

# The Role of Microtubule Associated Proteins in Plant Hypocotyl Elongation



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## Abstract

The elongation of Arabidopsis hypocotyls is regulated by many factors such as light, phytohormones, transcription factors and the cytoskeleton. Microtubule is a member of cytoskeleton which plays an important role in hypocotyls elongation. The organization and dynamics of microtubules are regulated by microtubule associated proteins (MAPs). Recent years, several MAPs involve in the regulation of hypocotyls elongation mediated by upstream signals are identified. This review summarizes the recent progress and classifies the MAPs participate in the regulation of hypocotyls elongation into two categories, the positive and negative regulators.

**Keywords:** Microtubule associated proteins; Hypocotyls; Arabidopsis

**Abbreviations:** MT: Micro Tubule; MAPs: Microtubule Associated Proteins; COP: Constitutive Photomorphogenic; BR: Brassinosteroid; WVD: Wave Dampened; EIN: Ethylene Insensitive

## Introduction

Hypocotyl is the part of a plant embryo or seedling plant that is between the cotyledons and the radicle or root. The regulation of hypocotyls elongation is crucial in the process of plant growth and development, because after the seeds germination, hypocotyls fully elongate to search of the soil surface and percept light then significantly inhibits hypocotyls elongation, the cotyledons unfold and the photosynthetic growth process could successfully begin. The Arabidopsis hypocotyls is widely used as a model for studies of cell elongation as hypocotyls cells elongate quickly without division during the postembryonic growth process [1,2]. Hypocotyl cells growth in the darkness start their elongation at the base and proceed in the acropetal direction reach their maximum length. The elongation of hypocotyls cells is regulated by both external and internal cues such as light, phytohormones, transcription factors, and the cytoskeleton [3-5].

Microtubule (MT) is one of the main members of cytoskeleton and plays important role in regulating cell expansion, division, and plant cell morphogenesis. Cortical microtubules regulate cell elongation by orientating cellulose fibrils and cellulose fibril arrays, thereby influencing the mechanical properties of the cell wall [6-9]. The orientations of cortical microtubules are associated with the growth status of etiolated hypocotyls [10,11]. The parallel array of cortical microtubules is dominantly transversely oriented to the hypocotyls longitudinal growth axis in elongating hypocotyls

cells and longitudinally oriented when cell elongation stops [10], suggesting the regulation of the organization and dynamics of cortical microtubules is crucial for hypocotyls cell growth. The organization and dynamics of cortical microtubules is regulated by microtubule associated proteins (MAPs) [12]. In this article, plants MAPs involve in hypocotyls elongation are classified, on the basis of their function, into two categories: one is positive regulator and the other is negative regulator in the elongation of hypocotyls. In addition, we also discuss how these proteins mediate the synergistic and antagonistic effects in hypocotyls elongation.

## MAPs Play Positive Roles In Hypocotyl Elongation

Until now, several MAPs play positive roles in regulation of Hypocotyl elongation have been identified. Arabidopsis SPIRAL1 (SPR1) encodes a plant-specific MT-localizing protein [13]. Plants over expressing SPR1 shows enhanced resistance to an MT-disrupting drug and increased Hypocotyl elongation. In addition, the site of high SPR1 expression moved up wards along dark-grown hypocotyls. The temporal and spatial distribution of SPR1-expressing cells in hypocotyls generally matches the zone of rapid cell elongation [13,14]. Moreover, microtubule destabilizing protein 40 (*MDP40*) as a positive regulator involves in Brassinosteroid (BR) mediated Hypocotyl elongation by destabilizing cortical microtubules [15]. *MDP40* is the target of Brassinazole-resistant1 (BZR1), a key transcription factor in BR signal transduction

pathway, the expression of *MDP40* is induced by BR treatment. *MDP40* primarily expresses in the upper region of the hypocotyls which is considered to be a fast growing region after 4 d. *MDP40* RNAi lines show the shorter etiolated Hypocotyl phenotype and the cortical MTs in the *MDP40* RNAi cells are less sensitive to the oryzalin treatment. This study identifies a novel positive regulator in Hypocotyl elongation and reveals a mechanism involving BR regulation of microtubules through *MDP40* to mediate Hypocotyl cell elongation [15].

### MAPs Play Negative Roles In Hypocotyl Elongation

Besides positive regulators, there are also several MAPs that negatively regulate the elongation of hypocotyls. Recent years, a microtubule destabilizing protein 25 (*MDP25*) which is a calcium regulatory protein is identified as a negative regulator of Hypocotyl cell elongation [16]. *MDP25* Overexpression results in shortening etiolated hypocotyls while *mdp25* mutant lines have the opposite phenotypes. In addition, *MDP25* is mostly expressed in the basal region of hypocotyls which is considered to be a non-growing region after 4 d of growth in the dark and the expression level of *MDP25* in light grown hypocotyls is significantly higher than in dark. The localization of *MDP25* is regulated by cellular calcium levels, increase calcium levels in cells cause *MDP25* partially moves from the plasma membrane into cytosol, binds to and destabilizes cortical MTs.

This finding suggests that *MDP25* link the change of cellular calcium levels mediated by light signal and cortical MTs in the regulation of hypocotyls elongation [16]. In addition, a recent study by Cao et al. identifies a novel Arabidopsis microtubule plus-end binding protein AUGMIN subunit8 (*AUG8*) that participates in inhibiting hypocotyls elongation by promoting the reorientation of cortical MTs [17]. The etiolated hypocotyls of *aug8* are significantly shorter than WT. *AUG8* binds to the plus ends of growing cortical MTs and promotes microtubule reorientation by regulating the dynamic instability of microtubule plus ends [17].

*WDL3* and *WDL5* belong to the microtubule-associated protein Wave-Dampened2 (WVD2)/WVD2-LIKE (WDL) family in Arabidopsis [18-21]. *WDL3* involves in light inhibited Hypocotyl elongation through the degraded by the ubiquitin-26S proteasome-dependent pathway in the dark [18]. Compare with wild type, *WDL3* RNAi seedlings have longer while Overexpression seedlings have shorter hypocotyls in the light, however, the Hypocotyl of WT, *WDL3* RNAi and Overexpression lines have no significant difference in the dark. The reason of different phenotypes of hypocotyls in the light and dark is that the *WDL3* protein is abundant in the light but is degraded through the 26S proteasome pathway in the dark [18].

In addition, Lian et al. analyzes the mechanism of *WDL3* in the dark and finds that Constitutive Photomorphogenic 1(COP1) targets *WDL3* for 26S proteasome-mediated degradation to control hypocotyls elongation in etiolated Arabidopsis seedlings. This study uncovers a function of COP1 in the cytoplasm to mediate hypocotyls elongation by regulating the abundance of MAPs *WDL3* [19,20]. In darkness, ethylene inhibits etiolated Hypocotyl elongation as part of the well-known "triple response" [10]. A recent study shows that

ethylene signaling participates in regulation of cortical microtubule reorientation and microtubule bundling plays important role in this process. The effects of ethylene on microtubule bundling are partially suppressed in a microtubule-bundling protein *WDL5* knockout mutant (*wdl5-1*) [21]. Another study demonstrates that *WDL5* plays a positive role in the phytohormones ethylene negatively regulated etiolated hypocotyls cell elongation. *WDL5* as the directly target of Ethylene-Insensitive 3 (EIN3), a key transcription factor in the ethylene signaling pathway, inhibits the elongation of etiolated hypocotyls by stabilizing and reorientation cortical MTs [20].

### Conclusion

In the past years, much progress has been made toward the MAPs involved in hypocotyls elongation. The elongation of hypocotyls is accurately regulated by positive and negative factors. Microtubule regulatory proteins function as positive or negative regulators that mediate hypocotyls cell elongation by altering microtubule organization and dynamics. In the process of hypocotyls elongation, the regulation of MAPs is not completely independent, on the one hand, MAPs are regulated by many internal or external signals involved in the signals mediated hypocotyls elongation, on the other hand, the stability of microtubules regulated by MAPs are important to the regulation of hypocotyls by the signal. In the future, as more MAPs involve in hypocotyls elongation mediated by different signals are identified, the mechanism of hypocotyls elongation regulation will be clearer.

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