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Review

The developmental context of cell-cycle control in plants

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Abstract

Plant growth is characterised both by continued growth and organogenesis throughout development, as well as by environmental influences on the rate and pattern of these processes. This necessitates a close relationship between cell cycle control, differentiation and development that can be readily observed and studied. The sequencing of the Arabidopsis genome has revealed the full complexity of cell cycle regulators in plants, creating a challenge to understand how these genes control plant growth and differentiation, and how they are integrated with intrinsic and external signals. Here, we review the control of the cell cycle and examine how it is integrated with proliferative activity within meristems, and during the differentiation processes leading to leaf and lateral root formation.

Keywords: Cell division; Arabidopsis; Cyclins; CDK; Differentiation; Leaf development; Root development

Contents

1. Introduction—the developmental context of plant cell cycling

Although as we shall see, the overall control of the cell cycle is broadly similar between plants and other eukaryotic organisms, the pattern of plant development dictates that it is organised spatially and temporally in radically different ways.

Plant development differs from that of animals in four main aspects. First, whereas animal development produces a mature embryo that already possesses the major organ systems of the post-embryonic organism, plant embryogenesis is mainly concerned with the production of groups of stem cells known as meristems at the apical and distal ends of the mature embryo which will then continue during adult growth to produce the organs that build the adult plant. Granted these stem cells are associated with an embryonic root and shoot that already possesses one or two seed leaves (cotyledons), but nevertheless plant post-embryonic growth involves not only increases in organism size but also the production of almost all organs. This leads us to the second major difference between plants and animals, which is that plant post-embryonic growth is associated with an organogenic continuum in which

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stem cells continuously produce new organs (leaves, roots, flowers) through de novo initiation, in contrast to the temporal restriction of animal organogenesis to the specific developmental stages of embryogenesis and pupation.

The third major difference is related to the sessile nature of plants and the importance of developmental responses to the environment in which they find themselves. Factors such as light, temperature and nutrient availability will impact on both the rate and, in some cases, the pattern of plant growth. Hence, such influences will impact on the cell cycle because of the importance of cell production in both growth and organogenic processes.

Finally, the nature of plant cells surrounded by a rigid cell wall imposes restrictions on the types of cell behaviour involved in developmental processes, in particular precluding cell migration as a mechanism for establishing pattern.

In broad terms, these represent the developmental context in which cell division must be placed in plants. We first explore the major differences between what is known of cell cycle control in plants and animals, and then examine aspects of cell division within meristems and during leaf and lateral root organogenesis.

2. The cellular perspective of the mitotic plant cell cycle

Plants share with all other eukaryotes the basic phases of the cell cycle (Table 1), and the control of transitions by cyclin-dependent kinase (CDK) complexes. Altogether, Arabidopsis has 49 cyclins in 10 classes [1], but cyclins with primary cell cycle roles are represented by the classes of A-, B-, and D-type cyclins, no plant cyclin E homologue has been identified. Plants also differ in their CDK repertoire compared to animals or yeasts, containing not only the archetypal *cdc2* (CDK1) homologue with the canonical PSTAIRE sequence (single-letter amino acid code) in their cyclin-binding domain and known in plants as CDKA, but also a plant-specific group of CDKs known as CDKB. Plants, therefore, lack equivalents of the cyclin D-binding CDK4 and CDK6, and plant D-type cyclins appear to bind primarily CDKA [2] and in some cases CDKB [3]. Given the constitutive nature of CDKA expression and activity, and the restricted expression of *CDKB* genes to S-phase and later, it is assumed that CDKA provides the major G1 kinase activity, and that this is joined in G2/M by additional CDKB activity.

Control of plant mitotic cycles is regulated at the G1/S transition by D-type cyclins (CYCD), represented in Arabidopsis by 10 genes in seven sub-classes. Plant CYCDs have low homology to vertebrate D-type cyclins, and not all contain the LxCxE Rb-binding domain [4]. Expression of several CYCDs is regulated by nutrient availability and hormones (reviewed [5]). When analysed in synchronous cell cultures, most CYCDs increase during cell cycle re-entry, but during the subsequent cell cycles expression remains relatively constant, consistent with a primary role in responding to external signals [6]. However, two members of the CYCD family show cyclical expression: CYCD5;1 has peak expression in G1 and CYCD4;1 in late G1/S-phase [7], suggesting possible roles as functional equivalents of cyclin E. Certainly overexpression of CYCDs is sufficient to drive cells into S-phase, resulting in a shortened G1-phase and dramatic effects on leaf development (see below).

Regulation of CYCD activity also occurs at the level of protein stability and kinase activity. CYCD3;1 is an unstable protein (half-life 7 min) and is targeted for ubiquitin-dependent proteasomal degradation after hyperphosphorylation. During the cell cycle, CYCD3;1 protein levels mirror expression, and several lines of evidence suggest it acts as a transducer of plant hormonal signals into the cell cycle. CYCD2;1 protein is more stable, fluctuating little during the cell cycle, but is regulated at the level of kinase activity [8].

The predominant kinase partner of most CYCDs is CDKA;1, the only Arabidopsis CDK containing the hallmark PSTAIRE motif [4]. Neither expression nor protein abundance fluctuates during the cell cycle, but kinase activity peaks in S-phase and in G2 [9]. While CYCD3;1-associated kinase activity mirrors protein abundance, CYCD2;1-

Table 1
List of Arabidopsis homologues of key cell cycle components and the phase of the cell cycle they are thought to play a role in

Homologue	Cell cycle phase of activity	Arabidopsis proteins
Cyclins: D-type	G1/S transition (and G2/M)	CycD1;1 CycD2;1 CycD3;1; -3;2; -3;3 CycD4;1; -4;2 CycD5;1 CycD6;1 CycD7;1
Cyclins: A-type	G1/S; S-phase	CycA1;1; -1;2 CycA2;1; -2;2; -2;3; -2;4 CycA3;1; -3;2; -3;3; -3;4
Cyclins: B-type	G2/M transition	CycB1;1; -1;2; -1;3; -1;4 CycB2;1; -2;2; -2;3; -2;4 CycB3;1
CDKs	G1/S transition; G2-phase	CDKA;1
Plant specific CDKs	G2/M transition G2-phase; mitosis	CDKB1;1; -1;2 CDKB2;1; -2;2
CAKs		CycH;1/CDKD;1; -2; -3; CDKF;1
KRPs	G1/S transition	KRP1; -2; -3; -4; -5; -6; -7
RBs	G1/S transition	RBR
E2F family	G1/S transition	E2Fa; -b; -c DPa; -b DEL1; -2; -3
WEE1	G2/M transition	WEE1
CDC25	G2/M transition	CDC25
FZR	Metaphase–anaphase	CCS52B