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Ecological patterns of seed microbiome diversity, transmission, and assembly

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Seeds are involved in the transmission of microorganisms from one plant generation to another and consequently act as the initial inoculum for the plant microbiota. The purpose of this mini-review is to provide an overview of current knowledge on the diversity, structure and role of the seed microbiota. The relative importance of the mode of transmission (vertical vs horizontal) of the microbial entities composing the seed microbiota as well as the potential connections existing between seed and other plant habitats such as the anthosphere and the spermosphere is discussed. Finally the governing processes (niche vs neutral) involved in the assembly and the dynamics of the seed microbiota are examined.

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Introduction

Plants harbor multiple microbial taxa, known as microbiota, which influence a number of plant traits such as biomass accumulation [1], metabolite production [2], drought tolerance [3] and flowering time [4,5]. In addition, the composition of the plant microbiota can enhanced host resistance to aboveground [6,7] and belowground [8,9] pathogens. The promise of plant benefits from plant microbiota opens new possibilities for increasing plant productivity or wellness through manipulation of the composition of these assemblages. However, this requires a fundamental knowledge on the processes that drive assembly of the plant microbiota throughout the plant developmental cycle.

To date many studies have investigated the composition and structure of microbiota associated with the phyllosphere and rhizosphere (Box 1) of numerous plant species during their vegetative or reproductive stages [10]. In contrast, analyses of microbiota associated with other plant habitats such as the anthosphere [11], the carposphere [12–15], the seed habitat [16] and the spermosphere [17••,18] have been relatively less studied. Nonetheless, these habitats are important for plant fitness since they are directly related to the production of offspring and then potentially associated to vertical transmission of the plant microbiota.

Why study the seed microbiota?

Historically, the seeds[3] have been traditionally viewed as a passive means of microbial dispersion, via contact of micro-organisms located in the surrounding environment (*e.g.*, threshing residues or soil) with the seed surface [19]. Seed surface-sterilization methods classically employed in reductionist approach to study specific plant-microbial strain interactions have led to the concept of 'germfree plants' [20]. However, seed-surface disinfection does not guarantee seed sterility since (i) seeds can produce numerous antimicrobial compounds that inhibit culture-dependent detection of micro-organisms [21], (ii) microbiota located in the integument, endosperm or embryo (Figure 1) could still survived robust disinfection procedures [22].

The composition of the seed microbiota [23•,24] can have direct impacts on seed quality. Perhaps the most frequent observation is related to the negative effect of microbial load on seed germination [25]. In contrast, some seed-borne microorganisms can promote homogenous germination rate through the release of seed dormancy via cytokinin production [26]. Occasionally, seed transmissions of mycotoxin (*e.g.*, *Aspergillus flavus*) or Shiga toxin (*e.g.*, *Escherichia coli* STEC) producers could dramatically impacted the sanitary quality of seed samples [27,28]. From an epidemiological angle, seed transmission of plant pathogens serves as a major method of dispersal and is therefore important for predicting disease emergence and spread. Indeed, very low

[3] In this document, the term seed will be restricted to sexually derived structures of spermatophytes, which can under favorable conditions germinate and produce new plants [19].

Box 1 Plant-associated microbial habitats

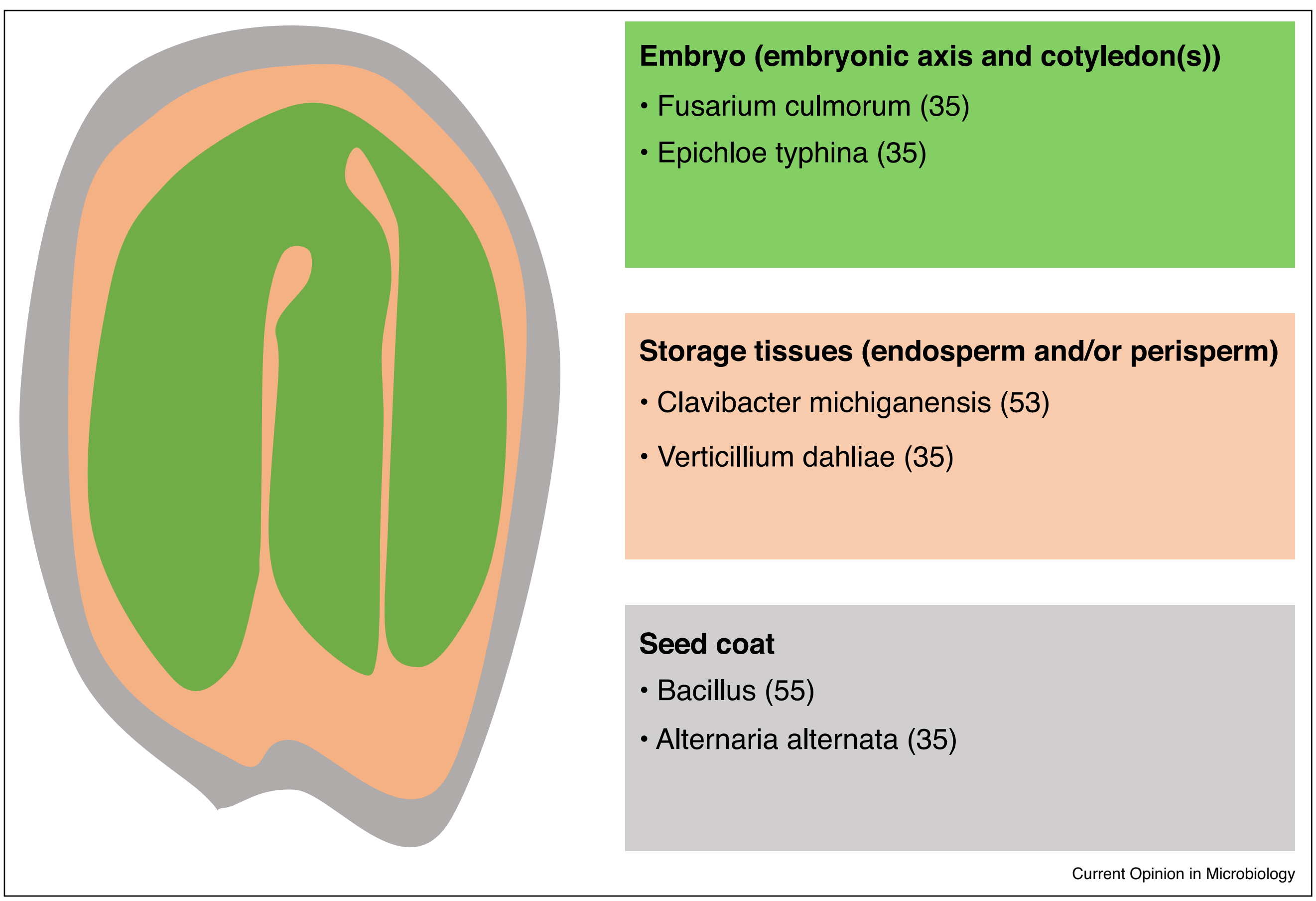
- **Anthosphere**: Microbial habitat associated to flowers.
- **Carposphere**: Microbial habitat associated to fruits.
- **Caulosphere**: Microbial habitat associated to stems.
- **Endosphere**: Microbial habitat located within plant tissues.
- **Phyllosphere**: Microbial habitat associated to leaves, includes phylloplane and endosphere.
- **Rhizoplane**: Microbial habitat associated to root surface.
- **Rhizosphere**: Zone of soil under the direct influence of the root system.
- **Spermosphere**: Zone of soil under the direct influence of germinating seeds.

degrees of seed contamination by bacterial pathogens can lead to efficient plant colonization [29]. Furthermore, seed transmission of phytopathogens can take place on non-host plants [30,31], which can then serve as a reservoir of plant pathogens.

Vertical versus horizontal inheritance of the plant microbiota

Members of the plant microbiota can be transmitted either horizontally (acquired from the surrounding environment) or vertically (acquired directly from the parent) [32]. For plants, the relative importance of horizontal and vertical transmission remains unclear [33], but both modes are likely to contribute to the ultimate composition of the seed microbiota (Figure 2). The horizontal or vertical transmission of any microbial entity is, in part, linked to the seed transmission pathway employed by this micro-organism. To date, three main transmission pathways have been described: (*i*) the internal pathway through the xylem or nonvascular tissue of the mother plant, (*ii*) the floral pathway via the stigma of the mother plant and (*iii*) the external pathway where seed is contaminated through contact with microbial inoculum

Figure 1



Localization of some seed-associated microorganisms.
Schematic representation of the three main compartments of mature seed: embryo (green), endosperm/perisperm (orange) and seed coat (grey). Of particular note is that this schematic representation does not reflect non-endospermic seeds (*e.g.*, Fabaceae), which are devoid of storage tissues. Micro-organisms located in the embryo compartment have been mostly found (with the exception of viruses) at the surface of the embryonic axis.