Modelling the spatial arrangement of vascular bundles in plants

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Highlights: The spatial arrangement of vascular bundles varies between plant species and organs. A novel reaction-diffusion 2D model is presented defining a set of logical and functional rules able to simulate the differentiation of procambium, phloem and xylem. The model shows that a common mechanism, lying behind the formation of vascular tissues, is able to qualitatively reproduce most stelar structures observed.

Keywords: PDE, reaction-diffusion, stele evolution, tissue differentiation

INTRODUCTION

Spontaneous spatial pattern formation as a result of the dynamic interactions of system components is common in nature at all scales. In plant development and morphogenesis, several regular patterns have been widely studied such as the establishment of the main axes, phyllotaxis, organ shape and venation. In the last decades, simulation models have proven to be useful tools for hypotheses testing on complex systems. Models have been often applied to unravel non-intuitive relations of local processes with the emergence of global forms and patterns. Several studies using computational modelling have been carried out on plant morphodynamics (Jönsson and Krupinski, 2010; Prusinkiewicz and Runions, 2012). Recent work (reviewed in: Jönsson et al., 2012) has focused on two topics: i) venation and phyllotaxis driven by auxin polar transport and ii) genetic regulation of stem cells in apical meristems. So far, no modeling effort has been done yet on the formation of primary vascular structures. We present a spatially explicit reaction-diffusion model defining a set of logical and functional rules able to simulate the differentiation of procambium, phloem and xylem. The model qualitatively reproduces most stelar structures observed in different plant taxa.
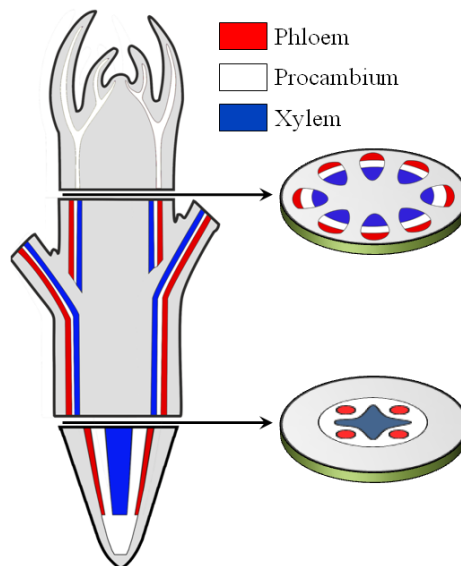
MODEL DESCRIPTION

Fig. 1. Schematic representation of vascular patterns in plants.

We developed a mathematical model that simulates the development of a group of undifferentiated cells in a sub-apical transverse section of stems and roots (Fig. 1). We used the activator–inhibitor and activator-substrate modelling approaches introduced by Gierer & Meinhardt (1972), and fully developed by Meinhardt

(1982). The main assumptions of our model are the following:
- mitotic index strongly relates to cell position within the meristem, being significantly higher in the outer zone than in the inner zone (Laufs et al., 1998);
- sugar metabolism, particularly cellular sugar status (Koch, 2004; Eveland and Jackson, 2012), plays a fundamental role in plant development and definition of spatial domains within plant organs (Pien et al., 2001);
- the emergence of vascular tissues depends on the juxtaposition of adaxial/central and abaxial/peripheral spatial domains which sets a cascade of species-specific and organ-specific genetic and molecular dynamic processes.

We defined a system of 9 PDEs that describe the spatio-temporal dynamics of different compounds in a group of meristematic cells. A first equation describes the sugar status of the cells. A set of three equations describes the dynamics of an activator-substrate system which leads to the differentiation of procambium. Another set of 5 equations drives the emergence of phloem and xylem and describe the dynamics of two locally mutually exclusive compounds with lateral reciprocal facilitation (Meinhardt and Gierer, 1980). Meristematic cells are in a continuous state of division and the velocity of cellular division depends on their position within the organ. Sucrose cleavage to hexoses is positively correlated to the division rate, then fast dividing cells have higher hexoses concentrations. An hexose threshold value results in the activation of genes marking the cell as either adaxial or abaxial. The two newly defined cell domains start producing specific signals which are necessary to produce an autocatalytic activator responsible for the activation of procambium-fate genes. Once differentiated, provascular cells start the production of two other competing autocatalytic activators responsible for the activation of phloem-fate and xylem-fate genes respectively. According to the prevalence of either one or the other activator, procambial cells differentiate into either phloem or xylem.
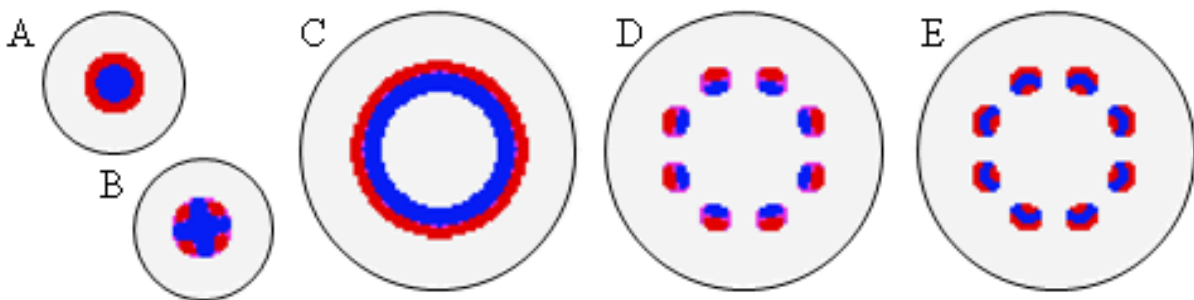
RESULTS AND DISCUSSION

Fig. 2. Examples of simulated steles. Grey: ground tissue; Red: phloem; Blue: xylem. A) Protostele; B) Actinostele; C) Siphonostele; D) Eustele with collateral bundles; E) Eustele with bicollateral bundles.

The arrangement of vascular bundles observed in plant steles, can be summed up in three basic types: i) protostele presenting a solid column of vascular tissue (Fig. 2A); ii) siphonostele characterised by an hollow cylinder of vascular tissue (Fig. 2C); iii) eustele showing separated strands of vascular tissue, usually arranged as a discontinuous cylinder (Fig. 2D) (Beck et al., 1982).

Model simulations were able to effectively reproduce most stelar types observed in plants showing that different vascular patterns can be developed by similar molecular and genetic processes (Fig. 2). Model numerical analysis and simulation results of the first set of equations, show that the emergence of protostelic opposed to siphonostelic or eustelic patterns depends on domain dimension where the process occurs (Fig. 2 A,C). Varying only the domain diameter, a protostelic structure emerges in small domains, while either siphonostelic or eustelic structures are formed in larger domains. The formation of these latter spatial patterns mainly depends on the parameter controlling the autocatalytic reaction between procambium activator and its substrates. Moreover, the differentiation of both phloem and xylem occurs in consistent arrangements within the abovementioned vascular structures. The different spatial organization of phloem and xylem, e.g. collateral bundles (Fig. 2D) and bicollateral bundles (Fig. 2E), depends on levels of diffusion and reaction rates of respective activators.

Future work will be focused on a better definition of sugar metabolism and on the simulation of secondary growth.

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