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## Root Growth and Development

- *John G. Torrey, Biological Laboratories, Harvard University, Cambridge 38, Massachusetts*

One can make a pretty good case for starting out a course on growth and development with the root and its development. There are a number of classic experiments with developing roots which bear repeating since each time they illustrate clearly and forcefully to the student some of the basic facts and features in the development of the vegetative plant body.

Seedling pea or bean roots, marked at millimeter intervals with India ink, and grown in a moist chamber for 2 days and then remeasured, illustrate just where along the root cell enlargement takes place. This simple manipulation of young tender seedlings is an excellent introduction to growing plants, the need for care in handling, protection from desiccation and damage, and some of the other simple facts of life. This experiment very quickly shows up the careless approach (7).

These same peas or beans can be usefully studied for the processes of mitosis and cell division. To make root tip squashes in class and study directly the stages of mitosis is an exciting experiment which anyone should do first hand. Any of a number of staining procedures can be used. Nicest for permanent mounts are Feulgen-stained root tip squashes (2). Quite good temporary squashes can be made with acetic-orcein, acetocarmine or lactic-acetic-orcein, in which all mitotic stages are nicely shown and where chromosome counts can be made and chromosome morphology studied. Since cell division and cell enlargement interacting together constitute the warp and woof of development, it is desirable to study them close together this way. It is useful to have prepared slides of well-stained transverse and longitudinal sections of the same root for related study, to allow an analysis of cellular detail in fixed material. The same procedures for root tip squashes, for studying elongation, and for tissue differentiation apply equally well to onion roots, which de-

velop rapidly from a young onion bulb (set) supported in a vial of water. The organization of the root apex, the differentiation of primary meristematic tissues and the primary tissues all are a part of the story of development in the root approached in this way.

With the ready availability of tritiated thymidine, it is a relatively simple procedure to feed roots, such as those above, a very small amount of H<sup>3</sup>-thymidine and then, using autoradiography, study the important process of the synthesis of DNA. The simplest process is to fix root tips some hours after having been provided the radioactively-labelled precursor, make root tip squashes as described above and then, using relatively crude photographic dark room facilities, use stripping film or pour liquid nuclear track bulk emulsion (Kodak Type-NTB 3) over the tissue squashes, expose the film to the H<sup>3</sup>-thymidine for a few days, develop, mount, and study the distribution of silver grains with respect to nuclei, chromosomes and cells in division (6). This procedure, carefully planned and timed, can be used to calculate the frequency of cell division in the root tip (8).

One of the neatest uses of this technique is that developed by Clowes (1) for studying the organization of the root apex. In a small class, his experiment demonstrating the existence of a "quiescent zone" of cells in the root apex, which show a very low rate of DNA synthesis, can be done in all of its steps, using H<sup>3</sup>-thymidine in preference to C<sup>14</sup>-labelled adenine. In a larger class, previously treated roots can be sectioned longitudinally and slides with mounted sections provided to students to let them prepare their own autoradiographs for study.

Somewhere during the study of early root development it is desirable to look at the process of seed germination. Here, germination of seeds with hard seed coats is informative, as is that of lettuce seed requiring red light for radicle development.

Intimately tied to the anatomical studies of the development of the primary tissues of the root, the differentiation of xylem and phloem, the formation of root hairs, and of lateral root initiation are simple experiments on the nutritional requirements of isolated roots grown in sterile culture. One such simple experiment is described in detail in Machlis and Torrey, (7), Exp. 26. It is informative to break open aseptically a ripe tomato and remove the mature seeds free of fruit pulp to sterile petri plates and allow the seeds to germinate in sterile water. The root tips of the germinated seeds are readily excised and, if sterile, can be grown in a nutrient medium (e.g., White's medium) which the class has made up earlier from prepared stock solutions. The elimination of an essential vitamin such as thiamin may show up as a deficiency in a single transfer after several weeks. Much is to be learned by the student about the synthetic capacities of isolated roots, about their heterotrophic nature, and about factors, genetic or otherwise, affecting their normal developmental patterns. Other roots and various media make interesting projects for individuals or for the class since, despite much work on cultured roots, the vast majority of plant species has never been tried.

The initiation of adventitious roots is a developmental process that concerns both shoot and root structure. The role of auxin in the process can be demonstrated with woody stem cuttings, but this takes time and good greenhouse facilities, such as rooting beds, bottom heat, and the like. I find a most intriguing experiment one which has been

used in research by a number of people. We have tried it in class, always have an unpredictable result, but always find something interesting. Much remains to be worked out as to what goes on. The experiment involves the rooting of hypocotyls of young bean seedlings with their leaves attached (7). More recent studies show that leaves are essential and not replaced by IAA (4), certain vitamins affect the initiation (5) and the auxin effect itself can be affected by related compounds (3). This is a good experiment which has much physiology and anatomy in it as well as a lot of unanswered questions.

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