

Auxine: généralités et transporteurs (2/2)

Source: Finet, C. & Jaillais, Y. AUXOLOGY: When auxin meets plant evo-devo. *Developmental Biology* **369**, 19–31 (2012)

Auxin pathway is controlled at many levels that include auxin biosynthesis, auxin metabolism, and auxin transport. Moreover, auxin was proposed to act as an integrator of the activities of multiple plant hormones, altogether suggesting a vast regulatory network of auxin during plant development (Jaillais and Chory, 2010).

[...]

Indole-3-acetic acid (IAA) is the most potent naturally occurring member of the auxin family. High IAA levels are detected in shoot and root meristematic tissues, in cotyledons, as well as in young leaves that have the highest biosynthetic capacity (Ljung et al., 2001). In mature leaves and roots, IAA remains present but in smaller amounts.

[...]

In plants, two distinct pathways are known to play a role in auxin transport: a passive distribution through vascular tissue and an active cell-to-cell polar transport. This polar auxin transport is fundamental for auxin distribution over both short and long distances. This transport occurs in a cell-to-cell manner and depends on specific influx and efflux carrier proteins that facilitate the uptake and release of auxin from/to the apoplast (Fig. 1B). Many auxin carriers are well characterized: the PIN-FORMED (PIN) proteins (Galweiler et al., 1998) and several proteins of the ABCB and ABCG transporter family (Cho et al., 2007, Geisler et al., 2005 and Ruzicka et al., 2010) are involved in auxin efflux from the cell and the AUX1/LIKE AUXIN PERMEASE (AUX1/LAX) proteins are involved in auxin influx (Bennett et al., 1996 and Swarup et al., 2001).

Among these carriers, PIN proteins have been proposed to be central rate-limiting components in polar auxin transport (Petrasek et al., 2006 and Wisniewska et al., 2006). A key characteristic of these proteins is their polar localization in the cell (Fig. 1B). This polar localization correlates with putative auxin fluxes in the plants and are key to establish local auxin concentrations (Wisniewska et al., 2006). The processes behind the establishment and maintenance of PIN polarity at the cell level are extremely complex and rely on connections with the cell wall, the actin cytoskeleton, phosphoinositide and calcium signaling, slow diffusion in the plasma membrane as well as intracellular trafficking (Fig. 1B) (Dhonukshe et al., 2008a, Kleine-Vehn et al., 2011, Mravec et al., 2011 and Zhang et al., 2011). A determinant factor for PIN polarity is their endocytic trafficking. The current model proposes that PIN proteins are secreted in a non-polar manner and that their subsequent endocytosis and recyling establish their polar localization at the rootward pole of the cell (Dhonukshe et al., 2008b). This polar recyling is dependent on the endosomal protein GNOM (Geldner et al., 2003 and Kleine-Vehn et al., 2009). Phosphorylation of PINs by several kinases, including PINOID (PID), targets these auxin carriers to a GNOM-independent recycling pathway that target them to the shootward pole of the cell (Fig. 1B) (Kleine-Vehn et al., 2009). This action is antagonistically controlled by the regulatory subunit of protein phosphatase 2A (PP2A) (Fig. 1B) (Michniewicz et al., 2007).

Endocytosis and recycling also control the quantity of PIN protein at the plasma membrane by regulating the balance of protein that is recycled back to the plasma membrane or targeted to the lytic vacuole for degradation (Fig. 1B) (Abas et al., 2006, Jaillais et al., 2006 and Jaillais et al., 2007). The retromer, a conserved protein complex, is involved in this balance as it promotes the retrieval of PIN proteins from late endosomes and reroute them toward the plasma membrane (Fig. 1B) (Jaillais et al., 2007). Auxin itself plays a key role in this regulation as it can inhibit endocytosis at certain concentration or promotes PIN proteins degradation at others (Abas et al., 2006, Paciorek et al., 2005 and Robert et al., 2010).