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MARSCHNER REVIEW

The seed microbiome: Origins, interactions, and impacts

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Abstract
Background The development and dispersal of seeds as well as their transition to seedlings represent perhaps the most critical stages of a plant's life cycle. The endophytic and epiphytic microbial interactions that take place in, on, and around seeds during these stages of the plant's life cycle may have profound impacts on plant ecology, health, and productivity. While our understanding of the seed microbiota has lagged far behind that of the rhizosphere and phyllosphere, many advances are now being made.
Scope This review explores the microbial associations with seeds through various stages of the plant life cycle, beginning with the earliest stages of seed development on the parent plant and continuing through the development and establishment of seedlings in soil. This review represents a broad synthesis of the ecological and agricultural literature focused on seed-microbe interactions as a means of better understanding how these interactions may ultimately influence plant ecology, health, and productivity in both natural and agricultural systems. Our current understanding of seed-microbe associations will be discussed, with an emphasis on recent findings that specifically highlight the emerging contemporary understanding of how seed-microbe associations may ultimately impact plant health and productivity.
Conclusions The diversity and dynamics of seed microbiomes represent the culmination of complex interactions with microbes throughout the plant life cycle. The richness and dynamics of seed microbiomes is revealing exciting new opportunities for research into plant-microbe interactions. Often neglected in plant microbiome studies, the renaissance of inquiry into seed microbiomes is offering exciting new insights into how the diversity and dynamics of the seed microbiome with plant and soil microbiomes as well as the microbiomes of dispersers and pollinators. It is clear that the interactions taking place in and around seeds indeed have significant impacts on plant health and productivity in both agricultural and natural ecosystems.

Keywords Seed microbiota · Seed-borne · Seed endophytes · Seed epiphytes · Seed bank · Seed germination · Seedling recruitment · Spermosphere

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Introduction

Seeds represent one of the most crucial stages of a plant's life history. In agricultural systems, seeds serve to initiate a new crop cycle, are most commonly produced commercially, heavily handled, processed, and uniformly planted across large geographic areas. However, in natural ecosystems, seeds not only serve to initiate the life cycle and reproduce the species, but also to facilitate dispersal, adaptation to, and persistence in

new environments (Fenner and Thompson 2005). Germinating seeds and seedlings are especially vulnerable to mortality from drought, granivores, and fungal seed-borne and soil pathogens (Bever et al. 2015). Even following germination, seedlings continue to face threats to their establishment from pathogens and herbivores, but also to resource limitation and deficiencies in overall habitat suitability, making the seed-to-seedling transition in both natural and agricultural systems one of the most important bottlenecks in a plant's life cycle (Leck et al. 2008). Therefore, the nature and impact of microbial interactions that take place before and during these vulnerable stages in plant development are critical in setting the trajectories for plant population and community dynamics in natural systems and crop success or failure in agricultural systems.

Microbes interact with seeds at all stages of plant development. These interactions may be casual or intimate, yet they all contribute to varying degrees to an evolving seed microbiome that may carry over to other developmental stages (Hardoim et al. 2015). This should not be surprising given the ubiquity of microbes and the many desirable microbial habitats that plants provide (Table 1). All of these microbial habitats that contribute to the plant microbiome may have significant connections to seed microbiome development.

A major motivation for exploring the seed microbiomes is to better understand how microbes acquired by seeds during their development and germination may influence overall plant microbiome structure and function, and also to better understand the impact of these microbial associations on plant function and ecology. Yet, despite the rapidly increasing emphasis on microbiome studies, seeds are rarely mentioned (e.g., (Berg et al. 2015; Lebeis 2015; Rout 2014; Schlaeppi and Bulgarelli 2015; Turner et al. 2013; van der Heijden and Hartmann 2016)), (with one notable exception (Mitter et al. 2016)), as a critical part of the plant microbiome and a potentially important determinant for plant microbiome assembly, structure, and function.

Microbes associated with seeds

Our understanding of the microorganisms residing in and on seeds has grown tremendously in recent years, with many excellent contemporary reviews of the bacterial (e.g., (Malfanova et al. 2013; Truyens et al. 2015)), fungal (e.g., (Porras-Alfaro and Bayman 2011; Rodriguez et al. 2009)), and oomycete (e.g., (Thines 2014)) microbiomes associated with seeds and other plant organs. Much of what we currently understand about seed microbiomes, particularly the endophytic microbiome, comes from a number of culture based studies across a range of mostly cultivated plant species (see (Truyens et al. 2015) for example). However, with new advances in sequencing and microscopy technologies, a deeper assessment of seed microbes has been possible, not only complementing but greatly expanding our catalog of microbial species in and on seeds. Yet, our understanding of their origins, routes of colonization, ecology, especially in natural ecosystems, and their impacts on plant growth and development are not as well developed.

In discussing seed microbiomes, it is important to distinguish between the endophytic microbiota (i.e., those microbial species that reside in internal seed tissues and vertically-transmitted to progeny seedlings) and epiphytic microbiota (i.e., those microbial species that colonize seed surfaces and may or may not become internalized within seed tissues and transmitted either vertically or horizontally). Although this is a rather artificial division, in part because endophytes can become epiphytes and vice versa, the reasoning for distinguishing them is that the endophytic microbiota may often originate from different seed tissues or environmental sources than those of the epiphytic microbiota. For example, microbes associated with the embryo and endosperm are more likely to be transmitted vertically than those associated with the seed coat, which are likely to be much more diverse and transmitted horizontally (Barret et al. 2016).

Endophytic microbes

The emerging view of the endophytic seed microbiota is that it is a species-rich consortium of bacteria and fungi (Hodgson et al. 2014; Malfanova et al. 2013; Rodriguez et al. 2009; Truyens et al. 2015). Although seeds are also known to contain many endophytic viruses (Sastry 2013) and oomycetes (Thines 2014), these will not be covered in this review. For many years, the endophytic seed microbiota has been viewed as being composed of taxa that are strict commensals or mutualists (Hume et al. 2016; Malfanova et al. 2013; Muller et al. 2016; Porras-Alfaro and Bayman 2011; Santoyo et al. 2016; Truyens et al. 2015), despite our recognition of endophytic viral, bacterial, and fungal seed-borne pathogens as early as the 1940s (Munkvold 2009). The endophytic

Table 1 Microbial habitats associated with different plant organs and tissues

Habitat	Definition	Original source
Aerosphere	The surface of the aerial parts of plants (synonymous with the phytosphere)	(Hollis 1952)
Anthosphere	The zone on and in flowers. The petal surface has been referred to as the anthoplane.	(van den Ende and Linskens 1974)
Carposphere	The internal portions of fruits	(Heywood 1969)
Calusphere	The zone within and around buds	(van den Ende and Linskens 1974)
Caulosphere	The zone within the stems of herbaceous plants and the bark of woody plants.	(Garner 1967)
Cormosphere	The entire plant surface and its immediate environment; region of exchange between biotic and abiotic components; also synonymous with the aerosphere and phytosphere.	(van den Ende and Linskens 1974)
Dermosphere	Tree bark; commonly refers to bark surface. Not to be confused with mammalian epidermal stem cell precursors that are also referred to as dermospheres.	(Lambais et al. 2014)
Endosphere	Internal tissues of the plant. Originated from the term "endorhizosphere", which was meant to represent the region inside roots. As this was semantically incorrect, a proposal to eliminate the term and replace it with such terms as endoroot, endorhiza, hypoepidermis, or hyporhizoplane was later put forth. However, the term endosphere was used earlier to encompass concepts embodied by the combined terms "endorhizosphere" and "endophyllosphere".	(Kloepper et al. 1992; Mohandas 1988; Partriquin and Dobereiner 1978)
Endospermosphere	The internal tissues of the seed. The same semantic issues exist as with the term "endorhizosphere". However, this term is not widely used and not typically used synonymously with endosphere.	(Normander and Prosser 2000)
Fructosphere	The surface and exocarp of a fruit	(definitive source unknown)
Geocarposphere	The zone of soil around underground fruit (e.g. peanuts).	(Griffin 1972)
Laimosphere	The zone of soil around underground portions of hypocotyls, epicotyls, stems, stolons, corms, bulbs, and rhizomes.	(Magyaros and Hancock 1972)
Mycorrhizosphere	The zone of soils surrounding mycorrhizal roots and hyphae of the directly connected mycorrhizal fungi	(Rambelli 1970)
Phyllosphere	The region on and around a leaf. The term phylloplane is often used to designate the surface of leaves.	(Last 1955; Ruinen 1953)
Phytosphere	The living plant cover of the earth; the surface of the aerial parts of plants in their entirety.	(Tikhomirov 1960)
Rhizosphere	The region of soil adjacent to and surrounding the root. The root surface is known as the rhizoplane.	(Hiltner 1904)
Spermosphere	The short-lived, rapidly changing zone of soil surrounding a germinating seed. The seed surface is referred to as the spermoplane.	(Slykhuis 1947; Verona 1958)

lifestyle does not necessarily imply ecology or a functional characterization of plant responses to the presence of the microbe (Schulz and Boyle 2005) and we now clearly recognize that mutualism and pathogenicity are not inherent microbial properties and are only expressed within certain contexts (Alvarez-Loayza et al. 2011; Eaton et al. 2011; Fesel and Zuccaro 2016; Malcolm et al. 2013). I believe this contemporary view better advances our understanding of the ecology of plant-microbe interactions in general but of seed-microbe interactions specifically. Therefore, for the purposes of this review, I will adopt this latter view.

Bacterial microbiota Currently, our knowledge of the bacteria associated with seeds is perhaps the most extensive. Across a wide range of plant taxa, seed-associated bacteria are found largely within the bacterial phyla Proteobacteria, Actinobacteria, Firmicutes, and Bacteroidetes (Barret et al. 2015; Bulgarelli et al. 2013; Johnston-Monje et al. 2016; Liu et al. 2012a). This can be explained, in part, by the dominance of these phyla in soil (Fierer et al. 2012) and aquatic (Shafi et al. 2017) ecosystems all over the globe, making members of these phyla the most likely taxa to encounter seeds during development and beyond. Yet, selective

recruitment from these environmental sources is evident since individual bacterial species vary from plant species to species (Links et al. 2014), genotype to genotype (Barret et al. 2015; Johnston-Monje and Raizada 2011), different stages of seed development (Hardoim et al. 2012; Liu et al. 2013), different geographical locations (Johnston-Monje and Raizada 2013; Klaedtke et al. 2016), and even in the presence of other phytopathogenic microbes (Rezki et al. 2016). Despite this, bacterial seed endophytes may be highly conserved in some plant species (Johnston-Monje and Raizada 2011; Links et al. 2014) and potentially providing the bulk of the species pool from which the seedling microbiome is recruited. Consistent with this is the observation that the seed endophytic microbiota is often distinct from the microbiota associated with the soil on which plants are grown (van Overbeek et al. 2011), suggesting the possibility that the seed microbiota may be recruited largely from the mother plant.

Currently, our knowledge about seed microbiome assembly remains incomplete, as some studies have indicated that bacteria may be recruited from the soils on which plants are grown (Johnston-Monje et al. 2016; Johnston-Monje et al. 2014), while others have indicated that neither local site conditions nor host genotypes fully explain the assembly of the bacterial seed microbiota (Klaedtke et al. 2016). Clearly, the connections between the seed and soil microbiomes is not yet fully understood. For example, some endophytes that colonize the endosphere of adult plants from the rhizosphere (Compant et al. 2010) may ultimately end up in flowers (Compant et al. 2008), thus contributing to the endophytic seed microbiome (Compant et al. 2011). In contrast, other bacterial seed endophytes may colonize seedlings systemically and exit the roots into the rhizosphere (Johnston-Monje and Raizada 2011; Johnston-Monje and Raizada 2013), linking seed-associated microbes across all plant organs with the soil environment. It is promising to see that this line of inquiry is being increasingly pursued making it more likely that these questions will be more clearly resolved as more plant-microbe systems are investigated.

Fungal microbiota Among the most well-studied fungal seed endophytes are species of *Epichlöe* and their asexual forms *Neotyphodium*, which have affinities for members of the Poaceae and provide many plant benefits including protection from pathogen infection (Perez et al. 2016; Saikkonen et al. 2016). Despite the focus on this group of fungi, there are many other ascomycete and basidiomycete fungal and yeast species associated with seeds (Links et al. 2014; Marquez et al. 2012; Rodriguez et al. 2009). Barrett et al. (Barret et al. 2015) demonstrated that seeds of plants within the Brassicaceae were dominated by ascomycetes in the classes Dothideomycetes, Eurotiomycetes, Leotiomycetes, and Sordariomycetes, as well as the basidiomycete class Tremellomycetes (e.g., *Cryptococcus* spp.). The Dothideomycetes are the largest known class of filamentous ascomycetes, which contains genera such as *Alternaria, Aureobasidium, Cladosporium, Epicoccum, Phaeosphaeria, Phoma, Pyrenophora,* and *Stagonospora*. The other ascomycete classes contain the commonly described endophytic genera *Chaetomium, Fusarium* (and associated teliomorphs)*, Microdochium, Stemphylium,* and *Xylaria*. In addition to being present in seeds, many of these fungal genera are commonly associated with soils where they are frequently transmitted horizontally to plants. In fact, recent studies have demonstrated that local site conditions and not host genotype may have a strong influence on the assembly of fungal seed microbiomes (Klaedtke et al. 2016). Although in many cases the physical location of fungi in the seed is not clear, they may largely reside on and in the seed coat (Rodriguez et al. 2009) where they may be both vertically and horizontally transmitted to subsequent generations.

Epiphytic microbes

Until recently, the epiphytic seed microbiome has rarely been considered explicitly in studies of the seed microbiome (except for (Cottyn et al. 2009; Hardoim et al. 2012; Kaga et al. 2009; Mano et al. 2006; Midha et al. 2016)), making it unclear whether seed microbes amplified during germination that may transfer to seedlings arose from the epiphytic or endophytic microbiomes (Lopez-Velasco et al. 2013). In a study to explicitly examine the nature of the epiphytic bacterial and fungal communities associated with several *Triticum* and *Brassica* species, Links et al. (Links et al. 2014) observed that species within each plant genus harbored unique endophytic bacterial communities, which, as in previous studies, were dominated by members of the Proteobacteria (e.g., species of *Pantoea*, *Pseudomonas*, *Massilia*, *Xanthomonas*, and *Telluria*). However, epiphytic bacterial communities were similar and large ($\sim 10^6$–10^8 bacterial genomes per g of seeds). In contrast,

the epiphytic fungal communities of both plant genera were similar and dominated by species of well-known plant pathogens in the genera *Fusarium*, *Phoma, Pyrenophora, Alternaria* and *Leptosphaeria*, suggesting that the epiphytic seed microbiota may not be as insignificant as perhaps once thought and the species filtering observed with endophytic microbes may also occur with epiphytic microbes. Again, this should be another exciting avenue of research in the future.

Population sizes of seed-associated microbes

Determining microbial population size on and in seeds is inherently problematic since population size estimates are nearly always based on selective plate counts where only a subset of the total population is assessed. In studies of the cultivable bacterial endophytic populations, estimates may range from 10^1 to 10^2 CFU/g seed (Compant et al. 2011; Ferreira et al. 2008; Rosenblueth et al. 2012) to as high as 10^6 to 10^8 CFU/g seed (Graner et al. 2003; Hameed et al. 2015; Links et al. 2014; Truyens et al. 2016; Truyens et al. 2015). Epiphytic bacterial populations have rarely been assessed but may range from 10^4 CFU/g seed (Cottyn et al. 2009; Silva et al. Chimwamurombe et al., 2016) up to 10^6 to 10^8 CFU/g seed (Mano et al. 2006). Using qPCR to quantify bacterial populations associated with seeds point to similar broad population size ranges (Ofek et al. 2011). To my knowledge, there are no clear estimates of fungal population sizes on or in seeds and although plant species and genotype, soil properties, and microbial strain may influence ultimate population levels and dynamics, this has not been systematically investigated.

A framework for understanding the assembly and structure of seed microbiomes

A few years ago, Aleklett and Hart (Aleklett and Hart 2013) made a case for the potential legacy effects of other stages of the plant's life cycle on the structure of the root microbiome. They utilized the plant life cycle to illustrate the potential microbial contributions to root microbiome assembly and the ecological forces that shape the rhizosphere community. I believe this is an equally useful framework for better understanding the assembly and structure of seed microbiomes and their potential impacts. Figure 1 illustrates the plant life cycle, emphasizing the important aspects of seed ecology. While our understanding of seed-microbe associations is more complete at some stages than others, this framework provides a means of generating new hypotheses concerning seed microbiome assembly, dynamics and function. It is likely that the forces that facilitate the assembly and structure of seed microbiomes will be quite complex, with microbes recruited not only from the soil microbiome (Hardoim et al. 2012; Klaedtke et al. 2016), but also dispersal agents (e.g., (Bangert et al. 1988; Czeczuga et al. 2009; Gandolfi et al. 2013), pollinator, and floral microbiomes, some members of which will ultimately be recruited into the developing seeds, multiply in the spermosphere during seed germination, and subsequently colonize seedlings (Darrasse et al. 2010). Microbes acquired along the way may all potentially contribute to the microbiome that eventually proliferates during seed germination and transfers to seedling and the various organs of mature plants. In the following sections, I'll explore the development of the seed microbiome through the plant's life cycle and how seeds may be influenced by these microbial associations along the way.

The anthosphere: An important habitat for seed-associated microbes

The importance of flowers and flower traits to angiosperm fitness is undeniable. Not only do flowers serve as the sites for seed development and dispersal, but they are also known to contain a very rich, diverse, and dynamic microbiome (Aleklett et al. 2014). This is due, in part, to their location on the plant, which facilitates microbial dispersal with wind, rain, seeds, and pollinators (McArt et al. 2014). Additionally, the morphology of most flowers serves as a protective environment for the developing seed, which concomitantly serves as a protected microbial habitat rich in carbon and nitrogen compounds for microbial growth (Alvarez-Perez et al. 2012; Fridman et al. 2012).

Flower microbiomes appear to be quite distinct from the microbiomes of other plant organs, especially those organs in closer contact with soil (Ottesen et al. 2013). Because of this rather unique habitat, the flower microbiome may contribute in unique ways to the seed microbiome during and after seed development. Although the floral microbiota is composed of many commensals and mutualists (Aleklett et al. 2014), they are

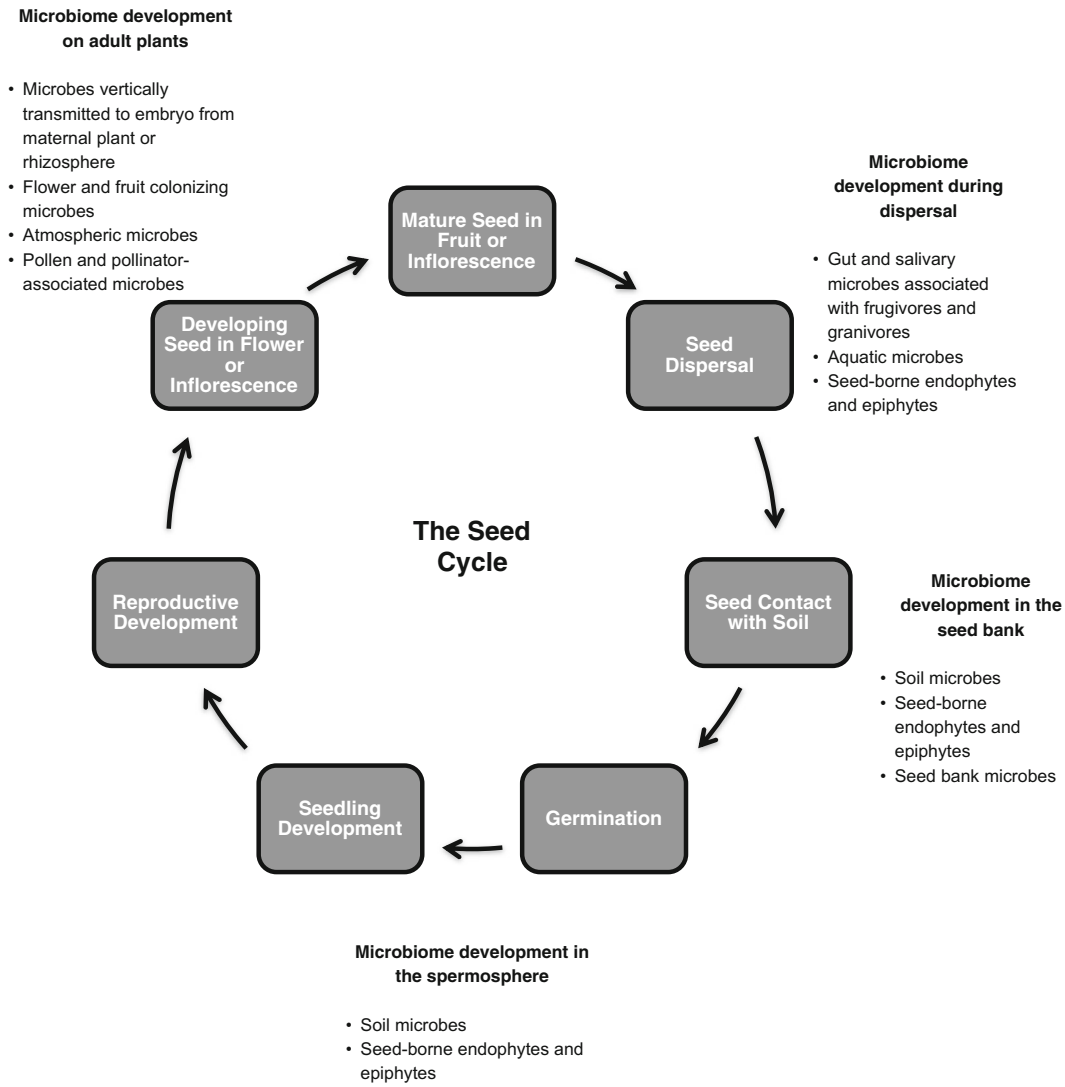

Fig. 1 Seed-to-seed development and opportunities for the acquisition of microbes by seeds

also comprised of many pathogenic species (Ngugi and Scherm 2006). In fact, much of our knowledge of floral microbiomes comes from studies of pathogenic species because of their readily-detectable impacts on flower and seed phenotypes (Ngugi and Scherm 2006). It is particularly clear from studies with pathogenic species that microbial interactions that take place in the flower may have significant impacts on longer-term seedling establishment (Darrasse et al. 2010; Dutta et al. 2014a).

Flower microbes

Although there are many studies of the culturable bacteria and fungi associated with flowers, estimates of the relative abundance and diversity of these microbes appear to be biased toward those species that are most easily cultivated. Other factors may also contribute to this bias, including biogeographic patterns of microbial species pools, stages of flower development sampled, plant species or genotype evaluated, types of pollinators, and surrounding vegetation. These confound comparisons among different studies. However, some general patterns are evident.

Species of bacteria within the Proteobacteria (particularly species of *Pseudomonas*) appear to dominate the floral microbiota of many different plant species (Compant et al. 2011; Junker et al. 2011; Ottesen et al. 2013; Zarraonaindia et al. 2015), whether detected by

cultivation-dependent or cultivation-independent means. Although a traditional view has been that the flower microbiota is rather non-diverse (e.g., (Pusey et al. 2009)), it is becoming clear that this is not the case. In one of the more pivotal and comprehensive studies of flower microbiomes, Shade et al. (Shade et al. 2013) assessed the bacterial diversity in whole apple flowers, beginning at the flower bud stages through flower senescence. They observed a large diversity of bacteria, dominated not only by Proteobacteria, but also by bacteria in the phyla Deinococcus-Thermus, TM7, Bacteroidetes, and Firmicutes. Species within these phyla display clear successional patterns through flower development. Many of the most dominant taxa were identified primarily as members of the Deinococcus-Thermus and TM7 phyla, both of which are known to contain plant endophytes (Miyambo et al. 2016) and rhizosphere epiphytes (Chauhan et al. 2011). However, to my knowledge, members of these phyla have never been described from seeds.

As more detailed and in-depth microbial assessments are made, our concepts of the species richness associated with various plant organs will likely change. Furthermore, although the significance of the apple flower microbiome to other stages of plant apple development such as seed and fruit development were not considered, these analyses provide a rich context from which to generate hypotheses about the potential contribution of floral microbes to seed microbiomes.

Origin of the flower microbiota

The floral microbiota may reside on the stigma (Stockwell et al. 1999), the pollen on anthers (Manirajan et al. 2016), floral petals (Junker et al. 2011), and in floral nectar (Herrera et al. 2009), where they all would likely have arisen from either atmospheric deposition (Otano et al. 2015), soil dispersal (Zarraonaindia et al. 2015), rainfall (Cho and Jang 2014; Kaushik et al. 2014), visitation from pollinators (McFrederick et al. 2017; Ushio et al. 2015), or from systemic colonization from the rhizosphere (Compant et al. 2010; Compant et al. 2008). Therefore, the assembly of the floral microbiome is likely to be very context dependent, with factors such as local vegetation, pollinator types, soil microbiome composition, and a myriad of local abiotic and biotic conditions being important drivers of assembly.

One of the more important drivers of floral microbiome assembly, however, may be the floral nectar. This is a sugar and amino acid rich mixture released from nectaries and is particularly important in providing an abundant source of available carbon and energy for microbial growth (Pozo et al. 2015) as well as for pollinators. This makes the interactions that take place between nectar molecules, microbes, and pollinators quite complex (Lievens et al. 2015) yet important in shaping the flower microbiome and perhaps subsequently, the seed microbiome. Therefore, some appreciation of the types of interactions that take place in floral nectar is important in understanding how certain seed microbes may have been recruited from the flower microbiota.

Microbiota of floral nectar

Descriptive studies of the nectar microbiota are based on a sizeable number of culture-based studies of bacterial (e.g., (Alvarez-Perez et al. 2012; Fridman et al. 2012; Lenaerts et al. 2016; Samuni-Blank et al. 2014)) and fungal (e.g., (Alvarez-Perez and Herrera 2013; Herrera et al. 2009; Peay et al. 2012; Pozo et al. 2011)) consortia across a range of plant species in both natural ecosystems and agroecosystems. A subset of these studies has focused on the role of nectar in facilitating flower infections by plant pathogens (Buban et al. 2003; Pusey et al. 2008; Stockwell et al. 1999). While the nectar microbiota are generally less diverse than that of the total floral microbiome, the general patterns again point to the dominance of bacterial species within the Proteobacteria, especially species of *Acinetobacter* and *Pseudomonas* (Fridman et al. 2012), and fungal species within the genera *Metschnikowia* and *Aureobasidium* (Alvarez-Perez and Herrera 2013; Bartlewicz et al. 2016; Belisle et al. 2012; Pozo et al. 2011). However, the actual microbial species composition may vary dramatically from one plant species to the next (Aizenberg-Gershtein et al. 2013; Fridman et al. 2012; Jacquemyn et al. 2013) and across geography (Samuni-Blank et al. 2014), both of which may be related, in part, to the strong priority effects known to regulate microbial succession in nectar (Peay et al. 2012). For example, with some yeast communities, those species arriving first and capable of utilizing molecules in the nectar will determine the subsequent dominance of later-colonizing species in the flower. This is especially true with *Metschnikowia reukaufii*, which is a highly competitive

yeast that often dominates floral nectar if it is one of the first species to arrive (Peay et al. 2012). This suggests that the nectar microbiome may be heavily modulated by pollinators, which may serve as the main vehicle for introducing bacteria and yeasts into flowers.

The importance of pollinator impacts on the assembly of the nectar microbiota cannot be underestimated (Samuni-Blank et al. 2014). Bees, for example, clearly contribute to the nectar bacterial community (Aizenberg-Gershtein et al. 2013). However, different types of pollinators (e.g., birds, insects, ants, etc.) are capable of introducing different proportions of yeasts and bacteria that can alter nectar sugar composition and make it either more or less attractive to subsequent pollination (Herrera et al. 2010; Vannette et al. 2013). Often in the presence of high densities of ascomycetous yeasts (sometimes in excess of 10^6 cells/ml of nectar (de Vega et al. 2009; Herrera et al. 2009)), floral nectar is more attractive to bee pollinators (Herrera et al. 2013), again pointing to the importance of priority effects and pollinator behavior in dictating the species composition within the floral microbiome.

Relationship of flower microbiomes to seed microbiomes

While much remains to be learned about the complex microbial interactions that take place in and on flowers during their ephemeral life, perhaps the more important questions arising from these studies are "How does the flower microbiota contribute ultimately to the seed microbiota?" and "Do the microbial associations that take place with seeds during development in the flower ultimately influence plant health and productivity?". Results of recent studies point to the possible answers to those questions.

We have known for many years that bacteria reside in and on seeds. However, few investigations of their origins and routes of colonization were ever carried out. Recent studies, have shown that several endophytic bacteria associated with flowers may colonize developing ovules and ultimately end up in fruits and seeds. Compant et al. (Compant et al. 2011) demonstrated that several *Pseudomonas* and *Bacillus* species present in flowers resided inside epidermal cells and inside the xylem vessels of ovaries. Furthermore, cells of *Bacillus* spp. were also detected inside seeds. The bacterial cells in association with epidermal cells in the seed may have most likely arisen from the flower itself whereas the *Bacillus* spp. present in xylem vessels may have been systemically transported to the seed from the rhizosphere (Compant et al. 2010). However, this hypothesis has not been tested directly.

A more direct way in which the significance of the flower microbiota to the seed microbiota has been demonstrated is through the introduction of known microbes into flowers and then monitoring their presence in the mature seed. In several studies, inoculation of flowers with either pathogenic or non-pathogenic bacteria resulted in significant levels of seed infestation (Dutta et al. 2014a; Dutta et al. 2014b; Mitter et al. 2017). Bacteria that reside on the stigma may enter seeds more rapidly than those residing elsewhere (Dutta et al. 2015). Yet, once inside the seed, residence in the embryo/endosperm enhances bacterial survival as opposed to localization in the testa (Dutta et al. 2016). The greater the bacterial populations introduced to flowers (from 10^3 to 10^9 cells/blossom), the greater the population of bacteria that ultimately colonize seeds and seedlings emerging from those seeds (Lessl et al. 2007). These observations suggest that bacteria that colonize both internal and external seed tissues in the flower, may be incorporated into the seed microbiome and, perhaps more importantly, may ultimately transfer to seedlings that develop from those seeds. This notion has also been supported with recent studies of the plant growth-promoting bacterium, *Paraburkholderia phytofirmans*, which, when introduced to flowers, colonizes developing seed embryos by penetrating through the stigma/style and establishing in mature seeds (Mitter et al. 2017). Once established within the endophytic seed microbiome, these and other bacteria can transfer naturally to seedlings during germination and promote seedling growth (Chimwamurombe et al. 2016; Mitter et al. 2017).

A brief mention of the carposphere microbiota

Although I have not mentioned the importance of the mature fruit that develops from the flower, there have been studies on the microbiology of the surfaces of fruits, primarily from the food safety perspective (Leff and Fierer 2013), that may influence the seed microbiome. For example, species of *Pseudomonas* and *Bacillus* are particularly prevalent in cucurbit fruits, especially within the seed cavity (Fürnkranz et al. 2012; Glassner et al. 2015). While species within these two bacterial genera have been shown to dominate flowers and fruits, they also colonize seeds and the endorhiza

where they're able to inhibit the growth of pathogenic fungi and bacteria and protect seedlings from infection (Fürnkranz et al. 2012). Similarly, species of *Pseudomonas* and *Bacillus* present in flowers were able to colonize fruits and seeds and move systemically throughout the plant to take up residence epiphytically on roots and endophytically in grape inflorescence stalks and fruits, even in the presence of an already established endophytic microbiome (Compant et al. 2011). While much more needs to be understood here, these initial results point to the importance of internal fruit tissues as routes for seed and seedling colonization of microbes.

Seed acquisition of microbes during dispersal

Although seed dispersal is not a life history stage that one considers in agricultural contexts, it is extremely important in natural systems because of its critical importance to the regeneration, maintenance, and dynamics of plant populations (Traveset et al. 2014). Surprisingly, the microbial colonization of seeds during dispersal events has never been considered and I discuss it here to point to the potential for this stage of the plant life cycle to be significant in the assembly of the seed microbiota of plants in natural ecosystems. An increasing literature on environmental microbiology and microbial ecology coupled with contemporary studies on vertebrate and invertebrate gut microbiomes of non-domesticated animals (Ley et al. 2008; Muegge et al. 2011) is providing a means to generate strong hypotheses about the type, magnitude, and impact of potential seed-microbe interactions during dispersal events.

There are a wide range of modes by which seeds may be dispersed (Poschlod et al. 2013; Traveset et al. 2014). Among the more well-known are wind dispersal, water dispersal, insect dispersal, animal dispersal, either by ingestion followed by defecation, regurgitation, or hitchhiking on the animal's fur or skin, or various multiple combinations and sequences of each. Each mode of dispersal or disperser species can potentially expose seeds to different microbial consortia, either because of the microbes directly associated with each dispersal agent (e.g., water or gut microbiota), but also the microbiota associated with the site of seed deposition and manner in which seeds are ultimately deposited (e.g., soil surface vs burial, in feces or regurgitated).

Wind and water dispersal

Seed dispersal of most plant species by wind or water generally occurs over shorter distances than seeds dispersed by animal vectors and is often limited to smaller-seeded species or those species whose seeds have morphological adaptations to facilitate greater flight time (Fenner and Thompson 2005). Although the atmosphere possesses a rich microbiome (Gandolfi et al. 2013), it is rather unlikely that microbes present in the atmosphere would contribute significantly to the seed surface microbiome during wind dispersal because of the very casual and ephemeral nature of any associations that may occur.

Water dispersal, on the other hand, provides suitable conditions for microbes to associate more intimately with seeds. Streams, rivers, lakes, and ponds contain a large diversity of fungal (Tsui et al. 2016), bacterial (Pernthaler 2013), and oomycete (Riethmuller and Langer 2005; Shrestha et al. 2013) species, all notorious for colonizing organic substrates, particularly seeds (Czeczuga et al. 2009) and often recruited from soil microbiomes (Ruiz-Gonzalez et al. 2015). Therefore, any significant residence time in surface waters, sediments, or flood waters could lead to significant microbial colonization of seeds. Given that many of the oomycetes found in freshwater environments are also notorious seed and seedling rotting pathogens (Crocker et al. 2016) or seed-borne pathogens of foliar plant parts (Thines 2014), it is likely that dispersal in water could potentially reduce germination percentages or seedling growth (Crocker et al. 2016) once seeds come to rest on soil, ultimately impacting establishment and recruitment.

Frugivorous/granivorous seed dispersal

Perhaps most important for seed acquisition of microbes during dispersal is that mediated by animals (Traveset et al. 2014), especially birds and mammals that consume seeds (granivores) or fruits (frugivores) where they deposit intact seeds in their feces at distant locations (Viana et al. 2016). Perhaps no other stage of the plant life cycle, other than a seed's residence time in soil, exposes seeds to such a rich diversity of microbes. During passage through the animal gut, seeds are exposed to a high diversity of microbes inhabiting the oral cavity and intestinal tract of the dispersing animal, creating opportunities for seed colonization, not only during gut passage, but also following defecation or

regurgitation. Seeds that manage to remain intact following gut passage are deposited into the microbially-rich feces of the frugivore or granivore (e.g., (Godon et al. 2016; Yildirim et al. 2010)). Microbial colonization occurring in this way may have significant impacts on plant ecology but, to my knowledge, they have not been studied. However, there are several compelling reasons to believe that seed gut passage could be a significant vehicle for seed microbe acquisitions with significant impacts on seed germination and seedling growth.

The types of bacteria that typically inhabit the guts of frugivores and/or granivores such as birds (e.g., (Hird et al. 2015; Kohl 2012; Lewis et al. 2016; Mirón et al. 2014; Waite and Taylor 2014; Waite and Taylor 2015)), mice (Kreisinger et al. 2014; Maurice et al. 2015), and other mammals (e.g., (Ley et al. 2008; Yildirim et al. 2010)) are all dominated by bacteria within the phyla Bacteroidetes, Firmicutes, and Proteobacteria. While the gut microbes of many mammals are obligate anaerobes, the gastrointestinal tract also harbors many facultative anaerobes, particularly among juveniles and older adults (Rodriguez et al. 2015). This is particularly true of birds, where aerobic and facultative anaerobic bacteria may also be abundant (Bangert et al. 1988; Waite and Taylor 2015). These bacteria include many of the same species already known to associate with plants (Berg et al. 2015), enhance plant health (Berendsen et al. 2012; Berg et al. 2014; Mendes et al. 2013), and protect germinating seeds and seedlings from fungal and oomycete pathogen infections (Nelson 2004). It is certainly likely that these bacteria could colonize seeds during gut passage. Plant ecologists have often observed increased seed germination and subsequent seedling growth following the passage of seeds through the guts of frugivores (Traveset 1998; Traveset et al. 2007). Among the explanations for this are the breaking of dormancy, the removal of germination inhibitors in fruits, the mechanical and/or chemical scarification of the seed coat, fecal protection from predators, removal of pathogens, or a fertilization effect from the nutrients in feces. However, from a microbe-centric perspective, the inoculation of seeds with pathogen-suppressive or growth promoting bacteria or fungi during gut passage and fecal deposition may be another explanation for such an observation.

As an example, seeds of chili pepper (*Capsicum chacoense*) that passed through the gut of an avian granivore and deposited in feces had a 370% increase in survival over seeds that did not passage through the bird gut (Fricke et al. 2013). As it had been shown previously that these seeds were susceptible to infection by *Fusarium semitectum* (Tewksbury et al. 2008), the authors attributed the increase in survival to the removal of *Fusarium semitectum* from seeds during gut passage. However, this was based solely on observations of the symptoms on seeds (not specifically verified to be attributable to *Fusarium*) recovered from bird feces compared with those that were not gut "processed". While such an interpretation may be likely in the absence of direct evidence, it is equally likely, especially given our current understanding of the microbial inhabitants of bird guts, that the enhanced survival could be due to pathogen protection from seed inoculation by protective gut or fecal microbes. Certainly, the potential for bacterial protection of germinating seeds from pathogens can occur by many of the same microbes found in feces (e.g., (Lewis et al. 2016; Ley et al. 2008)). In fact, agricultural applications of animal manures to soils commonly stimulates the microbially-induced protection of seeds and developing seedlings from pathogen attack (e.g., (Bonanomi et al. 2007; Darby et al. 2006)). So, there is considerable evidence to suggest that enhanced germination could be a function of the microbes acquired by seeds. Although such a hypothesis has not been tested, I raise it here to illustrate how a microbial perspective may be valuable in generating new hypotheses about the role of seed-associated microbes in ecological phenomena.

The interactions between seeds, their dispersal agents, and the microbes with which they associate are potentially significant and may impact plant population and community dynamics. As others have called for more attention to microbes in thinking about organismal and population biology (Duncan et al. 2013; McFall-Ngai 2015), I too feel it is now more important than ever for ecologists to consider how plants and animals interact with microbes at all stages of their life cycle in influencing the patterns and processes that we observe.

Seed-microbe interactions in the soil seed bank

In natural ecosystems, dispersed seeds may experience at least one of three fates: 1) they may be removed by granivory (Crawley 2014); 2) they may persist in a dormant or quiescent state until conditions for germination are appropriate (Nonogaki 2014); or 3) they may

germinate immediately. Regardless of their ultimate fate, they spend a certain amount of time in soil prior to germination and growth (Mall and Singh 2014; Saatkamp et al. 2014). Because of the high microbial diversity of soils, the deposition of seeds into the soil seed bank provides extended opportunities for seeds to interact directly with a wide range of soil microbes, from commensals and mutualists to pathogens and decomposers, all of which may subsequently impact seed germination, seedling establishment, recruitment, and demography (Chee-Sanford and Fu 2010; Wagner and Mitschunas 2008).

Although the importance of microbial interactions with seeds in the seed bank has been recognized for decades, we have made rather slow progress in understanding the nature of those interactions and the subsequent impacts for plant health and productivity. Part of this problem, I believe, is that often the impacts of seed-associated microbes (often fungi have been studied) on seed bank dynamics has been addressed by employing fungal exclusion experiments using fungicides (e.g., (Blaney and Kotanen 2001; Blaney and Kotanen 2002; Gallery et al. 2010; Mordecai 2012; Orrock et al. 2012; Schafer and Kotanen 2003)). In these experiments, seeds are buried in soils and either exposed to a fungicide treatment or left untreated. If seed germination or seedling survival is enhanced in the fungicide treatment relative to the control, the conclusion is that soil fungal pathogens are limiting the survival or germination of seeds in the seed bank. There are several shortcomings of this approach (Mitschunas et al. 2009), not the least of which is the inability to understand which microbes and their activities are involved.

Yet, some have attempted to understand which specific microbes may associate with seeds in the seed bank (Crist and Friese 1993; Kirkpatrick and Bazzaz 1979; Schafer and Kotanen 2004). Among the more commonly isolated fungi are species of *Acremonium, Alternaria, Cladosporium, Cochliobolus, Cylindrocarpon, Fusarium, Mucor, Penicillium*, *Phoma, Stemphylium,* among others, each of which include many seed-infecting pathogenic species (Schafer and Kotanen 2004). Similar observations have been made in more contemporary studies of seed bank fungi (Gallery et al. 2007) where seeds recovered from soils underneath several tropical pioneer trees were dominated by fungi in the genera *Alternaria, Botryosphaeria, Chaetomium, Clonostachys, Colletotrichum/Glomerella, Coniothyrium, Diaporthe, Fusarium* (including a number of *Fusarium* teliomorphs), *Mycosphaerella, Phomopsis*, and *Xylaria* as well as a large number of unidentified ascomycetes (Gallery et al. 2010; Kluger et al. 2008; U'ren et al. 2009). Again, many of the species isolated are known to be generalist plant pathogens. However, in none of these studies has fungal virulence been directly evaluated.

Perhaps most surprising from the numerous studies of seed bank microbes is the nearly complete absence of plant pathogenic oomycetes such as *Pythium* species, which are notorious seed-infecting organisms, at least of actively germinating seeds, from seeds in the seed bank. Only two studies have reported the infrequent detection of *Pythium* from seeds in the seedbank (Crocker et al. 2016; Schafer and Kotanen 2004), despite the rich diversity and abundance of oomycetes in most soils (Arcate et al. 2006; Coince et al. 2013; Nelson and Karp 2013; Sapkota and Nicolaisen 2015). Although plant pathogenic *Pythium* species are abundant in wetland soils (Nelson and Karp 2013) and can be highly virulent to both seeds and seedlings of *Phragmites australis* (Crocker et al. 2015), few appear as seed colonizers of wetland plant species in the seedbank (Crocker et al. 2016). Instead, seeds in wetlands are commonly colonized by a wide variety of mostly pathogenic fungi in the genera *Alternaria, Epicoccum, Fusarium*, and *Peyronellaea* (Crocker et al. 2016). Although specific fungal species recovered from seeds overwintering in the seed bank do not reduce seed germination, a number can be virulent to seedlings (Crocker et al. 2016). This has been observed by others (Kabeere et al. 1997; Kirkpatrick and Bazzaz 1979) and suggests that the seed bank may serve as a reservoir of pathogens that ultimately express their impacts as reduced seedling establishment and recruitment without directly reducing seed viability and germination while dormant in soil. This certainly deserves greater research attention in the future.

The seed bank ecology of *Pyrenophora semeniperda* and *Bromus tectorum*

One cannot discuss seed bank microbial ecology without mentioning the interaction of seeds of the invasive grass, *Bromus tectorum*, with the grass-infecting endophytic fungal pathogen *Pyrenophora semeniperda*. This pathosystem has become a model for seed bank pathobiology and ecology and a useful system for better understanding the impacts of seed-microbe interactions in the seed bank to plant ecology.

Bromus tectorum *Bromus tectorum* (cheat grass, downy brome) has become one of the more important and dominant invasive grass species in the Western United States (Meyer et al. 2007). Like most grasses, *B. tectorum* is a prolific seed producer (Meyer et al. 2007; Smith et al. 2008). Seed populations of *B. tectorum* generally mature during the high temperatures of summer. Mature seeds have varying levels of dormancy (Meyer et al. 1997) but, if they remain in a dry state at those high summer temperatures (referred to as a dry after-ripening period), they lose their dormancy and become increasingly germinable when seed water potentials are maintained above a critical threshold (Meyer and Allen 2009). Typically, after-ripened seeds then germinate rapidly in response to cooler temperatures and increased rainfall in the autumn (Allen and Meyer 2002). However, if exposed to intermittent summer rains, seeds may partially imbibe water but then return to a dry state without germinating. Under these conditions, seeds that fail to fully germinate enter a secondary dormancy, often leading to their carry over in the seed bank to the next season (Finch et al. 2013; Hawkins et al. 2013). These secondarily-dormant seeds lose their dormancy over time just as do recently matured seeds. However, seeds retaining some level of dormancy commonly germinate more slowly than those no longer dormant.

Pyrenophora semeniperda Although there are a number of important pathogens potentially influencing seed bank dynamics of *B. tectorum* (Meyer et al. 2016), *Pyrenophora semeniperda* is one of the more significant. *Pyrenophora semeniperda* is a globally-distributed fungal species with a host range of nearly 80 species within the Poaceae (Medd 1992; Medd and Campbell 2005; Medd et al. 2003). *P. semeniperda* is a seed borne endophyte that establishes in the seed during seed development in the flower (Medd and Campbell 2005; Meyer et al. 2008). Although present in developing seeds, aerially-dispersed conidia that contaminate seed surfaces are the likely source of seed-borne inoculum (Meyer et al. 2008) along with litter (Beckstead et al. 2012).

Although seeds are symptomless prior to dispersal, once they enter the seed bank in dormancy, the infection of dormant *B. tectorum* seeds by *P. semeniperda* occurs quite rapidly if sufficient water is available. Conidia germinate on the seed surface within 8 h of imbibition and the subsequent hyphal growth covers the seed, forms appressoria, and then penetrates through the seed coat. Within the next week, the fungus degrades the endosperm and forms stromata by 11 days (Medd et al. 2003). The embryo is completely degraded by 14 days and new conidia are produced on the seed surface between 21 and 28 days (Finch-Boekweg et al. 2016). These infections almost always kill dormant seeds, especially when water potentials are low (Finch et al. 2013).

Recently matured but dormant seeds may also be killed rapidly by *P. semeniperda* in the summer if a rainfall event stimulates conidial germination but seeds continue to experience dry conditions (Finch et al. 2013). The lack of water slows seed germination, increases infection and mortality, and results in less carry-over of dormant seeds to the following season (Beckstead et al. 2007; Meyer et al. 2007). However, once mature seeds lose their dormancy by early autumn, they may germinate rapidly if soil moisture remains available, and escape mortality by outgrowing the pathogen (Beckstead et al. 2007; Finch-Boekweg et al. 2013). However, if seeds are carried over in the seed bank, they may be rapidly killed in the late winter or early spring, regardless of the soil water status (Finch et al. 2013).

The virulence of *P. semeniperda* is negatively correlated with growth rate (Meyer et al. 2010), due, in part, to the production of the toxin cytochalasin B, which is required by *P. semeniperda* for virulence only when expressed on non-dormant seeds (Meyer et al. 2015). Although within any given seed bank population, *P. semeniperda* individuals may vary widely in their growth rates and virulence (Beckstead et al. 2010; Beckstead et al. 2014), it is the fast growing individuals of *P. semeniperda* that cause greater seed mortality on dormant seeds at low inoculum loads than the slow-growing individuals.

Pyrenophora semeniperda is also believed to have the potential to attack seeds of other susceptible native seed bank grass species (Beckstead et al. 2010). At sites invaded by *B. tectorum*, the seed densities of *B. tectorum* and frequencies of *P. semeniperda*-killed seeds are much greater than in non-invaded sites, leading to higher pathogen loads of *P. semeniperda* than those in non-invaded sites (Beckstead et al. 2010). From a plant community perspective, those plant species whose seeds germinate more rapidly from the seed bank are more likely to escape infection by the most virulent individuals of *P. semeniperda* whereas grasses more closely related to *B. tectorum* or species whose seeds germinate slowly are often more susceptible to *P. semeniperda* than distantly related species or species

whose seeds germinate rapidly (Beckstead et al. 2014). This might indicate that the *B. tectorum* seed bank may serve as an important reservoir for *P. semeniperda*, which would maintain the dominance of *B. tectorum* populations at invaded sites at the expense of native grass species. However, subsequent experimental and theoretical evidence does not support this (Beckstead et al. 2014; Mordecai 2013), instead predicting that such events are likely to happen only when the inoculum loads of *P. semeniperda* are extremely high.

I believe this pathosystem represents a valuable case study to illustrate the utility of thoroughly integrating ecological, pathological, and mycological research to enhance our understanding seed-microbe interactions influencing the dynamics of plant communities. An obvious gap in the work done to date is the role of other co-interacting members of the seed and soil microbiota, each of which may ultimately impact pathogen and seed dynamics in this system. Placing these interactions within the context of the changing temperature and moisture regimes that are important to the dynamics of this system will be equally informative. Finally, the current level of detailed understanding makes this an excellent system to model seed-bank dynamics, which will generate useful testable hypotheses to better explore this and other complex seed-microbe systems.

Development and activity of the spermosphere microbiota

Seed germination and seedling growth is the stage of the life cycle where all the previous interactions with microbes potentially have their ultimate impact. While microbial interactions during flowering, seed dispersal, and dormancy in the seed bank may all impact the microbial legacy of a seed, the interactions of seed-associated microbes with the soil microbiota during seed germination may have the strongest impacts on overall plant fitness. Both the endophytic and epiphytic seed microbiota as well as the soil microbiota are activated during seed imbibition and germination to create a spermosphere environment either beneficial or detrimental to the critical seed-to-seedling phase of the life cycle. Whether the origin of the spermosphere and seedling microbiota arises from the endophytic seed microbiome, the soil microbiome, or from a combination of both remains unresolved. However, recent studies are revealing new insights into this question and improving our understanding of how these interactions may ultimately influence plant health management in agriculture and ecological dynamics in natural ecosystems.

Over the years, there has been a rather limited research effort on the nature and dynamics of spermosphere microbes (Nelson 2004; Schiltz et al. 2015). Much of what we currently understand is based largely on culture-dependent descriptive studies of microbes amplified around germinating seeds. While the types of microbes that develop in the spermosphere may have profound impacts on the germinating seeds themselves, they also impact seedlings and adult plants that arise from those seeds. For example, there are numerous descriptions of bacteria proliferating in the spermosphere that actually enhance seed germination (e.g., (Mahmood et al. 2016; Rudolph et al. 2015)) or transfer to seedlings and enhance seedling growth (e.g., (Compant et al. 2010; de Souza et al. 2015; Glick 2015; Santoyo et al. 2016)). Furthermore, the literature is replete with studies demonstrating the amplification of seed, seedling and root pathogens in the spermosphere of agricultural plant species (Nelson 2004) and also in natural ecosystems (Bagchi et al. 2014; Liu et al. 2015; Spear 2017; Spear et al. 2015) as well as studies demonstrating the suppression of seed and root diseases from indigenous and seed-applied microorganisms (e.g., (Koch and Roberts 2014; Sharma et al. 2015)).

Despite our progress in describing the spermosphere microbiota and their impact on plants, our understanding of spermosphere chemistry has lagged far behind (Schiltz et al. 2015). And while our knowledge of the nature and complexity of compounds potentially released by seeds during germination is growing (Frank et al. 2011; Shu et al. 2008), the role of various compounds in supporting and regulating the interactions that take place in the spermosphere remains poorly understood. This is one of the greatest gaps in our understanding of spermosphere ecology and more research is needed in spermosphere chemistry if we are to develop a mechanistic understanding of the nature and dynamics of spermosphere interactions that influence downstream plant function and behavior. I will try to illustrate this point below.

Bacterial proliferation in the spermosphere

Much of our understanding of the microbial colonization of seeds during germination comes from studies focused largely on bacteria. A number of studies across a range of plant species and different soils have demonstrated that the bacteria proliferating on and around

germinating seeds are most commonly associated with three major bacterial phyla: Proteobacteria, Firmicutes, and Actinobacteria (Chen et al. 2012; Liu et al. 2012b; Lopez-Velasco et al. 2013; Ofek et al. 2011). Among the more frequently encountered taxa are species of *Agrobacterium, Bacillus, Burkholderia, Enterobacter, Paenibacillus, Pantoea,* and *Pseudomonas* among others (Nelson 2004). The presence of species within these genera should not be surprising since the phyla containing these genera not only dominate bacterial communities in most soils (Fierer et al. 2012), but they also dominate endophytic and epiphytic seed communities (Barret et al. 2015; Bulgarelli et al. 2013; Johnston-Monje et al. 2016; Liu et al. 2012a).

Currently, the degree to which either seed endophytic species or soil inhabiting species contribute to the proliferating spermosphere and/or spermoplane microbiota during seed germination is unknown. If the bacteria that proliferate and dominate the spermosphere are recruited largely from the seed endophytic and epiphytic microbiota, then microbial legacy effects during seed development and dispersal events may be especially important in understanding the nature of these spermosphere microbiomes. However, if the dominant spermosphere bacteria are recruited largely from the surrounding soil, then it is likely that the microbial properties of the soil rather than the seed would best inform our understanding of the microbes impacting seedlings and adult plants. If we assume that spermosphere bacterial communities are recruited from both seed and soil sources, which I have presented evidence for above, then competitive interactions among species originating from the seed and those originating from soil will ultimately determine the species that dominate the spermosphere and transfer to seedlings as epiphytes or endophytes.

For some time it has been believed that the spermosphere microbiota was derived largely from the soil (Buyer et al. 1999; Green et al. 2006; Normander and Prosser 2000). Although some results are consistent with this notion (Klaedtke et al. 2016), others have demonstrated the capacity of seed endophytic bacteria to proliferate during seed germination and colonize seedling rhizospheres (Barret et al. 2015; Compant et al. 2011; Cope-Selby et al. 2017; Darrasse et al. 2010; Ferreira et al. 2008; Hameed et al. 2015; Hardoim et al. 2012; Huang et al. 2016; Johnston-Monje et al. 2016; Johnston-Monje and Raizada 2011; Kaga et al. 2009). For example, Barret et al. (Barret et al. 2015) found that as seeds germinate, specific copiotrophic bacterial (e.g., species of *Bacillus, Massilia, Pantoea*, and *Pseudomonas*) species arising from the endophytic seed microbiome were amplified over 96 h of seed germination and enriched in seedlings. These taxa are well-known spermosphere colonists (Liu et al. 2012b; Lopez-Velasco et al. 2013; Ofek et al. 2011). Similar studies have demonstrated the spermosphere amplification of copiotrophic bacteria from the epiphytic and endophytic seed microbiome that are ultimately enriched in seedlings (Huang et al. 2016).

In contrast, it was demonstrated recently that bacteria amplified during seed germination and enriched in seedlings may arise from both the seed and the soil (Johnston-Monje et al. 2014). By growing different maize genotypes in different non-sterile soils as well as in sterile sand and then comparing the seedling endosphere bacterial communities with those of the parent seeds, they observed that a large proportion (>50%) of the seedling endophytic community of each genotype more closely resembled that of the parent seed, regardless of the soil in which seeds were sown. These vertically transmitted bacteria were largely in the genera *Enterobacter, Pantoea, Microbacterium, Paenibacillus, Klebsiella, Stenotrophomonas,* and *Bacillus*, all of which are well-known spermosphere bacteria (Nelson 2004). However, there were also members of the endophytic community (<25%) (in the genus *Agrobacterium*) that differed among the three genotypes depending on the soil in which seeds were sown, suggesting that maize seedlings, in addition to acquiring endophytes vertically, are also able to recruit bacteria from the surrounding soils.

This was followed up by an expanded study examining the bacterial communities of the spermosphere, seedling rhizosphere, phyllosphere, and root endosphere of different maize genotypes grown on different soils (Johnston-Monje et al. 2016). As before, comparisons were made between non-sterile soils and sterile sand as well as the bacterial communities of the soils on which the maize genotypes were grown. Despite the observation that endophytic and epiphytic seed communities are dominated by members of the Proteobacteria, Actinobacteria, Bacteroidetes, and Firmicutes, the microbiota from non-sterile seeds that proliferated during 24 h of seed germination were quite distinct from those of the corresponding soil, suggesting that these species arose from the seed epiphytic microbiome. The dominant bacteria from the epiphytic microbiome were species of *Burkholderia*, which was also found in seedling

rhizospheres. This, coupled with the observation of comparably dominant 16S rDNA sequences in seedling rhizospheres from both sterile and non-sterile soils, lead to the conclusion that the dominant bacterial populations in maize seedling rhizospheres are recruited from the seed.

While these results alone do not confirm that seed endophytes exit and multiply outside of the seed in the spermosphere where they then colonize developing seedlings, in part because such inferences are based only on partial 16S rDNA sequences with similarities of 97% or greater. Although such partial sequence similarities are unlikely to discriminate between bacterial genotypes as a means of confirming exact strain identity in both seeds and rhizospheres, it does demonstrate the likely transfer from seed to seedling during germination, raising testable hypotheses regarding the specific route of transmission from seed to seedling and whether seed endophytes exit the seed to subsequently multiply or whether they are transferred directly to seedling roots where they subsequently exit to proliferate in the rhizosphere. While the exit of endophytic strains from roots into the rhizosphere has been demonstrated (Hameed et al. 2015; Johnston-Monje and Raizada 2011), nothing is currently known about the exit of endophytes from seeds into the spermosphere during germination.

Fungal and oomycete proliferation in the spermosphere

Much of our understanding of fungal and oomycete proliferation in the spermosphere and the subsequent colonization and penetration of seeds and seedlings during germination comes largely from studies of fungal and oomycete plant pathogens as opposed to commensal or mutualistic fungi (Nelson 2004). From these early studies, it is clear that germinating seeds of all plant species elicit strong developmental responses by soil fungi and oomycetes, activated by the release of seed exudates (Nelson 1990). Again, because of the emphasis on soil pathogens, many of the fungal and oomycete species that have been studied in relation to spermosphere proliferation are pathogenic species of the fungal genera *Fusarium* and *Rhizoctonia* (Nelson 2004) and the oomycete genera *Pythium* and *Phytophthora* (Rojas et al. 2017a; Rojas et al. 2017b). Species within these genera are widely recognized as among the most significant and globally-distributed pathogens of germinating seeds and seedlings across both agricultural and natural ecosystems. However, other soil pathogens such as *Colletotrichum* and *Cylindrocarpon* may additionally be significant in some forest systems (Hersh et al. 2012; Ichihara and Yamaji 2009; Konno et al. 2011) whereas pathogens such as *Pyrenophora* (*Drechslera* anamorphs) and *Cochliobolus* (*Bipolaris*, *Curvularia* anamorphs) (Charchar et al. 2008; Kleczewski and Flory 2010) can be significant in grass ecosystems.

Responses of endophytic seed fungi during germination and their potential transfer to seedlings has been rarely studied. However, Barret et al. (Barret et al. 2015) found that seeds of different genotypes within the Brassicaceae were dominated by ascomycete fungi primarily in the class Dothideomycetes. Among the more abundant taxa detected in seeds were species of *Alternaria, Aureobasidium, Cladosporium, Epicoccum, Phaeosphaeria, Phoma, Pyrenophora, Stagonospora, Chaetomium, Fusarium* (and associated teliomorphs), *Microdochium, Stemphylium*, and *Xylaria*. During seed germination, species within the Dothideomycetes declined whereas members in the Eurotiomycetes increased. This was due mainly to the enrichment of *Penicillium* in seedlings. However, other fungal taxa were also enriched in seedlings, especially *Trichoderma viride, Chaetomium globosum, Daedaleopsis confragosa, Peniophora piceae,* and *Rhizopus oryzae*.

Furthermore, Huang et al., (Huang et al. 2016) demonstrated that, during wheat seed germination, both endophytic and epiphytic seed-associated fungi were transferred to seedlings. The endophytic seed fungal community was dominated by species of *Emericella, Zygosaccharomyces, Cladosporium*, and *Alternaria*. However, only *Emericella* and *Alternaria* were detected in seedlings, along with a species of *Leptosphaeria* that was not detected in seeds. Again, these results confirm that both endophytic and epiphytic seed microbes can transfer to seedlings, likely because of their rapid growth during the seed germination process. Although we don't know whether these fungi establish in seedlings beyond 96 h of development or whether they compete with indigenous soil fungi that may also enter seedling roots, it establishes that the seed endophytic fungal community can transfer to germinating seedlings.

Fungal and oomycete infections of seeds in natural ecosystems

For many ecological studies in natural ecosystem where questions revolve around the activities of the soil microbiota, either the specific microbes involved are rarely

studied directly or the seed stage of the plant life cycle is simply not considered. Often, the focus of studies with soil microbiota is on soil fungal and oomycete pathogens where, as with seed bank fungi, inferences about the role of these microbes in plant community dynamics are made largely on the basis of fungal exclusion experiments involving fungicides (e.g., (Bagchi et al. 2014; Bagchi et al. 2010; Bell et al. 2006; Pizano et al. 2014; Pringle et al. 2007)). In cases where the specific microbes have been identified, the focus is often not on seeds but seedling roots that may be infected with soil pathogens such as *Fusarium* (e.g., (Bezemer et al. 2013; Liu et al. 2016; Mangla et al. 2008; Morrien and van der Putten 2013)) or *Pythium* (e.g., (Mills and Bever 1998; Packer and Clay 2000; Packer and Clay 2003; Packer and Clay 2004; Reinhart and Clay 2009; Reinhart et al. 2010a; Reinhart et al. 2005; Westover and Bever 2001)), even though the infections most likely arose during seed germination.

Some of the more seminal studies of seed infections in natural ecosystems are from studies nearly 35 years ago with tropical tree species (Augspurger 1990). Many of these tree species lack significant periods of dormancy and disperse their seeds in a decreasing density gradient pattern from parent trees (Augspurger 1983; Augspurger 1984; Augspurger and Kelly 1984). The majority of seeds that are dispersed nearest to conspecific trees frequently die from infections by *Pythium* species (*P. torulosum* and *P. aphanidermatum*) within the first 2–7 weeks after dispersal (Augspurger 1983; Augspurger and Kelly 1984; Augspurger and Wilkinson 2007). However, this level of mortality does not occur under heterospecific trees or under conspecific trees at a distance away from the parent tree. Despite variation in host susceptibility to *Pythium* infection (Augspurger and Wilkinson 2007), mortality is generally greater in seedlings nearest conspecific trees and in shaded forested areas where soil moisture is more favorable for *Pythium* activity (Augspurger 1983; Augspurger 1984; Gomez-Aparicio et al. 2012; Kitajima and Augspurger 1989). The significance of these seed and seedling infections are expressed in seedling recruitment patterns, which influences tree spatial patterns and species diversity in tropical forests.

Similar phenomena have been subsequently explored in temperate forests with *Prunus serotina* (black cherry). As in the previous studies, seed and seedling infections by *Pythium* species are known to limit seedling recruitment near conspecific trees where the population sizes of specific species of *Pythium* accumulate in a plant host-specific manner (Mills and Bever 1998; Westover and Bever 2001). The more consecutive inputs of seeds to soils beneath conspecific trees, the greater the seedling mortality (Packer and Clay 2004). Although the density of *Pythium* populations and seedling mortality are quite variable and don't particularly decline in a distance-dependent manner (Reinhart and Clay 2009), seedling recruitment is much higher when seeds are dispersed some distance away from the parent plant (Packer and Clay 2000; Packer and Clay 2003). *Pythium attrantheridium* and *P. sylvaticum* have been shown to be among the more virulent species affecting *P. serotina* seeds and seedlings near conspecific trees (Reinhart et al. 2010a; Reinhart et al. 2010b; Reinhart et al. 2011).

Seed and seedling exudation – The driving force for microbial growth and interaction in the spermosphere

The release of molecules from imbibing and germinating seeds into the surrounding soil initiates a rapid explosion of microbial growth and activity in the spermosphere (Nelson 2004; Schiltz et al. 2015). One of the more important areas of study in spermosphere ecology is the investigation of the various molecules that support complex microbe-microbe and microbe-seed interactions that take place during seed germination. Without this understanding, progress toward a more mechanistic understanding of these interactions will be slow. Currently, we have a rather rudimentary understanding of the molecules released by seeds and the biological significance of many of these molecules are unknown. Below, I present a series of studies designed to better understand the roles of exudate molecules in stimulating pathogens and supporting bacteria growth in the spermosphere, but also in influencing the interactions that take place in the spermosphere that ultimately impacts plant health. I hope to use these studies to illustrate how such an approach can improve understanding seed-microbe interactions in the spermosphere and better understand the ecology of the seed-associated microbiota.

Pythium ultimum* – *A master spermosphere microbe An important question that has never been resolved completely, is "What molecules do seed-infecting pathogens utilize to proliferate in the spermosphere and infect seeds?" Of the work done to

date, much has focused on seed-infecting *Pythium* species where it has been observed that hyphal swellings of *P. ultimum* are stimulated to germinate rapidly in the spermosphere (Nelson et al. 1986; Nelson and Craft 1989; Nelson and Hsu 1994) in response to specific sets of unsaturated fatty acids, especially oleic acid and linoleic acids, which are the most common unsaturated fatty acid found in seed exudates (Ruttledge and Nelson 1997). This is a critical observation, not only in understanding how *P. ultimum* responds to germinating seeds, but to also serve as a useful sensor to subsequently study microbial interactions with *P. ultimum* in the spermosphere.

Enterobacter cloacae – A common seed associated bacterium To date, many of the studies of microbial interactions in the spermosphere have involved experimental studies with the bacterium, *Enterobacter cloacae*, introduced onto the seed and then studying not only the behavior of the bacterium, but its direct interactions with *P. ultimum* (Nelson 2004; Roberts et al. 1994). *E. cloacae* is a well-known plant endophyte, commonly found in seeds and other plant tissues (Cottyn et al. 2001; Hardoim et al. 2012; Hinton and Bacon 1995; Johnston-Monje and Raizada 2011; Leite et al. 2013; Santoyo et al. 2016) where it has been shown to enhance seed germination and seedling growth (Santoyo et al. 2016). The selection of *E. cloacae* as a model to study spermosphere ecology came from an early observation of the rapid proliferation of this bacterium in various osmotic solutions used to pre-germinate seeds prior to planting (Taylor et al. 1985). Although both endophytic and epiphytic populations of *E. cloacae* are associated with seeds, it is largely the copiotrophic epiphytic populations that are amplified during this pre-germination process. Perhaps more importantly, when pre-germinated seeds are colonized with *E. cloacae*, they are protected from infection by *P. ultimum* (Hadar et al. 1983; Taylor et al. 1985). It is this antagonistic activity of *E. cloacae* that has stimulated nearly all of the subsequent investigations of this seed bacterium in the spermosphere.

Given that seed exudates are rich in sugars, amino acids, and organic acids among others (Nelson 2004), early studies of *E. cloacae* were focused on carbohydrate and amino acid nutrition where it was shown that the growth of *E. cloacae* on simple mono-and oligosaccharides but not on polysaccharides (Roberts and Sheets 1991) paralleled the proliferation of *E. cloacae* in the spermosphere, suggesting that carbohydrate catabolism of specific exudate compounds was important to the growth and proliferation of *E. cloacae* in the spermosphere(Roberts et al. 1992). More detailed studies with a series of amino acid mutants (Roberts et al. 1996a; Roberts et al. 1996b; Roberts et al. 1996c) and several carbohydrate mutants of *E. cloacae* (Lohrke et al. 2002; Roberts et al. 1999; Roberts et al. 2011; Roberts et al. 2007) revealed that these key mutations decreased the level of spermosphere colonization by *E. cloacae* only on seeds (e.g., cucumber, radish) that release limited quantities growth-supporting carbon compounds essential for rapid growth in the spermosphere (Roberts et al. 2000) whereas high carbohydrate exudation seeds (e.g., pea, soybean, sunflower, corn) supported wild-type colonization of the mutants.

What these studies have revealed is that the spectrum of molecules released from the seeds of different plant species can differentially impact the growth and proliferation of spermosphere bacteria. Furthermore, not only the qualitative but the quantitative aspects of seed exudation can be significant (Roberts et al. 2009; Roberts et al. 1999). Seeds that release greater quantities of reduced carbon compounds into the spermosphere during germination support higher levels of bacterial growth and greater spermosphere populations of bacteria than those seeds releasing lower amounts.

P. ultimum – E. cloacae interaction – A unique interaction in the spermosphere These above observations are important not only in understanding *Pythium* responses to seeds and the growth and proliferation of *E. cloacae* in the spermosphere, but also what drives the *P. ultimum-E. cloacae* interaction that impacts seed germination and establishment. Early observations of the interaction between *P. ultimum* and *E. cloacae* pointed to carbohydrate catabolism as playing a central role in the success or failure of *Pythium* suppression by *E. cloacae* (Nelson et al. 1986) even though it has been suggested that *P. ultimum* suppression may be due to the generation of toxic levels of volatile ammonia by *E. cloacae* (Howell et al. 1988; Mukhopadhyay et al. 1996). However, this has never been confirmed and other potentially inhibitory molecules such as hydroxamate siderophores have been ruled out as an explanatory factor in *P. ultimum* suppression (Loper et al. 1993). However, knowing that long chain unsaturated fatty acids were the primary seed-derived stimulants of *P. ultimum* in the spermosphere, Van Dijk and

Nelson (van Dijk and Nelson 1998) assessed whether *E. cloacae* and other indigenous seed-associated bacteria, could inactivate the stimulatory activity of seed exudates to *P. ultimum* to indicate whether fatty acid catabolism may explain the suppressive effects of *E. cloacae* on *P. ultimum* germination. Both *E. cloacae* and other seed-associated bacteria (which included species of *Pseudomonas, Pantoea*, and *Acinetobacter* as well as other strains of *E. cloacae*) reduced or eliminated the stimulatory activity of seed exudates to *P. ultimum* hyphal swellings. The greater the bacterial population size the more rapidly the stimulatory activity could be eliminated and all the strains that reduced the stimulatory activity of cotton seed exudate (low sugar exudation seeds) all improved seedling stands, except on seeds that release high levels of exudate sugars during germination (Kageyama and Nelson 2003), suggesting that the elimination of seed exudate fatty acids on low sugar exudation seeds may be an important mechanism by which *E. cloacae* prevents seed infections by *P. ultimum*. This was later confirmed in a study where a series of β-oxidation mutants were designed to impair fatty acid metabolism by *E. cloacae* (van Dijk and Nelson 2000). Not only did these mutants fail to metabolize linoleic acid, but they also failed to inactivate seed exudate stimulation of *P. ultimum* and failed to protect seeds from infection. Genetic complementation of these mutants fully restored these phenotypes, pointing to the metabolism of linoleic acid as key to the success of *E. cloacae* in suppressing *P. ultimum* infections. Because *E. cloacae* positions itself on the seed surface in locations where much of the exudate release occurs, it is most likely able to catabolize important compounds such as linoleic acid before they can diffuse into soil to stimulate *P. ultimum* germination (Hood et al. 1998).

A few important observations are worth noting here. First, on large seeded plants such as corn, pea, and others that release high levels of sugars during germination, *E. cloacae* neither protects seeds from infection by *P. ultimum* (Nelson et al. 1986) nor inactivates the stimulatory activity of their exudates (Kageyama and Nelson 2003). Second, seed exudation is a temporal process with molecules released from seeds over time (Nelson 2004) such that the exudate molecules that most influence either *E. cloacae* or *P. ultimum* should be present when responses (*P. ultimum* hyphal swelling germination or *E. cloacae* proliferation) are elicited. Third, it is well known that in gram negative bacteria, the genes within the *fad* regulon, which are required for the uptake and degradation of fatty acids through the β-oxidation pathway, are transcriptionally regulated by the presence of both fatty acids and sugars (Clark and Cronan 2005). In the presence of sugars commonly found in seed exudates, the expression of *fad* genes could be repressed, thus eliminating the ability of a bacterium like *E. cloacae* to degrade fatty acids.

With these observations in mind, Windstam and Nelson (Windstam and Nelson 2008a; Windstam and Nelson 2008b) attempted to explain why *E. cloacae* was effective in preventing seed infections by *P. ultimum* on low sugar exudation seeds such as cucumber but not on high sugar exudation seeds such as corn. By examining the temporal response of *P. ultimum* germination in the presence or absence of *E. cloacae* they were able to demonstrate that *P. ultimum* hyphal swellings respond to germination elicitors (i.e., unsaturated fatty acids) in seed exudates within 30 min of exposure to the seed (Windstam and Nelson 2008a), indicating that even at that early time, sufficient linoleic acid was present for hyphal swelling germination to occur. This very early release of fatty acid elicitors was confirmed in a subsequent study (Windstam and Nelson 2008b). Throughout these early periods of seed imbibition, corn seeds released considerably more oleic and linoleic acid and key sugars (glucose, fructose, and sucrose) than cucumber seeds (Windstam and Nelson 2008b), with corn seeds releasing over 150 times the amount of glucose, fructose, and sucrose released from cucumber seeds within 30 min of imbibition. At these levels of glucose, fructose, and sucrose released into the corn spermosphere, degradation of linoleic acid by *E. cloacae* was dramatically reduced, leaving sufficient levels of linoleic acid still present to trigger *Pythium* germination.

Treating seeds with the wild type strain of *E. cloacae* resulted in the inactivation of *P. ultimum* germination, seed colonization and infection on cucumber but not corn seeds. In contrast, f*ad* mutants of *E. cloacae* neither inactivated exudates nor reduced *Pythium* colonization and infection of seeds of either plant species. Interestingly, when wild-type *E. cloacae* was introduced to cucumber spermospheres after *P. ultimum* hyphal swellings were fully activated to germinate (at about 2 h), no reductions in seed colonization or infection were observed relative to non-treated spermospheres, indicating that the suppression of *Pythium* seed infection by *E. cloacae* takes place within 2 h of the initiation of imbibition and that the failure of *E. cloacae* to protect

corn seedlings from *Pythium* damping-off is due to the repression of fatty acid degradation in *E. cloacae* by the exudate sugars released into the corn spermosphere. In spermospheres like cucumber, insufficient levels of exudate sugars are released, allowing *E. cloacae* to degrade any fatty acids that are present, which prevents the germination of hyphal swellings and subsequent seed colonization and infection by *P. ultimum*.

I believe this body of work is instructive in a few key ways. First, it highlights the utility of understanding spermosphere biochemistry as a means of developing a better mechanistic understanding of the microbial interactions that take place in the spermosphere. Second, and perhaps equally important, it points to the need to place the interactions under study into a temporal context. The spermosphere is not a static environment and, given the ephemerality of seed exudate compounds released into soil as well as the speed of specific microbial responses, it is essential that the release of specific molecules that may mediate a given interaction be synchronized with specific developmental or behavioral responses being studied. Third, the biology of key interacting entities must be understood at some level and perhaps studied in parallel. What is lacking in the work described above, is an understanding of the environmental variables that may influence these interactions, along with the other microbe-microbe and microbe-seed interactions taking place simultaneously that may influence the specific interactions under observation. Developing a focused and longer term research effort directed at these issues will be essential if we are to understand more of the significance of seed-associated microbes to overall plant health.

Conclusions

The principle reasons we study plant-microbe interactions, aside from the esoteric interests and curiosities of individual investigators, is that many believe that such interactions may have profound impacts on plant health, plant productivity, and fitness. An implicit outcome of these studies is the development of knowledge to better inform management strategies in agriculture or conservation and restoration strategies in natural ecosystems. Yet, relative to other stages in the plant life cycle, studies of seeds and their associated microbiota have been under-represented in the fields of plant ecology and plant-microbe interactions. Even despite increasing awareness of and emphasis on the importance of the plant holobiont to plant evolution, seeds are either not mentioned at all, or only mentioned in passing (Hacquard 2016; Rosenberg and Zilber-Rosenberg 2016; Vandenkoornhuyse et al. 2015).

Nonetheless, in this review, I have tried to highlight the importance of microbial interactions with seeds through the entire plant life cycle to better understand the breadth and diversity of microbes that associate with seeds, how they may become part of the seed microbiota, their potential or realized impacts on other plant developmental stages, and to point to areas of study that I feel need renewed investigation or may be productive avenues for new investigation. While it should be clear that seeds associate with a large diversity of both endophytic and epiphytic microbes, the connections between the two and their interconnectedness with the soil are just beginning to be realized. Research exploring the movement of seed endophytic microbes into the spermosphere and rhizosphere as well as recruitment from the spermosphere and rhizosphere and into the endophytic seed microbiome offer exciting possibilities for better understanding the dynamics of plant microbiomes. Additionally, research exploring the augmentation of flower microbiomes to ultimately structure the seed microbiome offers special opportunities for agriculture. While in natural ecosystems, research aimed at exploring the acquisition of microbes by seeds as they are dispersed through animal guts as well as a more detailed microbial perspective on seedling establishment and recruitment will provide new ways of explaining many phenomena related to plant community dynamics. Finally, just as studies of flower nectar chemistry have allowed for a better mechanistic understanding of the microbial and pollinator dynamics associated with flowers, studies aimed at elucidating spermosphere chemistry across a range of plant species will be key in ultimately understanding how the seed microbiome and the interacting soil microbiome ultimately influence plant health, productivity and fitness.

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