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Review

Saving for a rainy day: Control of energy needs in resurrection plants

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ABSTRACT

Plants constantly respond to threats in their environment by balancing their energy needs with growth, defence and survival. Some plants such as the small group of resilient angiosperms, the resurrection plants, do this better than most. Resurrection plants possess the capacity to tolerate desiccation in vegetative tissue and upon watering, regain full metabolic capacity within 72 h. Knowledge of how these plants survive such extremes has advanced in the last few decades, but the molecular mechanics remain elusive. Energy and water metabolism, cell cycle control, growth, senescence and cell death all play key roles in resurrection plant stress tolerance. Some resurrection plants suppress growth to improve energy efficiency and survival while sensitive species exhaust energy resources rapidly, have a diminished capacity to respond and die. How do the stress and energy metabolism responses employed by resurrection plants differ to those used by sensitive plants? In this perspective, we summarise recent findings defining the relationships between energy metabolism, stress tolerance and programmed cell death and speculate important roles for this regulation in resurrection plants. If we want to harness the strategies of resurrection plants for crop improvement, first we must understand the processes that underpin energy metabolism during growth and stress.

1. Introduction

We save because we cannot predict the future. Anon

All organisms face the daily challenge of balancing their energy expenditure between inputs [1]. In animals, this occurs between meals; in plants, this occurs at night and during stress. How well the organism regulates its energy balance, particularly when stressed, dictates its ability to elicit an appropriate response and survive [2]. In addition to stress, cells and proteins undergo routine wear and tear and require repair to maintain homeostasis. Cellular repair is an energy consuming process and the levels of repair rise during stress [3,4]. If the energy reserves available are insufficient to support an appropriate response, the organism may be willing but unable to repair the damage. At least some times, cells, and organisms, do not die from stress directly but rather from an energy deficit that prevents execution of the stress response [4]. One group of plants, the resurrection plants, have the capacity to withstand desiccation to an air-dry state and do not suffer the same fate as the majority of land plants. Although research has made significant progress, the mechanics underpinning the tolerance displayed by resurrection plants remains elusive. Putative explanations towards resurrection plant tolerance include; i) to the ability to slow their metabolism to a quiescent state during drying, ii) the production of copious amounts of osmolytes in the hydrated state that play cytoprotective roles and help control the rate of drying, iii) an ability to protect the cells from damaging UV rays by minimising surface area or disassembling the photosynthetic machinery while still producing enough energy to repair damage, iv) The use of an alternative energy metabolism system that is not utilised in sensitive plants v) a more efficient cellular repair system, vi) the ability to shut down cell death pathways, vii) A combination of all of the above. Here we speculate possible answers to these theories by highlighting the relationships between energy metabolism, desiccation tolerance and cell death in resurrection plants.

1.1. Living within their means – the balance between energy conservation and expenditure

1.1.1. Energy conservation

Sensitive and tolerant plant species employ stress responses that prevent damage and enhance survival, however, the strategies used and the outcomes produced are starkly different. Sensitive species can tolerate water losses of up to 40% relative water content (RWC). Desiccation tolerant plants on the other hand can survive losses of up to 95% of their RWC and are categorised into two classes, fully desiccation

Abbreviations: PCD, programmed cell death; mTOR, mechanistic target of rapamycin; SnRK1, Sucrose non fermenting 1–related kinase 1; TCA cycle, tricarboxylic acid cycle; M phase, Meiosis phase; S phase, synthesis phase; RWC, relative water content

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tolerant and modified desiccation tolerant, depending on the rate of drying tolerated [5,6]. Fully-desiccation tolerant plants, also known as constitutively desiccation tolerant plants, include non-vascular species such as mosses and bryophytes, can survive drying at any rate and utilise extensive repair mechanisms for tolerance [7]. In contrast, the vascular modified desiccation tolerant plants cannot tolerate rapid drying and thus employ control mechanisms that slow down the rate of water loss [5].

In contrast to sensitive species, modified desiccation tolerant plants such as resurrection plants use excess energy produced in the hydrated state to generate dehydration-associated metabolites [8]. Potentially, this enables them to be significantly more energy efficient and subsequently stress tolerant. By producing osmoprotectants in the hydrated state, resurrection plants can focus their limited energy resources during drying towards cell repair and cytoprotection [9].

A universal response to water deficit in plants is stomatal closure and the subsequent shutdown of photosynthesis. In resurrection plants, this shutdown occurs rapidly, upon water losses as little as 20–30% RWC [10]. For example, the photosynthetic rate of *Tripogon loliiformis* is reduced by 20% at 90% RWC and further declined to 50% when the RWC drop to 80%; at 70% RWC no photosynthesis was detected (Fig. 1) [11]. Conversely, many of the faster growing sensitive plants continue to photosynthesise, albeit inefficiently, until much lower relative water contents when it is too late to respond. In modified resurrection plants, the early shutdown of photosynthesis can promote survival. These plants cannot tolerate rapid drying, thus the rapid closure of stomata supports survival by providing additional time for the plant to employ adaptive measures. Once the plant has prepared for desiccation, water is rapidly lost from the 60– < 30% RWC stages. Fully-desiccation tolerant plants also shutdown photosynthesis, however, not as rapidly. Studies in the moss *Polytrichum formosum* demonstrated active photosynthesis until 40% RWC [12] The rapid photosynthetic shutdown and production of osmoprotectants in the hydrated state causes resurrection plants to grow slower than their sensitive counterparts [6]. This slow growth reduces their metabolic requirements and allows resurrection plants to maintain a tighter control of the dehydration of their vegetative tissue [6]. The compensation of cellular metabolic status and growth rate with minimised water loss is just one of the mechanisms employed by the *T.loliiformis* to tolerate desiccation.

In addition to controlling the rate of water loss, resurrection plants typically couple photosynthetic shutdown with a myriad of physiological and metabolic changes that protect the photosynthetic machinery and minimise damage [8,9]. Thus, the cells in resurrection plant vegetative tissue may not undergo as much damage from running an inefficient photosynthesis system compared to those present in sensitive species. Despite these advantages, the early shutdown of photosynthesis leads to caloric deficiency and energy deficit, which if left unchecked can lead to an inability to mount a stress response. To survive, resurrection plants must tap into alternative energy sources as well as reduce energy expenditure.

1.1.2. Resurrection plants control energy expenditure using modified metabolic pathways

In addition to serving as fuels for metabolism, sugars act as primary messengers for the regulation of plant growth and stress responses. With their different growth rates, it is apparent that sensitive species and resurrection plants utilise their metabolic resources differently. A key feature of many resurrection plants upon dehydration is the metabolic shift to sucrose and amino acid biosynthesis. This shift is sufficient to meet the cell's needs but also results in the creation of high sucrose/glucose ratios that trigger significant changes to the cell's metabolism [13,14]. Amongst other signals such as hormones and the available nitrogen content, the cell uses the ratio of sucrose/hexoses to help direct the metabolic status of the cell. High sucrose/low glucose ratios indicate a cellular energy imbalance, to help maintain homeostasis the cell directs its cell's metabolism towards cytoprotection rather than growth. Accordingly, leaves infiltrated with sucrose display increased expression of redox regulators, transcription factors including members of the NAC (NAP), MYB (AtMYB14, MYB90), bZIP (AtbZIP9 and 11) and WRKY (WKRY 26, 53 and 75) associated with energy metabolism as well as proteasome-mediated degradation, trehalose metabolism and autophagy [15] (Fig. 2). It is feasible that in resurrection plants, the high sucrose/glucose ratios created upon dehydration allow the plant to slow-down growth related activities and focus energy resources towards survival. For example, increased sugar levels upon dehydration of the resurrection grass *Sporobolus stapfianus* act as a signal to slow down cellular metabolism and trigger cytoprotective pathways[16].

Hormone signalling is an integral component of plant defence, responses to the environment and regulation of senescence and as such is expected to play a significant role in the desiccation tolerance mechanisms of resurrection plants. To date, however only limited studies have been performed [17,18]. During early drying, plants accumulate Abscissic Acid (ABA) to trigger the transcription of protective proteins and acts as a signal for the plant to initiate adaptive responses to water deficit [19,20]. Plant hormones may also play a role in the ability of

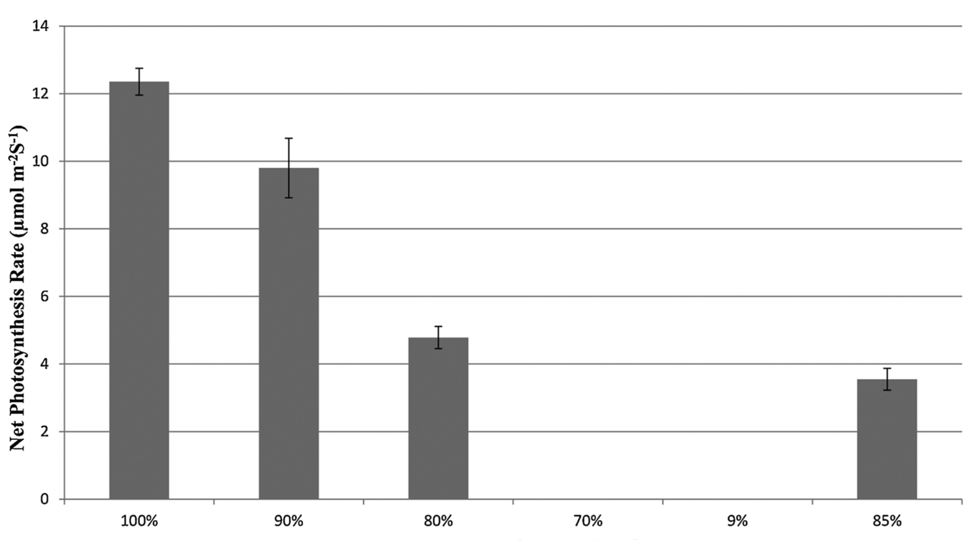

Fig. 1. Changes in net photosynthetic rate during dehydration and rehydration in *Tripogon loliiformis*.
The photosynthetic rate of Tripogon loliiformis is reduced by 20% at 90% RWC and further declined to 50% when the RWC drop to 80%; at 70% RWC no photosynthesis was detected.