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Seed endosymbiosis: a vital relationship in providing prenatal care to plants

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Abstract

Global food security is a challenge, especially under changing climatic conditions. Recent advances in plant technology using plant-microbiome interactions promise an increased crop production. Indeed, all healthy plants or crop genotypes carry a beneficial microbiome, encompassing root- and seed-associated endosymbionts, providing mycotrophy and mycovitality to plants, respectively. Recent studies have found that mycovitality, or the endosymbiotic seed-fungus relationship and its key translational functions, bear tangible biotechnological benefits. Thus, this paper underlines the role of endophytes as early plant growth promoters under stressful environments. Notably, it explores the concept of plant prenatal care towards enhanced seed vigor/germination and resilience, which results in an improved crop yield under stressful conditions. It presents an extensive research overview of endosymbiotic plant-fungi relationships with special focus on the wheat seed, an important source of staple food. Historical advances in terminology and scientific concepts on the subject are also presented to highlight the areas where further research is urgently needed.

Keywords: Seed; plant microbiome; endophytes; fungi, plant prenatal care; climate change

Abbreviations

ABA abscisic acid

AMF arbuscular mycorrhizal fungi

GA gibberellic acid

Introduction

The 21st century is challenging, for crops as much as for humans who depend on them. Global food production is being disrupted by extreme weather related to climate change, among other factors. At the same time, the Food and Agriculture Organization predicts that, by 2030, an extra billion tons of cereals will be needed worldwide each year (FAO 2013). China's current needs for food imports are further predicted to increase by 30-40% in years to come (Zhang 2011). As a remedy, agricultural sciences promote a "lab-to-farm" approach for crop improvement, largely dependent on the success of the captive-breeding and field program (Ronald 2014). Since these conventional ways may prove to be ill-equipped in handling current challenges alone, innovation aligning new scientific highways is crucial, notably one which focuses on the co-evolution between plants and microbes as a natural driving force allowing crops to deliver their full potential, especially under stress conditions (Jones 2013; Gopal et al. 2013; de Zelicourt et al. 2013; Berendsen et al. 2012). The diversity of plant-associated fungi and bacteria, in the magnitude of tens of thousands of species (Berendsen 2012), endows plants with a second genome of tremendous potential: the microbiome (Turner et al. 2013; Berg et al. 2014a). Microbial endophytes, which live asymptotically within plant tissue, are gradually being recognized as symbiotic contributors to plant performance. On the one hand, North-American microbial ecologists are uniting to use the power of microbial endophytes in making crops hardier (Jones 2013). On the other hand, the European Union's COST coalition for development of endophytes for use in biotechnology and agriculture (COST 2014), and the United Kingdom's BBSRC/NERC initiative to protect soils and safeguard global food security (BBSRC/NERC 2014) are highlighting the interactive effects of multiple endophytic symbioses in predicting an ecosystem's response to global climate change. Undoubtedly, microbial partners are key determinants of plant health and productivity (Sessitsch and Mitter 2015) as testified by rhizobacteria, endophytic fungi and arbuscular mycorrhiza (AM) fungal symbionts (Turner et al. 2013). According to Pirozynski and Malloch (1975), the origin of land plants is a matter of mycotrophy (Greek: mykós, "fungus" and τροφή trophe = "nutrition"), a fundamental phase in the movement of symbiotic plants onto land since at least 400 million years ago (Singh et al. 2011). Endophytic fungi that increase host competitive abilities, by increasing germination success, resistance to drought and water stress and resistance to seed predators, encompass a large number of plant species (Rodríguez et al. 2009). Though limited in number, the studies available suggest that endophytic fungi are prevalent in various habitats and can colonise a substantial proportion of the species: > 500 plant species, > 300 genera and > 100 families along with North Pole-South Pole latitudinal diversity gradient (Mandyam and Jumpponen 2005; Jumpponen and Trappe 1998). Canadian field and inoculation experiments with different plant hosts and endosymbionts showed that plant responses were specific to the individual hosts, their plant organs, and fungi involved (Currah and Tsuneda 1993; Fernando and Currah 1996; Vujanovic et al. 2000; Vujanovic and Brisson 2002; Vujanovic et al. 2007; Corredor et al. 2012; Vujanovic et al. 2012; Ellouze et al. 2013). This symbiotic relationship between root and fungi shaped the evolution of plant tolerance and nutrient acquisition, thus maximizing plant's productivity in terrestrial ecosystems. Nowadays, root-infecting *Rhizobium* bacteria and AM fungi are widely used in agriculture practice to facilitate the uptake of nutrients in plants, especially nitrogen and phosphorus. However, this paper aims to

provide new insights into the mutualism between seed and endophytic fungi, a less explored yet vital relationship in improving plant tolerance to abiotic stress. Given that healthy plants depend on healthy seeds, it directs attention to mycovitality, a seed-endophytic microbe relationship. Mycovitality, also known as a myco-mediated improvement in seed vigour and germination parameters (Vujanovic and Vujanovic 2007; Hubbard et al. 2012; Banerjee et al. 2014; Vujanovic et al. 2016), is a key regulatory mechanism in germinating seeds and seedlings driven by fungal endophytes. A critical first step in enhancing plant's developmental events and early resilience in response to environmental stressors affecting plant growth and productivity or yield (e.g. drought combined with heat), mycovitality is seen as the cornerstone of plant prenatal care.

The seed endosymbiosis: an underexplored reality

Despite efforts to improve crop yield through breeding, soil management, or fertilization (Asseng et al. 2014; Habash et al. 2009; Saint Pierre et al. 2008), climate change continues to affect food security (Wheeler and von Braun 2013). Thus, a climate-smart food system, first proposed by Wheeler and von Braun (2013), must be developed. Wheat, the primary food source for the human population (FAO 2015), has been hit the most by the scourge of heat and drought over the last decades (Lobell et al. 2011). The U.S. Department of Agriculture announced a drought-related farming alert in 2012, mobilizing researchers to create crop varieties that withstand extended dry periods without losing yield (Waltz 2014; Thomas 2015). So far, conventional breeding failed to recognize what might be gained by considering the beneficial effects of endophytes on desired traits of elite crop genotypes (Arnholdt-Schmitt et al. 2014). Though routine ways of ensuring crop resistance and performance are insufficient, innovative research is scarce, particularly when it comes to looking at the seed and how endophytes have been introduced into seeds (Mahmood et al. 2016). Although there is a great wealth of information available on Class I *clavicipitaceous* endophytes such as *Epichloë/Neotyphodium* species in wild-grasses (Rodriguez et al. 2009; Schardl et al. 2004), they are not in the scope of this review paper as producers of toxic alkaloids causing "chock disease" on grass inflorescence, reduced seed germination under water stress, and dwarfed phenotype in host plants at least during one of the endophytic growth stages (Baskin and Baskin 2014; Cheplick and Faeth 2009; Gudel et al. 2006; Simpson et al. 2014). Contrary to *clavicipitaceous* endophytes, we know little about the seed germination-promoting fungal endophytes on staple crops including wheat. Indeed, wheat genetics, breeding, and management still account for >90% of peer-reviewed publications (PRPs), while the association of microbial endophytes with wheat seeds represents ~0.02% of PRPs over the past decade or so (Fig. 1A). Similar results were obtained for the seed endosymbiosis in other plants, used in agriculture (e.g. maize/corn ~0.02, rice ~0.02, pulses ~0.002 and canola~0.002) and forestry (spruce ~0.001 and pine ~0.004) systems, based on scientific articles presented between 2000 and 2015 by the Web of Science (Thomson Reuters). This is striking considering that the seed is a key generative organ in regeneration, evolution, and dispersal of flowering plants (Baskin and Baskin 2014). Seed germination is also a vital phase of seedling recruitment and adaptation in natural or agricultural, as well as in undisturbed or disturbed soils (Southworth 2012). Thus, seed vigour is primordial for crop resilience and yield: humanity's best single food source. As focus is directed towards the seed, so should it be to its microbiome, notably its beneficial endophytic fungal partners.

Figure 1: 1A and 1B.**The mycodependency spectrum: from mycotrophy to mycovitality**

To understand the microbiome of the seed and germinant, one must understand the microbiome of the plant, particularly fungal endophytes (Vujanovic 2000; Selses and Rousset 2011). Endophytic fungal symbionts have unique features and ecological significance, as they form distinct mutualistic relationships with plants compared to arbuscular mycorrhiza fungal symbionts. Our understanding of the taxonomy and evolution of fungal endophytes is gradually progressing— specific terminology describing their symbiotic organs and beneficial functions is emerging (Fig. 2), though consensus towards the most comprehensive classification is pending.

Figure 2

The endophyte-plant cell interaction begins with chemical signals (van't Padje 2016), using volatile compounds for cell-to-cell communication (Ariebe et al. 2016; Banerjee et al. 2014), and endosphere cell-to-cell contact and colonization (Vujanovic et al. 2016). Abdellatif et al. (2009) found that fungal endophytes form unique, signature organs upon interaction with plant cells. They demonstrated that the existence and persistence of these organs, referred to as fungal endospheric hyphal compartmentalization (Fig. 1B), only manifests in healthy plants. They also identified shifts in the morphology and formation of inter- and intra-cellular symbiotic organs as a result of dynamic input from the host plant, which is intrinsically tied to plant's health status. Beneficial effects of endophytes on plants through increased nutrient uptake, known as mycotrophy (Pirozynski and Malloch 1975), are undeniable. The Basidiomycetous fungus *Piriformospora indica* confers drought tolerance to *Arabidopsis* and barley (*Hordeum vulgare* L.). Interestingly, it also does so during the seedling growth stages (Alikhani et al. 2013; Sherameti et al. 2008). Mycovitality is a symbiotic, seed-fungal endophyte relationship (Vujanovic and Vujanovic 2007) capable of enhancing seed vigor (Vujanovic et al. 2000), energy of germination and hydrothermal time of germination by better seedling water-use efficiency, in addition to an improved resilience to environmental stresses, such as drought and heat (Hubbard et al. 2012; Hubbard 2014a). Mycovitalism is unique to symbiotic endophytes (Abdellatif et al. 2009). Able to colonise multiple plant organs including seeds (seed-endosymbiosis), these endosymbiotic fungi belong to the multicellular Ascomycota and Basidiomycota, and form distinct symbiotic structures and organs (Abdellatif et al. 2009; Vujanovic et al. 2000) from those of the unicellular AMFs belonging to Glomeromycota (Merckx 2013; Parniske 2008). Contrary to AMF, endophytes demonstrate a tremendous diversity in symbiotic organs through cellular compartmentalization (Fig. 1B); one may stipulate that this plasticity translates into their capacity to colonize and interact with a broader range of plant species, as well as other eukaryotic hosts (Fig. 3) including insects and photosynthetic green algae or cyanobacteria in forming lichens. In fact, an extreme example is *Cypripedium* (Lady slippers) terrestrial orchids, which seeds obligately depend on mutualistic endophytic fungi for

germination (Vujanovic et al. 2000). By moderating the physiological stress response via mycovitality (Vujanovic and Vujanovic, 2007; Hubbard et al. 2012), the endophytic fungi improve wheat seed germination stages under drought and heat, yielding wheat plants with significantly improved agricultural traits (Hubbard et al. 2014a).

Figure 3

Furthermore, endophytic fungal symbiotes undergo mixed horizontal and vertical transmission, also named an “imperfect transmission” in Class I clavicipitaceous endophytic fungi-grass symbioses (Cheplick and Faeth 2009) when the symbiont is not transmitted to all offspring (Afkhani and Rudgers 2008), and show a biphasic lifestyle (Gundel et al. 2010; Zuccaro et al. 2011). The AMFs are considered to be asexual with horizontal transmission (Pawlowska and Taylor 2004). In the spectrum of plant’s mycodependence, mycovitality occurs at the level of the semosphere and spermosphere, as opposed to mycotrophy which occurs at the level of rhizosphere (Fig. 4) and regulates nutritional status of the phyllosphere (via enhanced nutrient availability for the host).

Figure 4

Discussion

Mycovitality: improving dormancy release and germination

Climate change, drought or excessive heat injure the seedling and decrease seedling emergence, prolonging seed dormancy (Hampton et al. 2013). To a certain extent, all plants possess seed dormancy— a stage of undetermined duration during which a plant or seed genotype depends on internal and/or external signals to begin or halt germination. From a plant ecology standpoint, dormancy, a mechanism blocking germination, has evolved differently across species and crops, through species’ adaptation to the prevailing environment (Finch-Savage and Leubner-Metzger 2006). Germination timing is an important adaptive early-life history trait, which determines plants’ fitness to grow in natural and agricultural ecosystems (Gao and Ayele 2014). Therefore, the challenge lies in breaking seed dormancy to ensure enhanced germination and post-germination (seedlings) phenophases (Graeber et al. 2014; Donohue et al. 2010).

The molecular and genomic diversity of plants, along with variation of environmental conditions, have led to the existence of several harmonized mechanisms controlling dormancy. Traditionally, seed dormancy was a measure of the seed’s innate mechanism of germination, regulated by naturally occurring chemical signals such as abscisic acid (ABA), as well as ethylene and gibberellic acid (GA) phytohormones. In addition, traditional or non-omics *in vitro*, chemical and physical approaches (Baskin and Baskin 2014) have contributed in advancing our understanding of dormancy (Graeber et al. 2014). However, genome wide-association mapping (Magwa et al. 2016) and multi-omics resources (North et al. 2010) have expanded our knowledge of seed dormancy. It is now seen as the result of diverse seed genetics, multiple molecular mechanisms, which themselves are associated with

several physiological pathways, epigenetic regulations, targeted oxidative modifications of seed mRNAs and proteins, redox regulation of seed protein thiols, and modulation of translational activities (Donohue et al. 2010; Finkelstein et al. 2008). Past knowledge had also emphasised on temperature and water activity regulators of dormancy and germination. However, given the complexity of natural systems, our current understanding is that dormancy is regulated by a combination of endogenous and exogenous abiotic (drought and heat, salinity, relative humidity, nutrients etc.) and biotic (volatile organic compounds, amino acids, hormones, enzymes, phenolics etc.) signals (Gill et al. 2016; Ortíz-Castro, 2009; Zhu 2016), with synergistic and/or competing effects (Oldroyd 2013).

Recent results on the regulation of seed dormancy show that an important biotic seed germination signal lies in mycovitality and bactovitality which refer to a form of fungal and bacterial endosymbiosis, respectively, using different endophytic strains with a variety of activities (Vujanovic and Germida 2013). The endosymbiotic partners are involved in seed biostratification and biopriming— through hormonal pathways regulation (Vujanovic et al. 2016; Mahmood et al. 2016). Biostratification is the exposure of seeds to beneficial microbial (fungal and/or bacterial) partners which creates conditions conducive to break the dormancy and enhance germination, whereas biopriming involves combined physical (hydration-dehydration) and microbial pretreatments to activate seed metabolism. The fungal inoculants were involved in transcriptional regulation (Chacon et al. 2007; Gill et al. 2016; Sarkar et al. 2014; Zuccaro et al. 2011) as well as epigenetic modification of chromatin structure and methylation; and appear capable of shaping the profile of transposon/retrotransposon elements, which mediate cell function and phenotypic variation in plants (Panke-Buisse et al. 2014). Hubbard et al. (2014b) found that the abundance of CACTA, Gypsy, Copia and cytochrome p450 transposable elements coincides with the altered DNA methylation in drought-stressed wheat seedlings. They also favor germination by scavenging reactive oxygen species (ROS) mediating stress in seeds. In addition, fungal endophytes are producers of antioxidants (Cui et al. 2015; Hamilton et al. 2012; Strobel 2002), resulting in down-regulation of antioxidant genes in germinating seeds under drought conditions (Radhakrishnan et al. 2013; Singh et al. 2011). The synchrony of breaking dormancy and increasing early stress resistance-induced by endophytes is possible for variety of cereal (wheat or barley), pulse (pea, lentil or chickpea), flax, and canola genotypes by modulating gene expression of hormonal *ent-kaurenoic* (KAO) regulator, repression of shoot growth (RSG), ABA, GA, 14-3-3 genes and nitric oxide (NO) molecules, and/or of stress resistance superoxide dismutase (SOD), manganese SOD (MnSOD), proline (Pro) and MYB genes (Vujanovic and Germida, 2013). Hence, endophytes control hydrothermal time (HTT) and stress resilience rendering seed germination (viability, vigour, energy of germination, uniformity and rate of germination) a predictable event to the point that plant-endophyte symbiosis has proved particularly efficient when subjected to unfavorable moisture and temperature parameters (Banerjee et al. 2014, Hubbard et al. 2012, Vujanovic et al. 2016). In essence, a conducive environment for offspring fitness cannot be reduced to the assessment of the plant genome, geographical location, physicochemical or nutritional factors of the spermosphere. Understanding the role of the spermosphere's microbiome, particularly that of the endophytic fungus (a biological factor), in reprogramming plant germination (Vujanovic et al. 2016), by increasing vigour—stress tolerance and nutrient uptake—, and by the accumulating net germination signals (Yu et al. 2014) is critical. This is especially true in the context of extreme environments, foreboded by climate change.

Space-grown, wheat seedlings harboring endophytes aboard a NASA (National Aeronautics and Space Administration) shuttle are a remarkable example of the extent to which an extreme environment can become amenable by the seed-endophyte symbiosis (Bishop et al. 1997).

The benefit of mycovitalism: plant prenatal care

Thus far, mycovitality or seed-endosymbiosis (Vujanovic and Vujanovic 2007) has been established as a player in the biological stratification, controlling the breakage of seed dormancy and alleviating environmental stress induced by climate change. Hubbard et al. (2014a) demonstrated that mycovitality improves both wheat's seed germination (Baskin and Baskin 2014), and overall host productivity and resilience against drought and heat. Further studies have shown that these advantages are transmitted to the offspring, thus potentially bringing about a plant epigenetic modification (Hubbard 2014b). In fact, endophytic fungi improve plant's yield and response to stress directly—by modulation of the plant's acclimatization, adaptation, and resistance capacities; as well as indirectly—by regulating global biogeochemical cycles (Rodriguez 2008; Smirnov 2014; Rai 2014; Rousk and Bengtson 2014) as pioneer decomposers of plant litter (Yang et al. 2016). These findings have crucial and far-reaching implications. Plants' (or crops') survival and selection is no longer just a matter of hardy genetics. Understanding all the richness that the seed microbiome brings to promotion of plant growth becomes an important stepping stone in our comprehension of plant development as the microbiome resides on the interface between crop health/ productivity, and the associated environment. Similarly to medical prenatal care, seeds should be cared for by ensuring that the best-matching microbiome is present in the environment where the seeds will be sown and grow. Like a healthy birth and growth of a baby, seeds are at the basis of a strong plant (Lugtenberg 2015; Lobell 2012; Aroca 2013; Lucero 2014). In agriculture and horticulture production systems, seeds may be seen as “agri-babies” whose proper development (fitness and resistance) and outcome (yield and sustainability) depend on the care delivered by its prenatal microbiome composed of fungal (notably endophytes and mycorrhizae), and other beneficial partners such as endophytic bacteria (Truyens et al. 2015), which ensure bactovitality. Consequently, the new generation of bioproducts should include endosymbiotic plant bioprotectors, resistance enhancers, and growth promoters, taking advantage of a plant's mycodependency over its entire lifecycle, as a *continuum* from mycovitality to mycotrophy. This implies that elite crop varieties could greatly profit from enhanced microbial activities and microbiome characteristics. In other words, further research should aim at advancing genomics-assisted breeding using beneficial microbiomes for crop improvement.

Conclusions

Climate change is ongoing. Crop plants must be improved to use inputs from the immediate environment, with much greater efficiency and less water demand. Despite their potential for crop resilience, improved crop yield and sustainable agriculture, plant endosymbiotic partners remain underexplored (Varma et

al. 2012; Kivlin et al. 2013; Lakshmanan et al. 2014; Lebeis 2014; Berg 2014b; Mendes and Raaijmakers 2015). Therefore, modern plant sciences should pay more attention to the microbiome's dynamic equilibrium with plant systems throughout annual reproductive→growth→reproductive phenophases. Seed is the alpha and omega in the life cycle of all plants, a vital phase for plant resilience and health with biostratification (Vujanovic et al. 2016) and biopriming (Mahmood et al. 2016) regulatory mechanisms, which may encourage laboratories to perform new screening and enrichment programs for plant prenatal care. The programs may consider employing comparative analyses of seed vs. root-associated endophytic microbiomes in variety of host genotypes and ecosystems. Screening and testing of microbial endophytic isolates for traits participating in plant growth promotion and health over the entire lifecycle may depict a *continuum* of the symbiosis benefits. In this regard, to account for modulations induced by environmental parameters, the natural evolution of this beneficial system needs to be studied in large-scale field experiment during multiple years and over multiple sites to further evaluate the contribution of the endosymbiosis to the plant-host genotype. As such, prenatal care seems to be a promising concept to advance endosymbiosis-based plant technology by exploring further opportunities for integrating mycovitality and mycotrophy, thus maximizing performance of plants and crops under changing environmental conditions.

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Author contribution statement Vladimir Vujanovic contributed to the generation of vocabulary related to mycovitality and plant prenatal care concepts. Both authors participated in the writing of this review.

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Figure. 2. Progress in the terminology describing plant-fungus symbiosis and major mechanisms by which various taxonomical groups of fungi improve host performance

Figure. 3. Plant mycodependency for total plant care: the role of mycovitality and mycotrophy

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Figure. 4. The stratified microbiome: the *semosphere* and *spermosphere* define *mycovitality*; while the *rhizosphere* and the *phyllosphere* define *mycotrophy*, along the continuum of endospheric (intimate interaction) zones and distinct aerial (light) and soil (dark) environmental niches.