Need for a new seed health strategy

This text is a draft for a new seed health strategy to be discussed with stakeholders

Stephanie Klaedtke[1] and Steven P.C. Groot[2]
[1]Institute Technique de l'Agriculture Biologique, France (stephanie.klaedtke@itab.asso.fr),
[2]Wageningen University & Research, The Netherlands (steven.groot@wur.nl)

Summary

Seed quality is important for seedling establishment - an essential step for crop production. Poor seedling emergence due to abiotic and biotic stress in the field can reduce crop stand, yield and farmers' income. Seed health and vigour, the ability of the seed and seedling to cope with such stresses, is of increasing importance for sustainable farming, in particular in the face of climate change. Although current knowledge is limited, it has become clear that the seed microbiome should also be taken into account when considering seed health. Until recently, seed health was almost exclusively oriented at controlling seed borne pathogens, but seeds can also contain beneficial micro-organisms that aid the seedling against pathogens or abiotic stresses. In an up-to-date seed health strategy, the seed microbiome should be considered as part of seed health. More attention and research are needed to produce and maintain seeds with an optimal seed microbiome. In this respect, soil biodiversity seems to be an important driver, as part of the seed microbiome originates from the soils. Knowing that organic soils have a higher biodiversity, the advantage for organic seeds should be explored. Organic seeds are often treated to control seed borne pathogens. Although it is likely that this also reduces a significant part of the seed microbiome, knowledge is lacking on how this influences seed vigour and seedling establishment. When such treatments can't be avoided, it might be useful to restore the microbiome by either biopriming or coating the seeds with beneficial microorganisms originating from seed microbiomes. In the annex, background scientific literature is provided, including the abstract to aid the reader.

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Introduction

Seed health and quality affect how well a crop will establish and perform, influencing crop yield, farmers' incomes and, ultimately, food security. In the framework of the LIVESEED project, Deliverable 2.5 has reported on 2 case studies into organic seed health issues – *Alternaria ssp*. with carrot and common bunt (*Tilletia* spp.) with soft wheat – and established an inventory of current problematic issues for the quality of organic seed. Based on these findings and on a review of scientific literature, we here aim at designing a strategy for organic seed health and quality.

To assess seed quality, routine seed testing evaluates seed germination rates and detects potential seedborne pathogens, according to crop species. If a problematic level of seedborne pathogen is detected, seed treatments can be used for disease control. In organic farming, these range from natural compounds (e.g., vinegar) and physical treatments (e.g., hot water treatments or brush cleaning) to the application of biologicals (e.g., antagonistic microorganisms). However, both practical experience and recent scientific findings tend to indicate that taking into account additional aspects to seed quality would benefit organic agriculture and other forms of sustainable agriculture (refraining from the use of chemical inputs).

Seed vigour is understood as the tolerance of seeds and seedlings to environmental constraints. Despite all the care taken by farmers before and during sowing, due to weather, field conditions can vary, which can put a strong restraint on the establishment of seedlings. Such uncertainties and unpredictable stress factors are expected to increase with global climate change. Research in the frame of the European project LIVESEED showed that high seed vigour not only provides more tolerance to abiotic stresses as drought and cold but can also make seedlings more tolerant to pathogens.

Unfortunately, farmers are not always aware of its importance or do not have access to high vigour seed. For instance, even when total seed emergence is good, slower emergence due to lower seed vigour will result in stronger competition by weeds, requiring more labour for weed removal. Awareness on the importance of seed vigour needs to increase with both seed producers and farmers, even more in the case of farm-saved seeds. Training to recognise seed vigour aspects and relatively simple test methods can aid in this.

Taking seed vigour more into account as a leverage for resilient organic agriculture has implications for seed production, processing, testing, treatments and storage. Seed vigour can also have a genetic basis, which can be incorporated into plant breeding programs for resilient varieties. Concerning seed production, the (most) healthy mother plants should be selected, and nutrient limitations avoided. Seeds need to be harvested at full maturity whenever possible. During storage, ageing of the seeds should be avoided by proper dry conditions and protection from pests.

The **plant microbiome** is understood as the microbial ecosystem, composed of bacteria and fungi, associated to plants. These micro-organisms can have a positive, neutral or negative effect on plant health. In the latter case they are referred to as pathogens. Plants transfer

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part of their microbiome to the next generation as the seed microbiome. Until present, attention was almost exclusively paid to pathogens in this seed microbiome, called seed borne pathogens. But the pathogenicity seems to depend on the concentration and the on the presence of other microorganisms in the seed microbiome. Seed can also contain micro-organisms that aid the seedling against pathogens or abiotic stresses. Although scientific research on the seed microbiome has started only recently, several important influences on seedling establishment have already been discovered.

Approaches and challenges

Based on the considerations above, seed vigour and seed microbiota are expected to have an important role to play in leveraging the potential and resilience of organic cropping systems. They are relevant elements to take into account for redesigning seed and cropping systems for agroecological transitions. At this stage, knowledge on seed vigour and microbiota has broadened our view on the complexity of seed and plant health. In the aim of leveraging this potential for the benefit of organic seed production, multiple new fields and topics arise for future research and development. These also have to be addressed at the different geographic scales, from local seed production on farm to entire seed systems.

<u>Interactions of seed vigour and seed microbiota</u>: It has become clear that both seed vigour and seed microbiota contribute to the health of seeds, seedlings and, ultimately, crops (Das Gupta and Austenson, 1973; Nelson et al., 2018). It remains unclear how the two mutually affect each other. Nevertheless, in the LIVESEED case study on carrot cited above, high vigour un-aged seeds were more tolerant to damping-off caused by *Alternaria radicina* than artificially degraded, low-vigour seeds. This illustrates that seed vigour and microbial activity on seeds and seedlings are inter-related, although it does not allow to determine which of the two is the driver (if any of the two should be considered the driver). These findings broaden the picture on seed and plant health beyond the mere detection of pathogens. They indicate that seed health and seed quality are intimately intertwined. The following infographic illustrates an understanding of seed and plant health as a continuum that is based on interaction with microbial life.

<u>Factors shaping microbiota:</u> More attention and research are needed to produce and maintain seeds with an optimal seed microbiome. A highly biodiverse microbiome seems to be advantageous for the seedling (Wassermann et al., 2019). Since the seed microbiome is partly originating from the soil and organic soils have a more biodiverse microbiome (Hartmann et al., 2015; Lupatini et al., 2017), this may give an advantage for organic produced seeds. Research into the factors shaping diverse seed or even optimised microbiomes, over the entire process from seed production to storage, would provide a basis for the elaboration of practical recommendations for seed producers and enterprises in order to benefit from microbial life for resilient crops. Integrating these factors into the production of healthy, vigorous seeds, seedlings and crops, will also require a paradigm shift from a point

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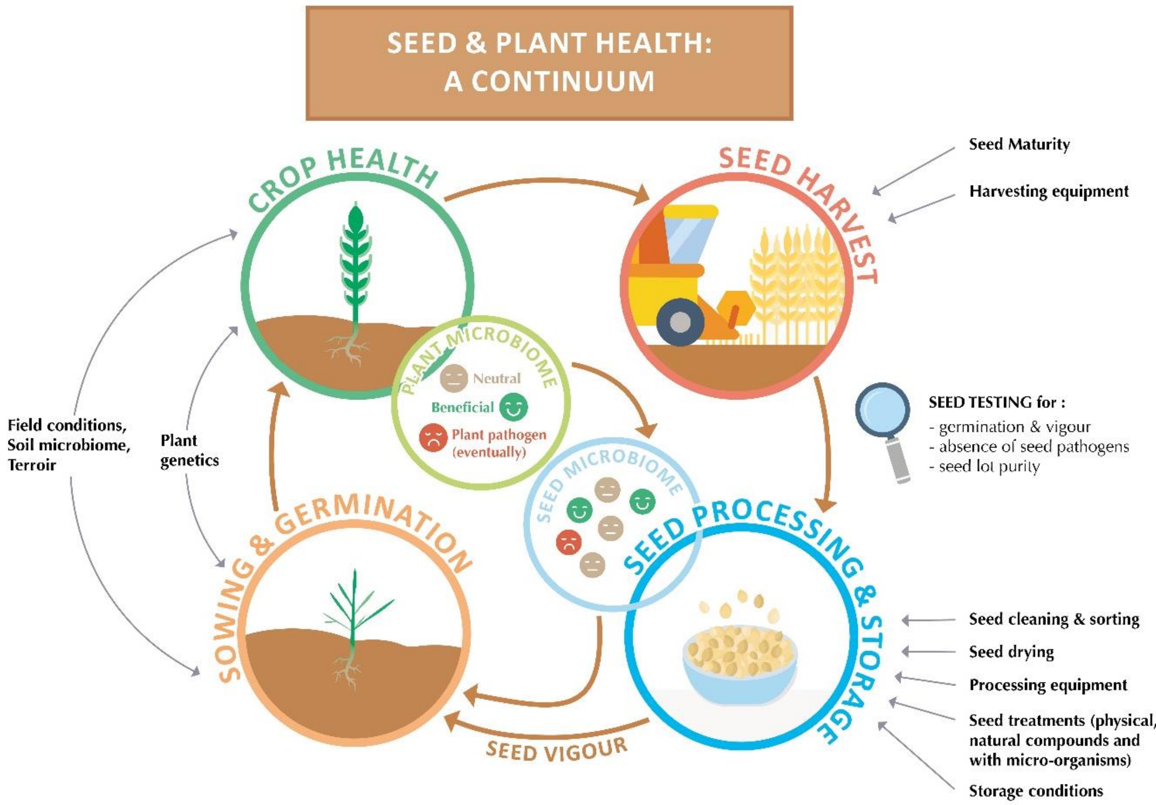
of view that mainly aims at avoiding plant diseases to a perspective of sustaining plant health processes. The dynamic process allowing living organisms to evolve towards health was initially described as *salutogenesis* in the context of human health (Antonovsky, 1996) and taken up by (Döring et al., 2012) in the context of plant health. With this in mind and in the long run, the science concerned with the health of plants may evolve from a stance of plant pathology – focussing on plant diseases – to a stance of *plant salutology* – focussing on health-sustaining processes.



<u>Implications for seed sanitation</u>

When seeds are infected, sanitation treatments may be necessary to control seed borne pathogens. Organic seeds may be treated with physical methods (e.g. heat, brush cleaning), natural compounds (e.g., vinegar, etheric oils) or biologicals (e.g., *Pseudomonas chlororaphis* strains). It is likely that treatments with some physical methods and natural compounds also reduce a significant part of the seed microbiome. Moreover, physical seed treatments often have negative influences on seed vigour. In the longer run, in terms of seed and plant health strategies, this poses the question of how to articulate the substitution of chemical seed treatments in conventional agriculture, on one hand, and the agroecological transformation of cropping systems towards systems based on microbial life, on the other. Fully basing cropping systems on resilient ecosystem interactions, and a thriving microbial

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environment in particular, may be in contradiction with seed sanitation treatments aiming at disinfecting seed surfaces. We argue that both strategies may be complementary. Bio-diverse, resilient cropping systems (in combination with sound organic cropping and seed production practices) may strongly reduce the need for "corrective" seed sanitation treatments. The latter are expected to remain sometimes necessary, at least as occasional support or safety net, e.g. for the management of common bunt in soft wheat. When such treatments can't be avoided, it might be useful to restore the microbiome by either biopriming or coating the seeds with beneficial microorganisms originating from seed microbiomes.

Implications for plant breeding

To date, considerations for plant and seed health in plant breeding have mainly led to breeding programs for genetic resistance to diseases, providing genetically resistant cultivars to facilitate the control of plant diseases in crops. Recent research with rice has shown that certain microbiomes transmitted by seeds may confer disease tolerance, or even resistance (Matsumoto et al., 2021). Integrating the role of seed-transmitted microbiota and genetic effects on seed vigour into breeding programs may be a way to ensure seed and plant health in the future, as a complement to resistance breeding.

Geographical scale of seed production

In the long run, fully integrating the seed and plant microbiomes in how we produce seeds may also affect recommendations on the geographical scale of seed production. Research with common bean has shown that local environmental factors described as ""terroir" shape the composition of seed microbiomes (Klaedtke et al., 2016). It remains widely unknown how the structure of plant microbial communities varies at different geographical scales and whether or not locally produced seeds provide some advantage in the form of microbial adaptation to local conditions. However, achieving such a level of comprehension of the seed microbiota still requires considerable research both into the factors shaping seed and plant microbiomes and their functional attributes.

Conclusion

We recommend the following strategy for an organic seed health and quality system:

- Integrate the role of the seed microbiome in seed quality aspects.
- Harness the potential of optimised seed microbiomes to aid in the protection of the seedling towards biotic (pathogens) and abiotic (e.g., climate) stresses, going towards more resilient cropping systems.
- Investigate into optimised seed microbiomes and their implications, taking into account local variation and adaptation.
- Investigate the effect of seed production conditions, harvesting, treatments and seed storage.
- Place more emphasis on producing and maintaining high seed vigour to further improve stress resilience of seedlings.

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- Study the interactions between crop genetics, the seed microbiome and seed vigour, in particular the role of crop diversity and overall diversity in production systems and incorporate this in breeding programs.
- Train seed producers, seed companies and farmers on the role of the seed microbiome and seed vigour.

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Annex

References with abstracts for background information

Antonovsky, A. (1996) The salutogenic model as a theory to guide health promotion. Health promotion international. 11, 11-18. https://doi.org/10.1093/heapro/11.1.11

This paper provides a critical look at the challenges facing the field of health promotion. Pointing to the persistence of the disease orientation and the limits of risk factor approaches for conceptualizing and conducting research on health, the salutogenic orientation is presented as a more viable paradigm for health promotion research and practice. The Sense of Coherence framework is offered as a useful theory for taking a salutogenic approach to health research.

Das Gupta, P.R. and Austenson, H.M. (1973) Analysis of Interrelationships among Seedling Vigor, Field Emergence, and Yield in Wheat1. Agron. J. 65, 417-422.

To evaluate various seed quality criteria, 86 samples of spring wheat (*Triticum aestivum* L. 'Manitou'), obtained from farmers in 1969, were grown in the same year with and without Panogen 15 seed treatment in replicated field trials at three locations in Saskatchewan. Untreated seed samples were grown again in 1970 at one of the locations. Determinations were made in the laboratory of various seed and seedling characteristics supposedly related to seedling vigor. Grain yield was increased significantly due to Panogen 15 treatment by 2.5 and 4.9% at two of the three locations. Seed samples high in 'unaided' vigor as reflected particularly by a modified germination test of untreated seeds, showed little response to the fungicidal treatment. Yield variations between samples were most consistently dependent on standard germination, 02 uptake, and field emergence. It was concluded that the standard germination test could be supplemented with other tests to more reliably assess expected crop performance. The rate of 02 uptake by seed during the 8th and 9th hours of imbibition was found satisfactory. Further research to develop a rapid and efficient method of determining early seedling growth in darkness is recommended.

Döring, T.F., Pautasso, M., Finckh, M.R. and Wolfe, M.S. (2012) Concepts of plant health – reviewing and challenging the foundations of plant protection. Plant Pathology. 61, 1-15. https://doi.org/10.1111/j.1365-3059.2011.02501.x

Plant health is a frequently used but ill-defined term. However, there is an extensive literature on general health definitions and health criteria in human medicine. Taking up ideas from these philosophical debates, concepts of plant health are reviewed and a framework developed to locate these concepts according to their position in several philosophical controversies. In particular, (i) the role of values in defining plant health in a naturalist versus a normativist approach; (ii) negative and positive definitions of plant health; (iii) reductionist

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versus holistic perspectives; (iv) the focus on functionality versus resilience, i.e. the ability of the plant to perform under stress with or without human interference; (v) materialist versus vitalist approaches; and (vi) biocentric versus anthropocentric views, are surveyed. The ways in which these perspectives relate to mainstream and alternative approaches to plant protection are explored and we suggest how the contradicting views might be reconciled. It is argued that none of these perspectives is without inherent contradictions, but that by combining contrasting approaches it is possible to provide a comprehensive though fuzzy concept. Rather than giving a new definition of plant health, a conceptual framework is developed that suggests what questions may be answered in debates on plant health issues and how such debates could be organized.

Hartmann, M., Frey, B., Mayer, J., Mäder, P. and Widmer, F. (2015) Distinct soil microbial diversity under long-term organic and conventional farming. The ISME journal. 9, 1177-1194. https://doi.org/10.1038/ismej.2014.210

Low-input agricultural systems aim at reducing the use of synthetic fertilizers and pesticides in order to improve sustainable production and ecosystem health. Despite the integral role of the soil microbiome in agricultural production, we still have a limited understanding of the complex response of microbial diversity to organic and conventional farming. Here we report on the structural response of the soil microbiome to more than two decades of different agricultural management in a long-term field experiment using a high-throughput pyrosequencing approach of bacterial and fungal ribosomal markers. Organic farming increased richness, decreased evenness, reduced dispersion and shifted the structure of the soil microbiota when compared with conventionally managed soils under exclusively mineral fertilization. This effect was largely attributed to the use and quality of organic fertilizers, as differences became smaller when conventionally managed soils under an integrated fertilization scheme were examined. The impact of the plant protection regime, characterized by moderate and targeted application of pesticides, was of subordinate importance. Systems not receiving manure harboured a dispersed and functionally versatile community characterized by presumably oligotrophic organisms adapted to nutrient-limited environments. Systems receiving organic fertilizer were characterized by specific microbial guilds known to be involved in degradation of complex organic compounds such as manure and compost. The throughput and resolution of the sequencing approach permitted to detect specific structural shifts at the level of individual microbial taxa that harbours a novel potential for managing the soil environment by means of promoting beneficial and suppressing detrimental organisms.

Klaedtke, S., Jacques, M.-A., Raggi, L., Préveaux, A., Bonneau, S., Negri, V., Chable, V. and Barret, M. (2016) Terroir is a key driver of seed-associated microbial assemblages. Environmental Microbiology. 18, 1792-1804. 10.1111/1462-2920.12977

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Seeds have evolved in association with diverse microbial assemblages that may influence plant growth and health. However, little is known about the composition of seed-associated microbial assemblages and the ecological processes shaping their structures. In this work, we monitored the relative influence of the host genotypes and terroir on the structure of the seed microbiota through metabarcoding analysis of different microbial assemblages associated to five different bean cultivars harvested in two distinct farms. Overall, few bacterial and fungal operational taxonomic units (OTUs) were conserved across all seed samples. The lack of shared OTUs between samples is explained by a significant effect of the farm site on the structure of microbial assemblage, which explained 12.2% and 39.7% of variance in bacterial and fungal diversity across samples. This site-specific effect is reflected by the significant enrichment of 70 OTUs in Brittany and 88 OTUs in Luxembourg that lead to differences in co-occurrence patterns. In contrast, variance in microbial assemblage structure was not explained by host genotype. Altogether, these results suggest that seed-associated microbial assemblage is determined by niche-based processes and that the terroir is a key driver of these selective forces.

Lupatini, M., Korthals, G.W., de Hollander, M., Janssens, T.K.S. and Kuramae, E.E. (2017) Soil Microbiome Is More Heterogeneous in Organic Than in Conventional Farming System. Frontiers in Microbiology. 7. https://doi.org/10.3389/fmicb.2016.02064

Organic farming system and sustainable management of soil pathogens aim at reducing the use of agricultural chemicals in order to improve ecosystem health. Despite the essential role of microbial communities in agro-ecosystems, we still have limited understanding of the complex response of microbial diversity and composition to organic and conventional farming systems and to alternative methods for controlling plant pathogens. In this study we assessed the microbial community structure, diversity and richness using 16S rRNA gene next generation sequences and report that conventional and organic farming systems had major influence on soil microbial diversity and community composition while the effects of the soil health treatments (sustainable alternatives for chemical control) in both farming systems were of smaller magnitude. Organically managed system increased taxonomic and phylogenetic richness, diversity and heterogeneity of the soil microbiota when compared with conventional farming system. The composition of microbial communities, but not the diversity nor heterogeneity, were altered by soil health treatments. Soil health treatments exhibited an overrepresentation of specific microbial taxa which are known to be involved in soil suppressiveness to pathogens (plant-parasitic nematodes and soil-borne fungi). Our results provide a comprehensive survey on the response of microbial communities to different agricultural systems and to soil treatments for controlling plant pathogens and give novel insights to improve the sustainability of agro-ecosystems by means of beneficial microorganisms.

Matsumoto, H., Fan, X., Wang, Y., Kusstatscher, P., Duan, J., Wu, S., Chen, S., Qiao, K., Wang, Y., Ma, B., Zhu, G., Hashidoko, Y., Berg, G., Cernava, T. and Wang, M. (2021)

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Bacterial seed endophyte shapes disease resistance in rice. Nature Plants. 7, 60-72. https://doi.org/10.1038/s41477-020-00826-5

Cereal crop production is severely affected by seed-borne bacterial diseases across the world. Locally occurring disease resistance in various crops remains elusive. Here, we have observed that rice plants of the same cultivar can be differentiated into disease-resistant and susceptible phenotypes under the same pathogen pressure. Following the identification of a seed-endophytic bacterium as the resistance-conferring agent, integration of high-throughput data, gene mutagenesis and molecular interaction assays facilitated the discovery of the underlying mode of action. Sphingomonas melonis that is accumulated and transmitted across generations in disease-resistant rice seeds confers resistance to disease-susceptible phenotypes by producing anthranilic acid. Without affecting cell growth, anthranilic acid interferes with the sigma factor RpoS of the seed-borne pathogen Burkholderia plantarii, probably leading to impairment of upstream cascades that are required for virulence factor biosynthesis. The overall findings highlight the hidden role of seed endophytes in the phytopathology paradigm of 'disease triangles', which encompass the plant, pathogens and environmental conditions. These insights are potentially exploitable for modern crop cultivation threatened by globally widespread bacterial diseases.

Nelson, E.B., Simoneau, P., Barret, M., Mitter, B. and Compant, S. (2018) Editorial special issue: the soil, the seed, the microbes and the plant. Plant and Soil. 422, 1-5. https://doi.org/10.1007/s11104-018-3576-y

Despite many decades of little interest and research attention, the microbiota of seeds is now developing into a major focus area for the exploration and understanding of plant microbiomes and beneficial plant-microbial interactions. Seeds, like no other plant organ, provide insights into the origin of plant microbiota, but also how the interactions of seed-associated microbes may be utilized to improve plant growth. This Special Issue focusing on soil, seeds, plant and microorganisms has highlighted important advances in understanding the complex plant-seed-soil-microbe interface. While important foundational data on microbial taxa, their putative functions and interactions with other plant parts and the soil are discussed. This Special Issue also points the way for additional studies to gain a more comprehensive knowledge and understanding of the ecology of seed microbiota. Presently, our knowledge of the ecology of seed microbiota lacks far behind our understanding of the rhizosphere and phyllosphere microbiota. And while the work highlighted in this Special Issue represents only the beginning of what may be a fruitful path forward in understanding the origin of seed microbiota, the routes and modes of seed colonizing, the sites of establishment within seeds, and the function of these microbes in plant and soil habitats, we can expect great advances in coming years. Many questions remain. For example, what factors determine efficient seed colonization by microorganisms and the successful establishment of populations in and on seeds? As with the rhizosphere and phyllosphere, does the plant physiotype shape the composition of microbial seed assemblages? Are seed microbiota different between plant families? What are the factors that allow microbes to

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persist in dormant seeds? What are the functional traits necessary for microbes to be able to invade and establish in plant seeds? Very often dormancy in seeds is concomitant with extreme drying begging the question of whether microbes require some level of desiccation tolerance to survive during seed dormancy. Some pioneer studies are indeed pointing to the capacity of some microorganisms to cope with stress conditions likely accompanying the seed maturation process as an essential component of efficient seed colonization (Pochon et al. 2012, 2013). What role do seed microbiota play in the assembly of the plant microbiota? Because the seed microbiota represent the initial microbial colonizers of emerging seedlings before they recruit microbes from the surrounding environment (rhizosphere or phyllosphere), the seed microbiota might play important roles in the assembly and function of the plant microbiome. While these and many other questions remain to be answered, the research highlighted in this Special Issue suggests that the future is bright for this emerging and productive area of inquiry.

Wassermann, B., Cernava, T., Müller, H., Berg, C. and Berg, G. (2019) Seeds of native alpine plants host unique microbial communities embedded in cross-kingdom networks. Microbiome. 7. https://doi.org/10.1186/s40168-019-0723-5

Background: The plant microbiota is crucial for plant health and growth. Recently, vertical transmission of a beneficial core microbiota was identified for crop seeds, but for native plants, complementary mechanisms are almost completely unknown. Methods: We studied the seeds of eight native plant species growing together for centuries under the same environmental conditions in Alpine meadows (Austria) by qPCR, FISH-CLSM, and amplicon sequencing targeting bacteria, archaea, and fungi. Results: Bacteria and fungi were determined with approx. 1010 gene copy numbers g-1 seed as abundant inhabitants. Archaea, which were newly discovered as seed endophytes, are less and represent only 1.1% of the signatures. The seed microbiome was highly diversified, and all seeds showed a species-specific, highly unique microbial signature, sharing an exceptionally small core microbiome. The plant genotype (species) was clearly identified as the main driver, while different life cycles (annual/perennial) had less impact on the microbiota composition, and fruit morphology (capsule/achene) had no significant impact. A network analysis revealed significant co-occurrence patterns for bacteria and archaea, contrasting with an independent fungal network that was dominated by mutual exclusions. Conclusions: These novel insights into the native seed microbiome contribute to a deeper understanding of seed microbial diversity and phytopathological processes for plant health, and beyond that for ecosystem plasticity and diversification within plant-specific microbiota.

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