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Anhydrobiosis and programmed cell death in plants: Commonalities and Differences

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ABSTRACT

Anhydrobiosis is an adaptive strategy of certain organisms or specialised propagules to survive in the absence of water while programmed cell death (PCD) is a finely tuned cellular process of the selective elimination of targeted cell during developmental programme and perturbed biotic and abiotic conditions. Particularly during water stress both the strategies serve single purpose *i.e.*, survival indicating PCD may also function as an adaptive process under certain conditions. During stress conditions PCD cause targeted cells death in order to keep the homeostatic balance required for the organism survival, whereas anhydrobiosis suspends cellular metabolic functions mimicking a state similar to death until reestablishment of the favourable conditions. Anhydrobiosis is commonly observed among organisms that have ability to revive their metabolism on rehydration after removal of all or almost all cellular water without damage. This feature is widely represented in terrestrial cyanobacteria and bryophytes where it is very common in both vegetative and reproductive stages of life-cycle. In the course of evolution, with the development of advanced vascular system in higher plants, anhydrobiosis was gradually lost from the vegetative phase of life-cycle. Though it is retained in resurrection plants that primarily belong to thallophytes and a small group of vascular angiosperm, it can be mostly found restricted in orthodox seeds of higher plants. On the contrary, PCD is a common process in all eukaryotes from unicellular to multicellular organisms including higher plants and mammals. In this review we discuss physiological and biochemical commonalities and differences between anhydrobiosis and PCD.

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1. Introduction

Life forms on earth encompass a wide diversity that inhabits its different climatic regions, ranging from cold ice caps to the hot springs and dry environment (*e.g.*, rocks, dessert) to wet ones (*e.g.*, ponds, lakes) in different geographical regions. This diversity reflects the adaptability of inhabitants at physiological, biochemical and genetic levels to cope with the prevailing environment. Occupying extreme environmental niche, certain organisms can survive removal of almost all of their cellular water without irreversible damage; such organisms are referred to as desiccation tolerant or anhydrobiotes [1–4] and the phenomenon itself as anhydrobiosis. Measurements of water potential by Gaff group indicated that even when plants are equilibrated at 50% relative humidity at 28 °C, they experience a water deficit equivalent to that of −100 MPa pressure which is lethal for the majority of angiosperms [5]. Desiccation or drought tolerant organisms on the other hand have the ability to survive dehydration, to the point where moisture content in the cytoplasm has no free water, *i.e.*, ∼0.3 g H_2O/g dry weight, a condition where most of the cellular water is bound with macro-molecules. Resumption of normal life after rehydration is a significant feature of desiccation tolerance [6].

In contrast to anhydrobiosis, programmed cell death (PCD) ubiquitously occurs throughout all eukaryotic lineages. Though a regulatory process, PCD also act as one of the survival mechanisms *in planta* during certain instances of biotic and abiotic stresses such as disease, water stress, salt and heat stress [7]. PCD generally involves targeted killing of unwanted or diseased cells and is used to control cell number in the given tissue, thus maintaining homeostasis. Additionally, PCD is also observed during certain developmental processes as well where defined cells die and the dead cells take over their assigned function such as tracheary cells, sclerenchyma fibres and cork cells *in planta* [8]. Considering sensitivity of all the major crop plants to drought, understanding the process of anhydrobiosis and that of PCD has the potential to open up the possibility of introducing the drought resistance character in crop plants which could solve the global food security problem.

Anhydrobiosis is more prevalent in lower plants, especially in thallophytes, although involvement of anhydrobiosis in higher plants is not ruled out, the phenomenon is mostly restricted to some reproductive propagules like seeds. During evolution, with the development of water conducting system in higher plants PCD became one of the prominent strategies for the cellular homeostasis while anhydrobiosis progressively became restricted to certain reproductive structures as a mechanism to tide over the water stress conditions such as unfavourable dry weather or dissemination of propagules over longer distances where they were prone to be exposed to low water availability. There are certain species that manifest both the survival strategies. The higher plants bearing orthodox seeds are the ideal examples – manifesting both phenomena at successive developmental stages, *i.e.*, anhydrobiosis and PCD in the endosperm during seed maturation phase, while PCD in aleurone layer cells during seed germination. Existence of such examples in nature opens up the possibility of incorporating features to regulate PCD and promote vegetative desiccation tolerance at least up to certain extent in crop plants that lack this faculty.

In this review we have attempted to show that anhydrobiosis as well as PCD are survival strategies that have evolved independently in plants as a means of adaptation to their frequently changing environment. We have endeavoured to sketch a parallelism between these two processes and highlight a possibility to explore the phenomenon of anhydrobiosis for the acquisition of desiccation-tolerance in higher crop plants.

2. Origin and evolution of desiccation tolerance and programmed cell death (PCD)

Desiccation tolerance is a primitive trait that evolved when organisms originated in water took over terrestrial habitats [9–11]. Migration to land exposed the organisms primarily adapted to aquatic life-style to frequent desiccations due to heat, sunlight and wind. Thus, in order to thrive (*i.e.*, colonize and survive) in terrestrial habitat, aquatic plants acquired tolerance for dry conditions [12]. As the primitive architecture of early aquatic plants could not prevent the water loss on exposure to the frequent drying, the early land invaders developed intrinsic mechanisms that resisted harsh and frequent fluctuations in terrestrial environment. For example, desiccation tolerant lichens and bryophytes have ability to rehydrate within 15 min, resume net photosynthesis in less than an hour and resume full photosynthetic functions in about 24 h [13–15]. Apparently, to survive desiccation, the early plants (*e.g.*, bryophytes and lichens) would have acquired the ability to dehydrate slowly and rehydrate quickly. The acquisition of the slow dehydration characteristics during low water condition could have been the key to successful development of desiccation tolerance as exemplified by an aquatic moss *Fontinalis* where slow dehydration protected cells against desiccation induced damages through reduced production of ROS and oxidative bursts [16]. Most of the early land plants were tolerant to desiccation in their vegetative, as well as reproductive phase of life, but the loss of desiccation tolerance in vegetative phase of higher plants occurred during evolution of water transport system, such as tracheid and xylem vessels [10]. Programmed cell death (PCD) is also a trait which is believed to have originated and evolved with the origin of the first cell [17]. Although supposed to be diverse in nature with respect to means, executioners and phenotypes, PCD invariably functions as a regulated cell death as a means to make other members fitter to survive in a given environment. In case of unicellular organism the display of PCD is generally 'altruistic' in nature to help other members of the colony survive in limiting growth conditions (light, nutrients). In bacteria PCD acts as interesting toxin/antitoxin 'addiction modules' to attain a kind of enforced symbiosis, where their disruption could result in death of 'host cell'. The functions of PCD in multicellular organisms has evolved and elaborated further to involve/control the development and tissue homeostasis including protection from the diseases. These aspects have been comprehensively reviewed elsewhere [17]. Although origin of PCD could have been the culmination of multiple processes/mechanisms, in its simplest form it could be summed as the result of unavoidable stochastic 'self-destruct' tendency of most of the cell effectors/processes when their activity is beyond the control of cell survival factors as beautifully put forward by 'original sin' hypothesis [17].

3. Distribution of anhydrobiosis and PCD in photosynthetic organisms

Desiccation tolerance is observed in a wide range of taxa, including bacteria, algae and higher plants [18–23]. It is a primitive trait