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Research review paper

Biotechnological aspects of cytoskeletal regulation in plants

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ABSTRACT

The cytoskeleton is a protein-based intracellular superstructure that evolved early after the appearance of bacterial prokaryotes. Eventually cytoskeletal proteins and their macromolecular assemblies were established in eukaryotes and assumed critical roles in cell movements, intracellular organization, cell division and cell differentiation. In biomedicine the small-molecules targeting cytoskeletal elements are in the frontline of anticancer research with plant-derived cytoskeletal drugs such as *Vinca* alkaloids and toxoids, being routinely used in the clinical practice. Moreover, plants are also major material, food and energy resources for human activities ranging from agriculture, textile industry, carpentry, energy production and new material development to name some few.

Most of these inheritable traits are associated with cell wall synthesis and chemical modification during primary and secondary plant growth and inevitably are associated with the dynamics, organization and interactions of the plant cytoskeleton. Taking into account the vast intracellular spread of microtubules and actin microfilaments the cytoskeleton collectively assumed central roles in plant growth and development, in determining the physical stance of plants against the forces of nature and becoming a battleground between pathogenic invaders and the defense mechanisms of plant cells.

This review aims to address the role of the plant cytoskeleton in manageable features of plants including cellulose biosynthesis with implications in wood and fiber properties, in biofuel production and the contribution of plant cytoskeletal elements in plant defense responses against pathogens or detrimental environmental conditions. Ultimately the present work surveys the potential of cytoskeletal proteins as platforms of plant genetic engineering, nominating certain cytoskeletal proteins as vectors of favorable traits in crops and other economically important plants.

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1. Introduction

1.1. Preface

Microtubules and actin (micro)filaments are fundamental components of the cytoskeletal infrastructure in every eukaryotic cell. The above cytoskeletal elements form wide-spread, non-covalent, filamentous polymers with significantly different sizes and explicit intracellular dynamicity.

As such, both cytoskeletal arrays form intricate and largely independent intracellular networks in plants, although in certain instances microtubules and actin microfilaments may colocalize and interact in space and time and function coordinately or independently during polar or diffuse cell expansion and differentiation, cell division plane determination and execution of mitosis and cytokinesis (Kojo et al., 2013; Sambade et al., 2014; Sampathkumar et al., 2011; Qin et al., 2014).

The cell-wide distribution of microtubules and actin microfilaments, their dominant participation in a multitude of functions and finally the intimate association of both elements and particularly of microtubules with the cell wall biosynthetic machinery have already pinpointed the potential of cytoskeletal proteins towards biotechnological applications as vectors of favorable traits of crops and other economically important plants.

1.2. Scope of the review

The present review aims to recapitulate research efforts addressing fundamental topics of plant cytoskeletal composition, organization and dynamics and the role of plant cytoskeletal elements in physiological processes of immense biotechnological interest and potential. It is therefore aimed to bring to light plant cytoskeletal proteins with already acknowledged or prospective biotechnological potential towards sustainable and green biofuel production, development of innovative cellulose-based materials and finally the engineering of crops with improved yield, pathogen resistance and sustainable growth potential under unfavorable abiotic conditions in order to feed an exponentially growing human population. As will be mentioned the plant cytoskeletal protein complement offers candidates for the genetic engineering of favorable traits in crops and industrially important plants.

2. Microtubules

2.1. Tubulins

Eukaryotic and hence plant α- and β-*TUBULIN* gene families contain multiple members with few exceptions. The genome of *Arabidopsis thaliana* encodes for six α-tubulin isoforms (designated as AtTUA1–AtTUA6; Kopczak et al., 1992), nine β-tubulin isoforms (designated as AtTUB1–AtTUB9; Snustad et al., 1992) and two functionally redundant γ-tubulin isoforms (Liu et al., 1994). Most of the tubulin isoforms are ubiquitously expressed throughout the *Arabidopsis* development with the exception of TUA1 and TUB9, which are predominantly expressed in reproductive organs (Carpenter et al., 1992; Cheng et al., 2001). In the fully resolved genome of rice (*Oryza sativa*) 3 α-tubulin (OsTUA1–OsTUA3) and 8 β-tubulin (OsTUB1–OsTUB8) isoforms are encoded which are again ubiquitous except for OsTUB8 which is specifically expressed in the anther (Guo et al., 2009; Yoshikawa et al., 2003). Moreover, complete *TUBULIN* families or individual *TUBULIN* genes have been elucidated independently of entire genomes in economically important angiosperms and gymnosperms (Breviario et al., 2013; He et al., 2008; Oakley et al., 2007).

Tubulin isoform diversity increases also through post-translational modifications (PTM; Magiera and Janke, 2014). One well-studied α-tubulin PTM with wide eukaryotic distribution involves the acetylation of a lysine residue residing at the 40th position from the aminoterminus (Lys40 or K40; L'Hernault and Rosenbaum, 1985).

Although a possible role of α-tubulin acetylation in microtubule dynamics and function is not fully clarified yet, there is evidence relating this PTM to microtubule longevity (Szyk et al., 2014) thus marking fairly stable microtubule subpopulations with substantially lower turnover rates than the rest.

In plants there is relatively little information concerning the occurrence and mostly the functional importance of tubulin PTMs, although major PTMs such as carboxylterminal tyrosination (Smertenko et al., 1997), α-tubulin acetylation and α-tubulin phosphorylation

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