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1 Research review paper

Q3 Biotechnological aspects of cytoskeletal regulation in plants

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A B S T R A C T

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 taxoids, 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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87 **1. Introduction**88 *1.1. Preface*

89 Microtubules and actin (micro)filaments are fundamental com-
 90 ponents of the cytoskeletal infrastructure in every eukaryotic cell.
 91 The above cytoskeletal elements form wide-spread, non-covalent,
 Q5 filamentous polymers with significantly different sizes and explicit
 92 intracellular dynamicity.

93 As such, both cytoskeletal arrays form intricate and largely indepen-
 94 dent intracellular networks in plants, although in certain instances
 95 microtubules and actin microfilaments may colocalize and interact in
 96 space and time and function coordinately or independently during
 97 polar or diffuse cell expansion and differentiation, cell division plane
 98 determination and execution of mitosis and cytokinesis (Kojo et al.,
 99 Q6 2013; Sambade et al., 2014; Sampathkumar et al., 2011; Qin et al., 2014).

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

108 *1.2. Scope of the review*

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

engineering of favorable traits in crops and industrially important 121
 plants. 122

123 **2. Microtubules**124 *2.1. Tubulins*

125 Eukaryotic and hence plant α - and β -*TUBULIN* gene families contain 125
 126 multiple members with few exceptions. The genome of *Arabidopsis*
 127 *thaliana* encodes for six α -tubulin isoforms (designated as AtTUA1–
 128 AtTUA6; Kopczak et al., 1992), nine β -tubulin isoforms (designated as
 129 AtTUB1–AtTUB9; Snustad et al., 1992) and two functionally redundant
 130 γ -tubulin isoforms (Liu et al., 1994). Most of the tubulin isoforms are Q7
 131 ubiquitously expressed throughout the *Arabidopsis* development with
 132 the exception of TUA1 and TUB9, which are predominantly expressed
 133 in reproductive organs (Carpenter et al., 1992; Cheng et al., 2001). In
 134 the fully resolved genome of rice (*Oryza sativa*) 3 α -tubulin (OsTUA1–
 135 OsTUA3) and 8 β -tubulin (OsTUB1–OsTUB8) isoforms are encoded
 136 which are again ubiquitous except for OsTUB8 which is specifically
 137 expressed in the anther (Guo et al., 2009; Yoshikawa et al., 2003).
 138 Moreover, complete *TUBULIN* families or individual *TUBULIN* genes
 139 have been elucidated independently of entire genomes in economically
 140 important angiosperms and gymnosperms (Brevario et al., 2013; He
 141 et al., 2008; Oakley et al., 2007).

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

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

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

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