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Spatial Peculiarities of Stem Cells in Plants and Animals

Anil Kumar[1], Sujata Mohanty[2*], S.K. Ray[1], S.M. Paul Khurana[1]

[1]Amity Institute of Biotechnology, Amity University, Gurgaon, Haryana, India
[2]Centre of Excellence for Stem Cell Research, AIIMS, New Delhi

[*]**Corresponding author:** Sujata Mohanty, Centre of Excellence for Stem Cell Research, AIIMS, New Delhi, E-mail: drmohantysujata@gmail.com

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Introduction

The life of any organism begins at the level of stem cells. The fertilized egg considered as ultimate stem cell, divides to give rise to lines of cells that form various differentiated organs. During these early divisions, each daughter cell retains totipotency. Then, through a series of divisions and differentiations, the embryonic stem cells (ESCs) lose potential and gain differentiated function. During normal tissue renewal in adult organs, tissue stem cells give rise to progeny that differentiate into mature functioning cells of that tissue. Stem cells which are not totipotent are called "progenitor cells"[1].

Stem cells display specific characteristic to be called as stem cells. The first characteristic of stem cells is that they are naïve cells- meaning that they either expresses very little cell surface markers of differentiation or no cell surface marker of differentiation. Second characteristic is asymmetric cell division, which is responsible for the self renewal of the stem cell pool[1,2]. During early embryonic development, each cell divides and gives rise to two daughter cells with the same potential: symmetric division. During normal tissue renewal in the adult, each progenitor cell gives rise to one daughter cell that remains a progenitor cell, and one daughter cell that begins the process of determination to a terminally differentiated cell-asymmetric division. The number of cells increases exponentially during early embryogenesis, but the cell number remains constant during normal tissue renewal, as the number of new progenitor cells equals the number of cells destined to die. So, stem cells are "slow-cycling" in nature[3,4,5]. The third main characteristic is the plasticity, ability to give rise to different cell types in a culture. The stem cells in culture have the ability to differentiate into different cell types of the same germ lineage or the ability to transdifferentiate, which is the ability to differentiate into cell types across the lineage[6-11].

The characteristics of stem cells noted in the above paragraph have been derived from studies have done on the animal cells. Plant stem cells have not been studied in much in detail. Stem cell homeostasis in plant systems does not involve cell behaviors shown by animal system such as asymmetric cell divisions, oriented cell divisions and cell migration[12-14]. Specially the cell surface markers and niche identification has progressed substantially in case of animal stem cells. Most of the stem cell studies in plants are limited to shoot apical meristem (SAM) or root apical meristem (RAM) in the model plant Arabidopsis thaliana[15-20].

Stem cell: Origin of Life

First recorded attempt to understand the origin of life and the early development of the human, was most likely made by Aristotle (384 – 322 BC)[21]. He was the first to contemplate that the individual was formed de novo or was pre-formed in the mother and only enlarged during development[21]. Aristotle deduced that the embryo was derived from the mother's menstrual blood, a hypothesis known in the middle ages as "spontaneous generation". The hypothesis that life did not arise spontaneously, but rather only from preexisting life (omne vivum *ex vivo*) was proposed by Leydig in 1855. Rudolf Virchow (1855) extended this to postulate that all cells in an organism are derived from preexisting cells (omnis cellula e cellula); so, in the beginning it was some cell which was giving rise to the complete organism. Now we understand that cell as stem cells. The hypothesis of spontaneous generation was formally disproved in 1864, when Louis Pasteur with controlled experiments demonstrated failure of microorganisms to grow in sterilized broth if ambient organisms prevented from entering[22]. According to the principles derived from Leydig, Virchow, and Pasteur, life neither ends nor begins but is continuous. The product of the union of a sperm with an egg is the ultimate or Holy Grail totipotent stem cell [Reviewed by (Sell 2004)][1].

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Spatial Location of Stem cells

Stem Cells, in case of humans, as of today, has been found to be located in almost all the organs, starting from the dip bone marrow to the uppermost cells of the body the hair follicular cells and skin. In case of plants the SAM acts as a reservoir for stem cells. The central zone (CZ) harbors stem cells. The stem cell progenitors differentiate in the adjacent peripheral zone and in the rib meristem located just beneath the CZ[13]. Yadav et al.,[10] did profiling of gene expression from different cell samples of shoot apical meristems further expanded the use of this approach. They isolated three cell type populations from shoot apical meristems and demonstrated that cell-type-expression profiling is sensitive in identifying transcripts expressed in specific subsets of shoot-meristem cells[23].

The Arabidopsis RAM is well suited for the analysis of biological, and especially developmental, processes within individual cell types due to its relatively simple radial organization and its mode of continuous development from a set of stem cells[24,25] Birnbaum et al.,[24] localized the expression map of more than 22,000 genes in five different cell types of the Arabidopsis root and three developmental zones. Their findings strongly suggested that patterns of gene expression crossed anatomical boundaries. They could correlate group of genes for specific destined cell fates[23]. Following this work, Brady et al.,[25] studied microarray expression profiles of root developmental time points and provided a comprehensive map of nearly all cell types within the Arabidopsis root[23].

Locating stem cell zones

That the signals from other cells are required to maintain the plant stem cells come from the studies on Arabidospis. This was revealed by work on mutant Arabidopsis plants that are unable to maintain the apical meristem. Laux and colleagues isolated Arabidopsis plants with mutations in the WUSCHEL (WUS) gene[26]. In these plants, the shoot apical meristem starts to form, but then the meristem cells differentiate and the stem cells are lost. WUS turned out to encode a transcription factor (a protein that controls the activity of other genes) that is expressed in only a small number of cells just beneath the stem cells in the shoot meristem[27]. Because the WUS mutation affects the adjacent stem cells, where the gene is not expressed WUS must be required to produce a signal that functions between cells to maintain the shoot stem cells[28,18,29,30].

In the root, evidence that stem cells are maintained by intercellular signals came from experiments in which the cells making the signal were selectively killed. Van den Berg and colleagues used a laser beam to kill single cells within the root meristem[31]. When they killed specific cells that flank the stem cells (called the quiescent center cells or QC cells) the adjacent stem cells differentiated. This was not simply a result of the injury caused by the laser, because killing neighboring cells other than the QC did not induce differentiation. Therefore, the QC must be the source of a signal that prevents differentiation of the root stem cells[28-30].

Stem cells in Animals have been isolated at different stages of the life cycle. Scientists have isolated the stem cells from different developmental stages i.e., Embryo, fetus and adult. The stem cells isolated from the embryo are called embryonic stem cells and the stem cells from the fetal tissue and adult tissue or organ are categorized as adult/ somatic stem cells. Regarding the categorization of cord stem cells and cord blood stem cells, still there are different schools of thoughts for their characterization and some authors prefer to characterize them separately.

Human Embryonic stem cells (ESCs) lines holds promise for disease modeling, basic scientific research, drug development, toxicity studies, and may serve as an unlimited renewable source of cells for transplantation therapy[32]. It is more than three decades, since murine ESCs were first described when they were isolated and grown *in vitro*[33,34]. In 1998 Thomson et al. isolated human ESCs from the inner cell mass of in vitro fertilized embryos (blastocysts), that were donated for research purposes[35,36]. These cells are characterized by the expression of a stage-specific embryonic antigens (SSEA), expression of undifferentiated cell gene markers (OCT4, Nanog, Rex1), and activity of telomerase and alkaline phosphatase enzymes. These cells also remain undifferentiated and karyotypically stable during prolonged passages, and readily differentiate *in vivo* and *in vitro* to cells representing the three germ layers[36,37]. However, the same potential for differentiation that makes ESCs useful, also render them difficult to control. Often the transplantation of ESCs in nude mice results in teratoma formation, a hurdle that must be overcome before widespread clinical application[38]. Other difficulties include the rejection of ESCs by the host immune system after transplantation, and the use of a feeder layer to retain an undifferentiated state in vitro. Above all the major difficulty associated with ESCs research is the ethical argument posed by critics that deriving a cell line from a blastocyst is the moral equivalent of destroying a human life. These difficulties slow down the process of investigation for ESCs, which is necessary before the safety of any type of human trial can be accurately assessed.

Adult Stem cells

One alternative to ESCs for use in clinical studies is adult stem cells[39]. 'Adult' stem cells include haematopoietic stem cells[40], bone marrow stromal (mesenchymal) stem cells[41], neural stem cells[42] dermal and hair follicular (keratinocyte and melanocyte) stem cells[43-46], fetal cord blood stem cells[47] and several others[48]. Like Embryonic stem cells, they are capable of self-renewal throughout the organism's life, and also capable of differentiating into different mature cell types. However, adult stem cells are already committed to a certain cell lineage and thus they are restricted in their differentiation range[49]. Adult stem cells reside within mature tissues and serve as a limitless source for new mature cells, enabling maintenance and repair of the tissue by continuously regenerating mature tissues either as part of normal physiology or as part of repair after injury. Adult stem cells have been identified in many animal and human tissues, including bone marrow, blood, brain, skin, hair, intestine, muscle and tooth[39].

Evidence for Animal Stem Cells

Most of the adult tissues and organs are under constant wear and tear. The neurons of the central nervous system, liver and many endocrine glands consist of functional cells that do not divide; if such organs are damaged, the functional cells can proliferate, restoring cellular number and function. Such organs are considered to be conditionally self-renewing. The functional cells of other systems, such as the skin, gastrointestinal tract, and

hematopoiesis, are both short-lived and incapable of proliferation. These organs are maintained by a small population of cells with extensive capacity for proliferation together with the ability to have daughters that are functional or whose progeny acquire characters that are needed for function.

Hematopoiesis has many features that facilitate the experimental study of obligatory renewal. Two schools of thought were soon established; members of one taught that a single stem cell was the origin of all the cells of the blood. Others were equally committed to the doctrine that each lineage was headed by its own stem cell. The issue could be resolved only if new experimental evidence was found. In 1961, J. E. Till and E. A. McCulloch reported experiments in which small numbers of normal mouse marrow cells were transplanted into heavily irradiated mice; when these recipients were killed after 10–14 d, their spleens were seen to contain nodules that could easily be counted. A linear relationship was established between the number of marrow cells injected and the number of nodules found in the recipients' spleens. When the spleens were examined histologically, the nodules were found to consist of maturing and mature blood cells. This was one of the early evidence for the existence of stem cells in bone marrow[50-53]. In 1959, for the first time, Edward Donnall Thomas used HSCs for treating postradiative marrow failure in man with leukemia and lymphomas through bone marrow transplantation, which was first clinical application of stem cells and another evidence for their existence[54].

Evidence for Stem Cells in Plants

Evidence that the whole shoot descends from a small set of constantly dividing cells within the apical meristem came from clonal analyses by Stewart and Dermen[55]. They looked at variegated plants, plants whose leaves and stems are not uniformly green, but have patches of white tissue, a feature often selected in ornamental plants. These white tissues descend from mutant cells that are unable to produce chloroplasts. Most of the time, the plants produce small colorless patches, but Stewart and Dermen also found plants with colorless sectors composing nearly a third to half of the whole shoot, and which were continuously produced by the meristem over long periods of time. These large, stable sectors of mutant cells could only be formed if all cells that make up the shoot descended from a small population of relatively stable, long-term progenitors-the shoot stem cells. Comparable experiments showed that root tissues also descend from a small set of stem cells. For example, Dolan, Scheres and Kidner used a reporter gene to mark cell lineages in the roots of the model plant Arabidopsis[56-59] First the reporter gene was blocked by a transposon (a piece of DNA that can move around in the genome). Then the cells became genetically marked when the transposon moved, unblocking expression of the reporter in only a few cells of the root meristem. This allowed these cells and their descendants to express the reporter gene. Once again, a few large and stable sectors allowed the scientists to trace the progenitors of root tissues to just a few stem cells in the center of the root meristem[29,30].

Molecular regulation of plant and animal stem cells

In context to a few gene expressions plant and animal stem cells have been found to behave in a similar fashion. One such gene that is conserved between plants and animals and has a central role in deciding whether a cell continues to divide or differentiates encodes the Retinoblastoma (Rb) protein. When activated, Rb represses genes required to replicate DNA, in addition to other less-well-characterised functions that lead to cell differentiation[60]. In Arabidopsis, if the gene encoding Rb is inactivated in the root meristem, the descendants of root stem cells cannot differentiate; conversely, if Rb is artificially activated in the stem cells, they stop dividing and differentiate[61]. A similar mechanism operates in plants wherein Rb appears to promote exit from stem cell state in animals[62].

The property of pluripotency is believed to depend at least in part on the way the chromatin is organized, that is, how the DNA is packaged in the nucleus and how this affects the access of regulatory proteins to genes required for cell differentiation. Polycomb proteins play an important role in regulating the chromatin to repress differentiation genes and therefore maintain the pluripotency of animal stem cells[62]. In plants, Polycomb proteins also regulate the transition between pluripotent and differentiated states, but unlike in animals, they are required in the differentiating cells to repress genes that are normally expressed in the meristem. This is shown by Arabidopsis plants with mutated polycomb genes: in these plants, shoot meristem genes continue to be expressed in cells that are due to form leaves and consequently leaf development is abnormal[63]. In conclusion, at least some of the genes that control the stem cell state in animals are also relevant for plant stem cells, but there may be variations in the way these genes are deployed. The Rb protein seems to function similarly in plants and animals to stop cell division and start differentiation in cells that leave the stem cell niche. Polycomb proteins are used to maintain a repressive chromatin state in both kingdoms but appear to function differently in the stem cells: they repress differentiation genes in animal stem cells, whereas in plants they are used to inhibit meristem genes in differentiated cells. It must be said, however, that we are far from understanding the molecular basis of pluripotency in any organism, so we cannot yet be sure whether pluripotency is controlled differently in plants and animals[29,30].

The recent advances in biotechnology, such as genomics, proteomics, *in vivo* epidermal targeting, GFP labelling and adeno- and retro-viral gene transfers, will allow for much better understanding of SC biology. These novel technological approaches will allow the identification of specific molecular markers which will aid further in the isolation of SCs, thus, opening unlimited possibilities for therapeutic approaches. The possibility that stem cells can be used to repair virtually all tissues has recently received enormous attention and is expected that development in this field will ultimately lead to understanding of developmental biology, the way we perceive the disease and their management which will have tremendous impact on the humans and may be on plants, as well.

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