Autoreproductive cells and plant meristem construction: the case of the tomato cap meristem

P. W. Barlow¹*, H. B. Lück², and J. Lück²

¹ Institute of Arable Crops Research, Long Ashton Research Station, Department of Agricultural Sciences, University of Bristol, Bristol and ² Le Beausset

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Dedicated to Professor Brian E. S. Gunning on the occasion of his 65th birthday

Summary. Root apical meristems are composed of two zones in which either formative or proliferative cell divisions occur. Within the formative zone, autoreproductive initial cells (a-cells) occupy distinctive locations. By means of graph-L-systems, the behavior of one such type of a-cells has been investigated, with particular reference to root caps within the developing primordia of lateral roots of Lycopersicon esculentum cultivated in vitro. Here, the a-cells constitute the “protoderm initials”, cells which are found also in the root cap of many angiosperm species. A set of cuboidal (i.e., six-sided) a-cells develops early in the ontogeny of a lateral-root primordium. Then, according to both anatomical observations and theoretical simulations obtained by the application of graph-L-systems, sequential production of descendents from each a-cell leads to the formation of a new autoreproductive cell (a), a cap columella initial (c), and two mother cells (e and f) whose respective descendents differentiate as root epidermis and cap flank cells. In this graph-L-system, there is specification of the location of sister cells with respect to the three orthogonal directions of a cuboidal. In the early stage of root cap formation, only a few rounds of these formative cell divisions by each a-cell and its four types of descendents are required to provide the basic set of cells necessary for full cap development. After the lateral root emerges from the parent root, there may be a temporary cessation of the formative divisions of the a-cells which give rise to columella initials. Columella production is then supported entirely by its own independent set of autoreproductive c-initials. At the same time, division of the autoreproductive protoderm initial cell is directed towards maintaining the cap flank and the epidermal cell files. The regulation of the types of formative division by the a-cell may be represented by means of a division counter which may be specific for a given species.

Keywords: Autoreproductive cell; Epidermis; Lateral-root primordium; L-system; Root cap; Tomato.

Introduction

Many aspects of plant growth and development appear to be so regular that they can be codified by a set of deterministic rules. L-systems (Rozenberg and Salomaa 1980) are composed of such sets of rules and these may apply at different levels of plant organization. They are especially relevant to the description of branching events which play such an important part in plant growth.

Generally, L-systems are composed of algorithms that reproduce, within an ordered time-frame, recurrent events in the development of constructions composed of elements. In the case where the elements are walls, or wall segments, the corresponding constructions are cells; where the elements are cells, the constructions are organs; and where the elements are organs and their meristems, the constructions are organisms. If growth and development at each organizational level is to realize its full potential, the constructions at each level must participate in branching events which increase the number of constructions and, hence, their scope for further differentiation. Sets of branching events within a hierarchy of constructions are thus natural and highly regulated accompaniments to plant growth. Branching is accomplished by the insertion of new elements which results in the construction being separated into two independent portions. L-system algorithms can precisely specify the location of the inserted elements, as well as the growth and development of the constructions prior to their
branching. Some of the more evident branching events in plants are those associated with the generation of new leaves, buds, and shoots.

In the present paper, branching events at the organizational level of the cell will be considered: namely, the sets of cell divisions which accompany tissue and organ construction. However, the precise orientation of elements in three dimensions is not given by L-systems, even those systems that apply to filaments which eventually branch. Therefore, the nonrandom placement of successive generations of cell division walls needs further definition. This is generally furnished by consideration either of cellular graph productions with cell gluing rules, as used in Graph Grammars (e.g., Lück and Lück 1979), or by wall matching rules, as used in Cellworks (e.g., Lück and Lück 1996). Using the three orthogonal directions of cuboidal cells for cellular location in a three-dimensional space, we propose here much simpler systems than have been described previously. We call these graph-L-systems. The outcome of their application is an ordered series of organogenetic cell divisions which, in turn, is accompanied by an ordered pattern of cells.

On the basis of the regularity of cellular arrangements resulting from cell divisions within plant tissues, it is reasonable to assume that such arrangements have relevance not only to the branching and self-maintenance of the organ within which these tissues reside, but also to the functions of the tissues themselves. The particular construction which we have explored, from the point of view of establishing the rules for its assemblage, is that which is composed of the cap and epidermis of tomato roots. Cells contained within the pericycle of maturing root tips are taken as the starting point for this construction. Algorithms have been developed for the tomato root cap which utilize cells with specific orientations associated with their division walls. These are the elements from which the cellular patterns of the cap and epidermal tissues are generated by simulation, a methodology which plays an important part in validating the algorithms used in this type of analysis.

Material and methods

Cap tissue development was analyzed in lateral-root primordia, as well as in emerging and recently emerged roots, of *Lycopersicon esculentum* Mill. (cv. Moneymaker). The source root material was grown in vitro in modified White’s solution supplemented with sucrose, as described in Barlow (1992). Root segments, 5 cm long and known to contain primordia, were excised from behind the root tip, fixed in formaldehyde-ethanol-acetic acid and embedded in paraffin wax. Using a rotary microtome, transverse sections, 10 μm thick, were prepared from the whole length of each segment. All the sections were placed serially on microscope slides, stained with safranin-tannic acid-orange G (Sharman 1943), dehydrated, and finally mounted in Canada Balsam under a coverslip. Sections prepared from a number of roots containing lateral root primordia at all stages of development were examined with the ×25 and ×40 objective lenses of a Zeiss Photomicroscope. Because the growth axes of both the primordia and the young roots are perpendicular to that of their parent root axis, these younger roots were always cut longitudinally during the sectioning procedure. Their median sections were located and photographed on Pan F film (50 ASA; Ilford). The exposed film was then developed in Acutol (Paterson, Telford). Boundaries of the cell packets were traced on glossy prints prepared from the negatives. Numbers of cells mentioned in reference to packets of cells apply only to those which have been seen in a single median longitudinal section of the lateral root.

Results

The objective of this study of young roots of tomato grown in vitro was to arrive at a formal model of root cap construction. Graph-L-system methodology was proposed because this class of L-systems, besides having recurrent growth functions which predict the number of cells produced by an initial mother cell, also specifies the position of the daughter cells in several spatial directions. Although the final outcome of the L-system model for the root cap is sketched in Fig. 6, it will be useful to refer to this figure in the various sections that follow. It should be noted, however, that negative states in Fig. 6 refer to observed or extrapolated states which have not been simulated by the L-system.

Summary of primordium construction and root cap development in young lateral roots

There is a progression of development – less to more advanced – along the distal-proximal axis of the parent root. Thus, cross sections of in vitro grown tomato roots (Figs. 1–3), cut from tip to base, revealed all stages of lateral-root development, from the primordial stage up to the emergence of young lateral roots from the confines of the parent root tissue.

The earliest primordial stages could be identified in the pericycle (Fig. 6, step –4) and adjacent endodermis by the relatively strong affinity of some cells for cytoplasmic stains (that is, relative to the weaker staining of neighboring, nonprimordial cells). Whether these cells were dividing anticlinally, as is the case in the earliest stages of primordium development (Lloret et al. 1989, Malamy and Benfey 1997), was not determined.