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REVIEW

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Microbial effects on plant phenology and fitness

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Abstract

Plant development and the timing of developmental events (phenology) are tightly coupled with plant fitness. A variety of internal and external factors determine the timing and fitness consequences of these life-history transitions. Microbes interact with plants throughout their life history and impact host phenology. This review summarizes current mechanistic and theoretical knowledge surrounding microbe-driven changes in plant phenology. Overall, there are examples of microbes impacting every phenological transition. While most studies have focused on flowering time, microbial effects remain important for host survival and fitness across all phenological phases. Microbe-mediated changes in nutrient acquisition and phytohormone signaling can release plants from stressful conditions and alter plant stress responses inducing shifts in developmental events. The frequency and direction of phenological effects appear to be partly determined by the lifestyle and the underlying nature of a plant–microbe interaction (i.e., mutualistic or pathogenic), in addition to the taxonomic group of the microbe (fungi vs. bacteria). Finally, we highlight biases, gaps in knowledge, and future directions. This biotic source of plasticity for plant adaptation will serve an important role in sustaining plant biodiversity and managing agriculture under the pressures of climate change.

KEYWORDS

flowering, life history, microbiome, phenology, phyllosphere, plant development, plant growth promoting bacteria, plant–microbe interactions, reproduction, rhizosphere

Plant–microbe associations played an important role in the initial colonization of land by the ancestors of terrestrial plants (Wang et al., 2010) and remain critical for plant nutrition acquisition, defenses, and overall health (Smith and Read, 2010). Microbes can influence plant traits, ecology, and even the evolution of plant lineages (Osborne et al., 2018; Magnoli and Lau, 2020). Plant phenology—the timing of plant developmental events—is determined by both genotype and environmental factors (Burghardt et al., 2016; Taylor et al., 2017). Temperature, moisture, and photoperiod are major, but not the sole, external regulators of plant signaling pathways and nutrient uptake, which subsequently promote or suppress phenological progression. Compounding evidence suggests that microbes can manipulate environmental cues, impact host gene expression, and otherwise affect traits associated with life-history transitions (i.e., phenological traits [Table 1]; Gundel et al., 2006; Pinedo et al., 2015; Lu et al., 2018).

Microbial activities may narrow or widen the duration of plant life-history stages and accelerate or delay life-history events, which could have fitness consequences. For example, laboratory manipulations of soil microbes affect flowering time and selection on flowering time (Lau and Lennon, 2011, 2012; Wagner et al., 2014; Chaney and Baucom, 2020). Alterations in flowering time can impact pollinator populations and plant yield and may lead to premature or prolonged allergy seasons (Derocles et al., 2018; Shrestha et al., 2018; Sapkota et al., 2019). However, flowering is merely a single phenophase; timing of events throughout the entire life cycle matter for plant survival and reproductive success, as changes in earlier phenological transitions (germination, budburst, and vegetative stages) have downstream effects on the environments experienced by subsequent developmental stages (flowering, fruiting, and senescence; Burghardt et al., 2016; Taylor et al., 2017). For these reasons, phenological traits are crucial to the productivity of crop plants and the persistence of wild plants, particularly in the face of ongoing climate change.

Due to the ubiquitous nature of microbes across plant-associated environments and the importance of phenology, the effects of microbes on plant life-history timing deserve attention. Here, we review microbial impacts on phenological traits and synthesize these results based on theoretical predictions from

TABLE 1 Definitions of phenological traits discussed in this review

Term	Definition
Life-history timing	The timing of any developmental event with respect to either the age of the organism or the time of year
Phenology	The seasonal timing of a life-history event
Flowering time	Date of first flower
Fruiting time	Time to fruit maturity or seed abscission
Maturation time	Age at first flowering (perennials)
Senescence	Either the onset of seasonal dormancy (perennials), or death (annuals)
Mid-flowering events	Subdivided stages within flowering (e.g., date that the most flowers are open, date that the first individual flower senesces)
Phyllochron	Transition through distinct vegetative developmental stages (e.g., from juvenile to adult type leaves)
Budburst	Emergence of shoot tissue from a dormant vegetative state (i.e., a twig or rhizome)
Germination time	Days after planting until germination or date of germination within a single season
Germination probability/proportion	Proportion of seeds germinating within a defined timeframe (e.g., a single season or duration of an experiment)
Phenophase	Any distinct phase of the life cycle

resource allocation and life-history theory, mechanisms, and context-dependency. We briefly discuss how plant phenology can also affect microbial communities and microbial life histories. Finally, we consider the implications of this biotic source of plasticity for agriculture and plant adaptation to climate change.

PREDICTIONS FROM LIFE-HISTORY THEORY

Life-history theory predicts that delays in phenological transitions should only be favored if they offset the costs of slower time to reproduction (Roff, 1993). Thus, we would expect the effects of microbes on optimal timing of phenology transitions to depend on the nature of the interaction (e.g., parasites increasing mortality vs. symbionts providing resources), the life history and reproductive strategy of the plant, and the particular stage in development (Figure 1). Changes in optimal phenological timing across contrasting microbial environments in space or time may generate selection pressures, and plants may also respond plastically.

The first phenological “decision” in the life of a plant is when to germinate. Germination timing determines the conditions that a young seedling will experience and has downstream effects on the conditions experienced by subsequent plant life stages (Burghardt et al., 2016). Early germination can lengthen growing seasons and let plants secure more resources, ultimately increasing reproductive fitness (Akiyama and Ågren, 2014), and earlier germinants may escape predator- or parasite-induced mortality, increasing survival to reproduction (Beckstead et al., 2007). Alternatively, earlier germination can decrease fitness if early germinants experience harsher conditions, such as chilling or drought (Thomson et al., 2017). Thus, if seeds are exposed to microbes that ameliorate cold or drought stress (such as certain bacteria and fungi, Hubbard et al., 2012; Subramanian et al., 2016), the optimal germination time will be earlier. If seeds are instead or additionally infected with pathogenic microbes, optimal germination timing might depend on whether the risks to late germinants and dormant seeds are greater than they are for early germinants (as for some fungal pathogens; Enebak et al., 1998; Enebak and Carey, 2004). Perennial plants in seasonal environments repeat such growth initiation patterns yearly and face similar fitness trade-offs in timing, with earlier budburst increasing potential growth but risking frost damage (Caffarra and Donnelly, 2011). Like seeds, they may sometimes benefit from extended dormancy (Shefferson et al., 2018). On the other hand, root phenology and shoot phenology are often unlinked, and roots are not as tightly constrained by seasons as shoot tissues (Radville et al., 2016). Thus, plants may have fewer or no costs for advancing root phenology early in the season if beneficial microbes are present.

Later in the plant's life, microbes can modify the amounts and kinds of resources available for plants, changing the relative costs and benefits of delays in life-history transitions (Charlesworth et al., 1991). Without trade-offs, earlier and longer duration of reproduction is best. However, many factors can favor a delayed onset of flowers. For example, plants might delay reproduction if larger size increases total seed output (Fournier-Level et al., 2013), if there are strong trade-offs between reproduction and survival in perennials (Primack, 1979) or if there are physiological limits: flower and fruit development requires sufficient resources, but reproductive tissue generally acquires negligible resources. In such cases, if plants associate with microbes that provide nutrients or ameliorate stressors, then the optimal onset of

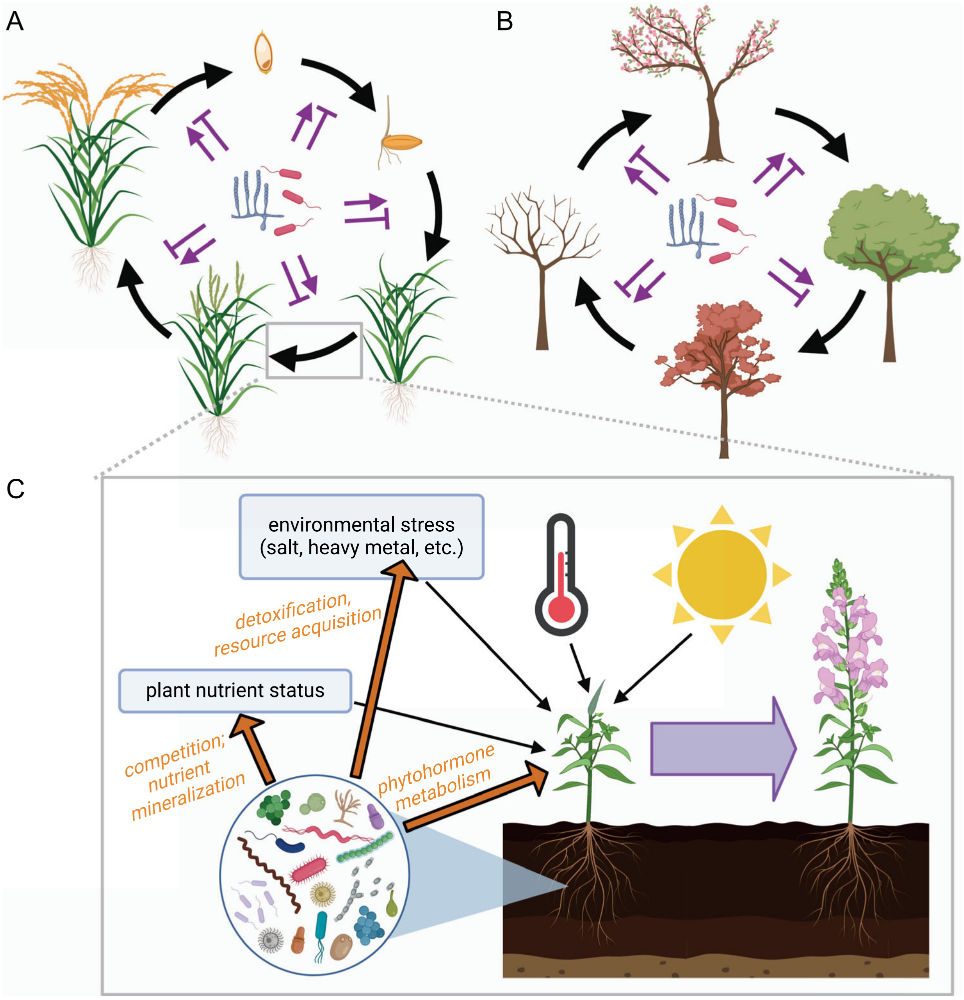

FIGURE 1 Microbial symbionts and neighbors can alter the timing of all life-history transitions. (A) In annual plants, microbes influence (clockwise from top left) fruiting and senescence, germination, vegetative growth stages, and transition to flowering. (B) In perennial plants, microbes additionally influence (clockwise from top left) emergence from dormancy and flowering, budburst and vegetative growth, leaf senescence, and return to dormancy. (C) Microbes can affect plant phenology via a number of mechanisms, some of which are direct (e.g., production or degradation of key phytohormones) and some of which are indirect (e.g., modifying the plant's immediate environment, such as water or nutrient availability, or modifying the ability of the plant to perceive and respond to environmental cues, such as by blocking light and temperature sensing or priming plant stress defenses). Microbial taxa vary in which pathways they influence and in magnitude and direction of effects; for instance, they can either ameliorate or exacerbate stress. Plants integrate microbial effects with other direct cues such as temperature and photoperiod to time life-history transitions, such as flowering

reproduction may be shifted earlier and the optimal duration longer. If plants are instead infected with pathogenic microbes that reduce survival, the optimal time to reproduction may be reduced because high mortality risks late in the growing season can obviate many benefits of reproductive delays (Fournier-Level et al., 2013).

APPROACH

Our literature search of the Web of Science (Institute of Scientific Information [Philadelphia, PA], 2020) required either reference to "phenology" or "life history," or words describing phenological events in plants (e.g., "flower*", "fruit*") and words describing microbes (e.g., "microb*", "inoculat*") within 30 words of each other (approximately one English sentence; Moore, 2011) and returned 935 records. We scored the first 500 (sorted by "relevance" in Web of Science) into two broad categories: (1) studies that experimentally tested microbial effects on plant phenology and (2) studies about other links between plants, phenology and microbes, such as how plant or microbial phenology influenced which plants and microbes interact. We discarded those that fit neither category. For both categories, we recorded microbial taxonomy and the plant organ location of the microbes (e.g., seed, root, leaf). For records that fell into the first category, we further recorded the phenological trait(s) measured (Table 1), direction of effect (earlier or delayed; expanded or narrowed), and the primary mechanism of microbial effects (nutrient provision, phytohormones, other beneficial, pathogen). We also recorded the method of microbial manipulation and other aspects of each study (Appendix S1). We evaluated whether scored aspects of studies explained the

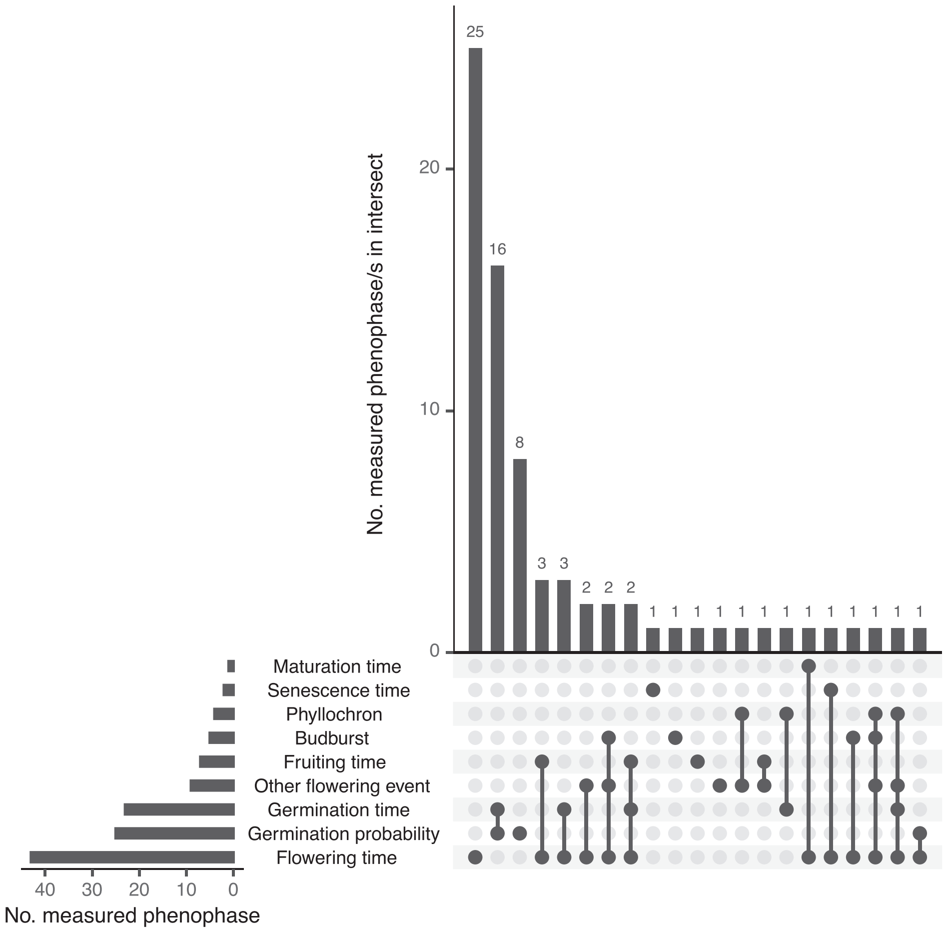

FIGURE 2 The number of studies among 500 scored records that included tests for microbial effects on a particular phenophase is shown in the lower left-hand graph. In the main, right-hand plot, the studies are separated into those including tests of microbial effects on multiple phenophases (combinations of phenophases indicated by connected dots) or of only one phenophase (single dots). Plotting software: UpSetR (Conway et al., 2017)

proportion of significant earlier or delayed effects (two separate presence–absence response variables) using linear models with a Bernoulli distribution (Appendix S1; Hadfield, 2010; R Core Team, 2017). Lastly, we noted whether selection on plant phenological traits was measured, and if so, what fitness component(s) was used. Because this type of study was scarce, we inspected the forward and reverse citations of each for additional studies quantifying microbe-driven shifts in selection on phenology.

We uncovered a rich literature on phenological links between plants and microbes (data available at https://zenodo.org/record/507165). Strikingly, microbe-induced shifts in phenology were reported in 88% of the studies that tested for them, although this may be an overestimate due to the bias against publishing negative results (Fanelli, 2012). These effects are widespread across diverse microbial and plant taxa and have important implications for the ecology and evolution of these organisms, including in the context of climate change and agricultural sustainability. Our search identified several high-priority topics for future work, motivated by the current lack of available information, their particular importance, or both.

MICROBES CAN INFLUENCE TIMING OF ALL PLANT LIFE-HISTORY TRANSITIONS

From seed to seed, plants are exposed to microbes at every point of their life cycles. Microorganisms have been documented to alter every life-history transition or phenological trait, from the probability or timing of germination (25/26 and 17/19 studies, respectively, finding an effect of microbes) to flowering time (37/43 studies) to fruit maturation and senescence (6/7 and 1/2 studies, respectively). Bacteria and mycorrhizal fungi were the microbial groups that most reliably affected plant phenology, with significant effects observed in 24/25 and 16/20 studies, respectively. Bacteria were also more commonly evaluated than non-mycorrhizal fungi and microbial mixtures (18 and 16 studies, respectively). Flowering time was the most-studied phenological trait and frequently sensitive to microbes. All stages other than flowering and germination were relatively understudied (Figure 2) and could not be included in most of our models. Yet some stages appear to be more responsive to microbes than flowering and germination time (fruiting time and phyllochron, Appendix S2), and a few studies reported microbial effects on other traits (senescence time, maturation time, mid-flowering events), suggesting that these life stages deserve greater attention. For example, in the two studies considering senescence, mycorrhizal fungi had no impact on timing in corn (Colombo et al., 2017), but growth-promoting bacteria advanced senescence in *Arabidopsis thaliana* (Poupin et al., 2013). Microbial effects on phenology of ferns, mosses, and other non-seed plants are critically understudied: these plant groups were missing from our search results (Appendix S3).

MECHANISMS OF MICROBE-INDUCED PHENOLOGICAL SHIFTS

Plant development is orchestrated by intricate source–sink pathways: the bidirectional movement of photosynthates via the phloem provides nutrients and energy to different plant tissue destinations as phenological stages progress. During vegetative growth, resources are directed to new leaves and root storage, whereas costly flowers and fruits are the major sinks during reproductive growth (Zamski and Schaffer, 2017). This source–sink resource partitioning is regulated by hormonal, sugar, and environmental cues (e.g., temperature, moisture, bioavailable nitrogen). The impacts of photoperiod and temperature on plant circadian clocks and other signaling pathways involved in growth and development have been well documented (Figure 1; Singh et al., 2017; Cao et al., 2021). Emerging research indicates that microbes can interrupt these signaling pathways (Huot et al., 2014) by supplying or degrading plant hormones and nutrients (Egamberdieva et al., 2017; Kuypers et al., 2018). In turn, plant hormones can modulate the plant-associated microbiome (Huot et al., 2014; Carvalhais et al., 2015; Lebeis et al., 2015). Therefore, not surprisingly, numerous bacteria and fungi that shift host phenology have also been linked to alterations in nutrient acquisition and hormonal cues related to growth and defense.

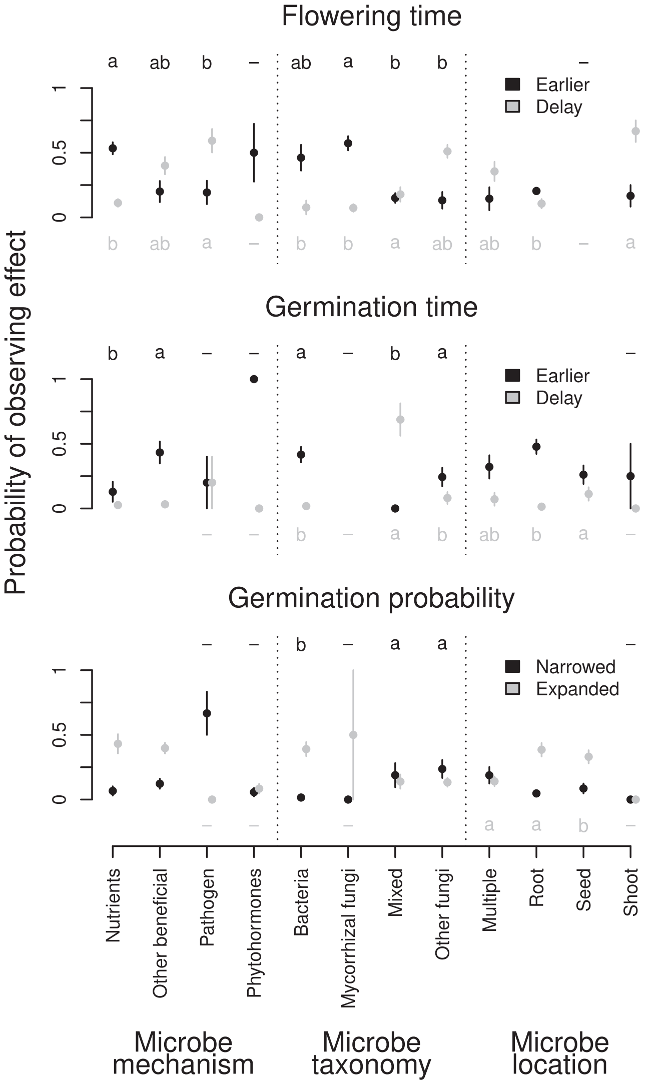

FIGURE 3 The probability that a test found flowering time (top) or germination time (middle) to happen significantly earlier (black) or to happen significantly later (gray) when a microbial treatment was applied. On the bottom, the probability that a test found a narrowed (black) or expanded (gray) likelihood of germination. Sections separated by vertical lines indicate separate model tests for differences between categories. Letters indicate significant differences in binomial models, where the difference is significant (90% highest posterior density interval, HPDI; see Appendix S6 for 95% HPDI) at the latent variable level, and the letters are ordered from highest probability to lowest. Categories with 10 or fewer data points (indicated by "-") were excluded from model tests, and so differences from other categories cannot be tested. Points and bars are study-weighted means and ± standard errors of the mean, respectively. Note that because model random effects are fit on the logistic scale, model-fit differences and study-weighted mean probabilities do not perfectly align

Nutritional mechanisms

Microbial alleviation of nutrient limitation—especially bioavailable nitrogen, which is required in large amounts for flower and fruit production (Zamski and Schaffer, 2017)—can allow phenological transitions. We hypothesized that microbes supplying nutrients would be likely to defray costs of early flowering and early germination and would be more likely to accelerate phenological events than pathogens or other microbes. A number of results supported this hypothesis. Microbes known to supply nutrients were marginally more likely to accelerate flowering and least likely to delay it, though other beneficial microbes (where mechanism of benefit is unknown, or not nutrients or phytohormones) were marginally more likely to increase the speed of germination (Figure 3; Appendix S4). Likewise, mycorrhizal fungi were likely to accelerate flowering time, whereas inoculations with mixed taxonomic groups or whole communities were more likely to delay this transition (Figure 3). Notably, both the bacteria and non-mycorrhizal fungi taxonomic categories included both nutritional mutualists and pathogens (Appendix S5). Bacteria on average accelerated germination time (Figure 3); however, bacterial effects on germination could not be directly compared to the effects of mycorrhizal fungi due to a scarcity of studies.

Often, microbial effects on phenology were specifically linked to nutrients, including for stages that were infrequently studied (fruiting, 7 studies; vegetative stages, 9 studies). Rhizobia and a beneficial *Pseudomonas* strain accelerated flowering in lentils and other legumes by increasing uptake of nitrogen and phosphorus (Thakur et al., 1999; Singh et al., 2008). Inoculation of orchid seeds with mycorrhizal fungi in low-nutrient media restored germination and early developmental growth to levels seen on high-nutrient media (Guimarães et al., 2013). The acceleration of budburst and flowering by mycorrhizal fungi can also be due to enhanced nutrient uptake (Sohn et al., 2003; Vaingankar and Rodrigues, 2012; Yguel et al., 2014) or increased carbon resources in storage organs (Scagel, 2003; Scagel and Schreiner, 2006), but mycorrhizal fungi do not always accelerate budburst (Berdeni et al., 2018). Nutrient effects of microbes on phenology may even pass through seeds and extend across generations (Shumway and Koide, 1994). Cumulative nutrient-acquisition effects may be more likely in perennials and especially evergreen perennials, which maintain active tissue year-round. While fewer studies focused on these types of plants (28 and 4, respectively), their phenological responses to microbes may differ from those of annuals (Appendix S6). Indeed, because timing shifts could generally accumulate across life stages, it is unclear whether similar effects (e.g., mixed microbial taxa treatments delay both germination and flowering) are independent effects, as only eight studies considered both early-life and late-life phenological stages (Figure 2).

Hormonal mechanisms

Notably, microbes known to affect phytohormone signaling had similar effects on flowering time as microbes known to affect nutrients (Figure 3). Hormones and nutrients often interact in the signaling cascades leading to major phenology events. Studies that clearly link microbe-driven nutrient acquisition to both hormonal pathways and phenology are rare, but suggest that microbial manipulation of hormones and nutrients may generally co-mediate flower induction. For instance, Lu et al. (2018) found that root exudates of certain plant varieties can select distinct microbiota that increase nitrogen availability through nitrification. The increased nitrogen availability, in turn, delays flowering via tryptophan-dependent production of indole acetic acid, a phytohormone that stimulates vegetative growth and suppresses flowering. In another example, arbuscular mycorrhizal fungi (AMF) accelerated flowering in wild-type tomato but not in mutants deficient in the perception of ethylene and light, which also failed to acquire phosphorus from the AMF (Chialva et al., 2016).

Hormone signaling in plants additionally relates information about biotic and abiotic stressors. Stress-related hormones (e.g., salicylic acid [SA] and jasmonic acid [JA]) can suppress growth hormones (e.g., auxin and gibberellin), and resource allocation to physical defenses can stunt or delay plant development. Recent evidence shows that SA and JA also affect microbial community assembly (Huot et al., 2014; Carvalhais et al., 2015; Lebeis et al., 2015). During stress, altered hormone levels trigger immune defenses, affect microbial colonization, and could have downstream consequences on flowering time. For example, the fungus *Pochonia chlamydosporia* accelerates flowering in *Arabidopsis thaliana*, but its successful recruitment to the microbiome depends on JA (Zavala-Gonzalez et al., 2017). Similarly, the plant-growth-promoting *Burkholderia phytofirmans* strain PsJN induces early bolting in multiple hosts, an effect linked to JA signaling, auxin homeostasis, and gibberellin biosynthesis (Poupin et al., 2013; Pinedo et al., 2015). Indeed, recruitment of microbes that manipulate flowering time may be an important stress response strategy.

Other mechanisms

Microbes can alter plant phenology through mechanisms not primarily related to hormones and nutrition, as phenology can be limited by other factors that microbes modify, such as water availability for early germinants (Hubbard et al., 2012; Thomson et al., 2017). For example, rhizobia effects on soybean germination, flowering, and fruiting time were similar to effects of a chemical treatment that attracted water to seeds and seedlings (Gayathri et al., 2008), and plant-associated microbes capable of heavy metal detoxification improved germination probability and seedling survival (Sánchez-López et al., 2018). Clearly, microbes regulate host phenology through a variety of mechanisms, and much more work is needed to understand why and how distinct microbes affect plant phenology. Characterizing underlying mechanisms is even more challenging considering that pathway regulation and impacts can be transient and context-dependent.

CONTEXT DEPENDENCY: INTERACTIONS WITH THE ABIOTIC AND BIOTIC ENVIRONMENT

Context dependency is rampant in all categories of species interactions (Chamberlain et al., 2014). Plant–microbe interactions are no exception and depend on adjacent biotic interactions and abiotic properties of the local environment (Morris et al., 2007; Shantz et al., 2016). Conditionality of microbial phenological effects across biotic and abiotic environments may be especially important in light of the fact that most studies (56/74) had no field component: both the biotic and abiotic environment experienced by plants in the field can be radically different from controlled environments.

Abiotic sources of context dependency

It has long been hypothesized that biotic interactions are more likely to be mutually beneficial when the abiotic environment is stressful to one or both partners (Bertness and Callaway, 1994). Furthermore, increasing benefits in stressful sites might result in the evolution of increased mutualism (O'Brien et al., 2018).

Accumulating evidence suggests that microbial effects on plant phenological traits may be a key mechanism supporting these hypotheses, particularly for germination. Soil and endophytic microbes may enhance germination in nutrient-deficient soils, as observed in the Florida rosemary scrub ecosystem (David et al., 2020) and under salt stress (Piernik et al., 2017). Beneficial microbes, including pre-treatment of seeds with the best local strains (Balshor et al., 2017) could be useful to improve seed germination, a major bottleneck in large-scale ecosystem restoration plantings (Larson et al., 2015) especially in stressful environments. Conversely, these effects could contribute to invasion success across distinct habitats: the same soil microbiota that improved germination of St. John's wort in limestone barrens had the opposite effect in more hospitable old-field environments (Petipas et al., 2020).

Microbial effects on flowering time were also linked to improving stress tolerance. In *Arabidopsis thaliana*, a mixed microbial community accelerated flowering only under drought conditions (Fitzpatrick et al., 2019). Likewise, a *Burkholderia* strain accelerated bolting in *A. thaliana* only under salt stress (Pinedo et al., 2015), a soil slurry restored normal flowering time in *Elsholtzia splendens* under copper stress (Jin et al., 2015), and mycorrhizal alleviation of nutrient and water stress was tied to earlier flowering and higher fitness in *Erodium oxyrrhynchum* (Sun et al., 2008). Notably, either faster or slower flowering can be an adaptive response to stress (Charlesworth et al., 1991; Fournier-Level et al., 2013; Gezon et al., 2016), and various studies document microbe-induced reproductive delays that increase host fitness under stressful conditions. For instance, under drought, *Phyllobacterium brassicacearum* increases not only the duration of vegetative growth, but also biomass and water-use efficiency of *A. thaliana* (Bresson et al., 2013). Importantly, not every study that tested stress-dependent effects and benefits observed them: effects of AMF on *Medicago truncatula* flowering and biomass were consistent across nutrient treatments (Liu et al., 2017), and in *Zantedeschia* sp., nutrient availability impacted microbial effects on flowering time, but not fitness (Scagel and Schreiner, 2006).

While microbes generally ameliorate plant stressors (Porter et al., 2020), microbes can exist on a mutualist–parasite spectrum (David et al., 2018); for example, the effects of AMF shift from mutualism to parasitism under certain, rare, conditions (Johnson et al., 1997; Frederickson, 2017). Stress exacerbation could also act through phenology; for example, microbial communities more often reduced germination of several plant species in the presence of a stressful allelopathic chemical (David et al., 2018). While there are few similar examples, our results might be biased toward studies testing species with known plant-growth-promoting effects. We also note that fitness effects may trade-off across life stages; for instance, an endophyte that increased growth also reduced germination probabilities (Kazenel et al., 2015).

Mechanistically, microbes may have stress-dependent effects by constitutively priming plant stress responses, as was seen in response to salt (Pinedo et al., 2015). Alternatively, microbes may alter the ability of plants to sense the abiotic environment. Endophytic fungi delayed germination in *Lolium multiflorum* by altering the ability of seeds to sense and respond to chilling and light requirements (Gundel et al., 2006). Such microbial signal-blocking could explain effects of fungi on germination timing that were only observed under certain cold treatments in *Elymus canadensis* (Connolly and Orrock, 2015).

Biotic sources of context-dependency

Not all context-dependency in species interactions is due to abiotic conditions; biotic context can also have dramatic impacts on outcomes (Cardinale et al., 2003; Morris et al., 2007). Indeed, complex communities were more likely to delay flowering and germination (Appendix S6). For example, a whole soil community generally reduced germination rate and success across 19 species, but a single strain from the community mostly increased germination (Balshor et al., 2017). Sub-additive effects were common, such as among phyllosphere fungi that delayed flowering in *Arabidopsis thaliana* (Zahn and Amend, 2019) and for acceleration of flowering in lentils by *Rhizobium* and *Pseudomonas* (Singh et al., 2008).

However, effects can be more complex: AMF influence on a range of phenological traits in *Brodiaea laxa* and *Zephyranthes* spp. sometimes weakened, strengthened, or even shifted in direction when the native soil community was present (Scagel, 2003, 2004). Even the abundance of a single microbe can change the direction of the effect on flowering (Garrido et al., 2010). Such complex interactions suggest that microbe–microbe interactions can alter microbe–plant interactions, emphasize the importance of studying natural communities, and highlight the need for caution when interpreting single-inoculant experiments (Vorholt et al., 2017).

Some microbe-induced shifts in flowering time, or the corresponding fitness consequences, accrue via other types of biotic context, such as herbivory and competition. In *Datura stramonium*, the effects of AMF reversed from accelerating to delaying flowering when 50% of leaf area was removed to mimic herbivory (Garrido et al., 2010). Inoculation with *Bradyrhizobium* strengthened the effects of neighboring plants on the timing of soybean flowering and fruiting (Viana et al., 2009). The fitness consequences of germination timing—which often responds to soil biota—depend on the density and growth rate of neighboring plants (Weinig, 2000). For outcrossing zoophilous plants, flowering overlap with pollinator activity is critical for reproduction (Rafferty and Ives, 2011). Reciprocally, changes to flowering time could have indirect impacts on plant fitness by altering pollinator survival (Davis et al., 2019). Although very few studies considered the consequences of microbe-induced phenological shifts for plant interactions with macroorganisms, these forms of context-dependence are likely to be ecologically and evolutionarily important.

PATHOGENS, COMMENSALS, AND MUTUALISTS AS DRIVERS OF PLANT PHENOLOGY EVOLUTION

Like insect herbivores, phytopathogenic microbes have played a critical role in shaping plant evolution (Upson et al., 2018). The most virulent pathogens can devastate entire plant populations, creating extremely strong selection pressure favoring genetic variants that confer resistance. On the other end of the spectrum, some mutualistic microbes (e.g., rhizobia and mycorrhizal fungi) confer such strong growth benefits that plants have evolved intricate molecular and physiological machinery to communicate with them (Streng et al., 2011). These important groups of microbes are not particularly noted for their effects on plant phenology; yet, many examples of such effects exist (Thakur et al., 1999; Liu et al., 2017; Berdeni et al., 2018; Davis et al., 2019). Thus, selection for optimal phenology may also have shaped plant interactions with pathogens, rhizobia, mycorrhizal fungi, and other phenology-shifting microorganisms.

Microbes as drivers of selection on plant phenology

The few studies that have explicitly linked phenological impacts of microbes to evolutionary processes have found that selection on phenology can change across microbial contexts. Several studies report that manipulation of the soil microbiota changed directional selection on flowering time from positive to neutral or even negative (Lau and Lennon, 2011, 2012; Wagner et al., 2014). In both *Ipomoea purpurea* and *Arabidopsis thaliana*, selection for earlier flowering was stronger in the presence of a complex soil microbiome, relative to sterile conditions (Fitzpatrick et al., 2019; Chaney and Baucom, 2020). And in maize, viral infection reversed the sign of the genetic correlation between flowering time and breeder-selected performance traits (Horn et al., 2013). So far, the mechanism linking microbes to the relationship between fecundity and flowering time has not been determined, but links between microbes, fitness, and germination are clearer.

Multiple studies reported a negative impact of fungal pathogens on germination probability, suggesting that pressure to avoid pathogens has likely shaped selection on germination timing. More generally, non-mycorrhizal fungi more often reduced the likelihood of germination than increased it (Figure 3). In *Elymus canadensis*, for example, fungicide treatment increased both the speed and probability of germination (Connolly and Orrock, 2015). Alternatively, some microbes (particularly bacteria) induce faster germination, which can help plants escape pathogens that specialize on new germinants, as observed in loblolly pine (Enebak et al., 1998; Enebak and Carey, 2004). In cases where pathogens establish more slowly in a season, responsiveness to germination-accelerating microbes should be evolutionarily favored.

Microbe-driven plasticity of phenological traits has fitness consequences for plants

In addition to their direct evolutionary impacts as agents of selection, microbes can alter plant fitness by simply shifting a phenological trait that is under selection for any reason. In plant populations where germination timing is under selection to ensure proper plant size during cold winter temperatures (Donohue et al., 2005), microbes that delay or speed germination could either reinforce or disrupt this coordination, depending on the direction of their effect. Similarly, in dry environments selection often favors earlier-flowering phenotypes that can reproduce before late-season drought becomes too severe. In one such habitat, soil microbiota shifted flowering time of a perennial mustard by up to 3 days, corresponding to a 12% change in fecundity under the local selective regime (Wagner et al., 2014). In crop breeding programs, slow or unreliable germination can preclude an otherwise high-performing genotype from selection for the next generation. Observations of microbe-induced germination delays are common in crops including soybean and corn (Naveed et al., 2014; Andrade et al., 2019). Notably, many ostensibly nonpathogenic microbes with no direct negative effects could nevertheless decrease plant fitness if they shift phenological traits in an unfavorable direction. However, the extent to which microbe-induced shifts in phenology align with selective pressures on phenology is currently unclear, due to the rarity of studies that quantified selection on phenological traits in any microbial context.

Beyond causing selection on and phenotypic plasticity of phenological traits, microbes can drive plant evolution in more subtle ways. In teosinte, for instance, rhizosphere communities altered patterns of genetic variance and covariance among flowering time and other traits (O'Brien et al., 2019), which determine these traits' potential to respond to both direct and indirect selection. The activity of floral microbes affects pollinator behavior, with implications for patterns of gene flow within and among plant populations (Rebolleda-Gómez et al., 2019; Russell and Ashman, 2019); seed and fruit microbes may have similar effects on dispersal and migration. Overall, genetic variation within plant species for phenological responses to microbes appears to be plentiful (Krauss et al., 2007; Chialva et al., 2016; Fitzpatrick et al., 2019; O'Brien et al., 2019), reinforcing the need for more research into the evolutionary causes and implications of these interactions.

Selective pressures on microbes

Plant phenology has the potential to influence microbial fitness, and microbial effects on phenology may evolve in microbial genomes, or as joint traits (Metcalf et al., 2019; Rebolleda-Gómez et al., 2019; O'Brien et al., 2021). For microbes, it can be advantageous to manipulate the development of the host plant to increase resources. For example, in annual plants, soil priming (exudation of organic C from roots) intensified throughout the vegetative growth period and started to decline after flowering (Cheng et al., 2003). Indeed, pathogens have evolved to manipulate life-history transitions to increase their probability of transmission (Jennersten, 1988). For such joint traits, we have often expected genes in closer temporal or physical proximity to the trait to have greater impacts (Dawkins, 1982), suggesting that microbes located aboveground would be more likely to influence flowering time. Compared to microbes in shoots, microbes in roots were less likely, and multi-location microbes equally likely, to affect flowering time. Similarly, microbes in seeds were more likely than root microbes to affect germination timing, but less likely to affect germination probability (Figure 3). However, few studies considered flower-inhabiting microbes, which manipulate the attraction of pollinators (Rering et al., 2018; Tsuji and Fukami, 2018; Cellini et al., 2019; Russell and Ashman, 2019). Floral microbes can be mutualistic or pathogenic, and some can migrate to the vascular bundles, becoming systemic and even passing on to seeds (Piqué et al., 2015; Kim et al., 2019; Chesneau et al., 2020). Thus, they have high potential for downstream consequences on plant traits, such as the timing of floral senescence and fruiting.

THE OTHER SIDE OF THE COIN: PLANTS INFLUENCE PHENOLOGY OF MICROBES

When considering all studies relevant to microbes, plants, and phenology, half addressed how microbes influence plant phenology (74 of 148), and the rest addressed the reverse: how plant or microbial phenology influence interaction outcomes (82 of 148). We suspect "reversed" effects might be equally common, as the timing of interactions relative to organism development can alter the strength or even the sign of the outcome across types of species interactions (Rudolf, 2019). Biases in these additional relevant records were similar to biases observed for effects of microbes on phenology alone: most studies considered soil or root microbes (118 of 148), especially mycorrhizae (50 studies), and only 21 considered microbes residing in multiple plant organs (Appendices S7, S8).

While microbial activities can affect plant phenology and selection on plant phenology, the reciprocal is also true: plants influence microbial phenology. It is well-known that roots influence germination of AMF spores (Gianinazzi-Pearson et al., 1989), and the absence or presence of carbon supplied by plants often promotes or breaks dormancy, respectively, in many microbes (Bever et al., 2012; Dijkstra et al., 2013). Plant influences on microbial phenology likely have evolutionary consequences for the microbes. For example, changes in source–sink sugar transport across plant phenophases or tissues could select between microbes that initiate growth more rapidly versus those that tolerate long periods of low nutrients (Moreno-Gámez et al., 2020). In the wider context of ecology and evolution of species interactions, adaptation of plants and microbes to influence or be influenced by each other's phenology may not be surprising. Biotic interactions with large impacts on fitness can be important cues for adaptive phenological plasticity (e.g., near-instant early hatching in response to egg predators; Warkentin, 1995) and may favor adaptive manipulation of interacting species' phenology (bee handling induces early flowering; Pashalidou et al., 2020) more often than generally appreciated.

Microbial community composition also changes across plant development. For example, microbial succession patterns in rice can accurately predict plant age (Edwards et al., 2018). Rhizosphere microbiome composition was associated with plant age in sorghum (Schlemper et al., 2017; Xu et al., 2018) and *Boechera stricta* (Wagner et al., 2016) and with flower age in apples (Shade et al., 2013). However, while the presence and time of residency of *Arabis alpina* were important factors in structuring soil communities, the transition to flowering did not affect the microbial community composition of the roots (Dombrowski et al., 2017). This observation calls into question whether tissue age or background fluxes in microbial propagules, rather than plant phenology per se, drives shifting patterns of microbial colonization through time. We recommend that more studies leverage flowering mutants, which have revealed short-term influences of the circadian clock on microbiomes (Hubbard et al., 2018), or evergreen plants, because both separate tissue age from reproductive stage effects.

IMPLICATIONS FOR AGRICULTURE AND GLOBAL CHANGE

Plant–microbe interactions may alter phenological shifts induced by global change. As plants migrate or expand ranges, new habitats may have novel microbial communities, or local microbial communities may change (Castro et al., 2010). These community shifts could alter microbial effects; for example, if the expected loss of mycorrhizal species (Steidinger et al., 2020) biases overall community effects toward delays (mycorrhizal fungi more often cause earlier flowering, Figure 3). Warming can also cause phenological mismatches between plants and microbes, such as earlier timing of microbial mineralization but not root growth (Groffman et al., 2012).

In contrast, plant responses to elevated CO_2 may shift microbial phenology. Elevated CO_2 can increase plant photosynthesis and rhizodeposition in the growing season, fueling booms for rhizosphere microbes (Phillips et al., 2011); yet elevated CO_2 can reduce litter quality (Prieto et al., 2019; Dijkstra et al., 2013), potentially suppressing rhizosphere microbes when plants senesce. Warming temperatures and increasing CO_2 and nitrogen deposition may also alter benefits and nutrient exchange in plant–microbe interactions (Kivlin et al., 2013; Shantz et al., 2016), which could feed forward to alter plant phenology. Microbes also may influence plant evolutionary trajectories in response to global change. Phenological traits have evolved in part due to pressure to escape stressors such as drought, pathogens, and temperature extremes, which are expected to worsen over the coming decades (Pau et al., 2011; Dantec et al., 2015). Microbial effects on the future evolution of phenology will depend on whether soil microbes' effects on phenology are generally aligned with the direction of selection on phenology in a given habitat, and how often microbes alter the associations between phenology and fitness, as discussed above.

Reciprocally, microbe-driven shifts on budburst and senescence (Poupin et al., 2013; Yguel et al., 2014) could impact the duration of the seasonal window in which plants sequester atmospheric C and therefore the progression of climate change. While our understanding of microbe-induced phenology shifts currently remains rudimentary, the fact that plant phenology so often responds to microbes suggests that microbial manipulation could become an important tool for tackling the climate crisis. Across studies, the magnitude of microbial effects is often at the scale of days to weeks, which is about the same magnitude as the average effects of past climate warming (CaraDonna et al., 2014).

In addition to their relevance for climate change, microbe-induced phenological shifts have many potential applications for sustainable agriculture. Yield-increasing microbial inoculants are already used on some commercial farms and have high potential to displace a larger proportion of chemical inputs in future years (Parnell et al., 2016). Food crop phenological models tailored to particular growing regions and planting seasons can optimally time pesticide sprays, irrigation, fertilizer treatment, and harvest, increasing both quality and yield (Mechlia and Carroll, 1989; Soltani et al., 2020). However, these models fail to incorporate microbial activities that influence plant growth and reproduction across a variety of food crops and microbial types, as discussed above (Chialva et al., 2016; Andrade et al., 2019).

Additionally, biological control agents can have nontarget phenological consequences; for example, fungal entomopathogens can shift germination timing and decrease germination probability (Heinz et al., 2018). On the other hand, phenology regulation can be an advantageous mode of action. Babalola et al. (2007) discovered three rhizobacteria strains that cause a parasitic weed to germinate early, before a host is available to colonize. Even disease agents could be useful: a weakened viral pathogen increased yield in zucchini by delaying flowering (Spence et al., 1996). Testing biocontrols for negative phenological impacts and exploitation of microbial control of plant phenology could lead to novel crop management strategies. Organic farming and precision agriculture could greatly benefit from improved understanding of microbe–host-phenology interactions.

NEXT STEPS FOR RESEARCH ON MICROBE-DEPENDENT PLANT PHENOLOGY

We have three main recommendations for future research in this area. First, more work is needed on less-studied phenological transitions (vegetative, fruiting, and senescence) and microbe locations (reproductive structures, phyllosphere, and other shoot tissues). Knowledge of what happens at intermediate phenophases is particularly essential for applying whole life-cycle models (Burghardt et al., 2016). Second, there is a need for more studies that measure microbe-mediated selection on phenology, which appears potentially important based on evidence from the few existing studies. All that is required is to (1) include at least two plant genotypes in multiple microbial conditions (they do not even have to be the same genotypes in each microbe treatment), (2) measure both a phenological trait and a fitness trait (e.g., biomass, survival, fecundity, yield), and (3) test whether the microbial treatment alters the regression of fitness onto phenology. We note that many of the studies reviewed here collected all the necessary data to do this and were only missing the analytical step. For example, Kalkal et al. (2018) measured time to flowering and yield in 20 chickpea genotypes, as affected by two rhizobia strains or one AMF strain. They concluded that there was sufficient genetic variation to select for the phenological response to microbes, but did not test for associations between flowering time and fitness or yield. All that is needed to address this gap is awareness; this extra analysis could provide valuable insights for minimal extra effort. Third, finer-resolution methods for fractionating microbiomes are needed to learn more about mechanisms. It is much easier to identify the mechanistic basis of the effect in one or a few microbes, than to tease out microbes with similar effects from complex communities. In particular, synthetic community approaches (Vorholt et al., 2017) and community enrichments (Estrela et al., 2021) are likely to be useful for studying microbial effects on plant phenology in a tractable yet ecologically realistic system. Progress in each of these three priority areas will be crucial for gaining a clearer picture of this important phenomenon.

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AUTHOR CONTRIBUTIONS

A.M.O. performed statistical analyses. All authors reviewed and synthesized literature and contributed to manuscript writing and editing.

DATA AVAILABILITY STATEMENT

Search results and associated extracted data are available in the Zenodo repository at https://zenodo.org/record/5071265. Code is available at GitHub at https://github.com/amob/MicrobesAndPhenology.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Detailed methods of the literature search and analysis.

Appendix S2. Summary of microbial effects on plant phenology across different plant phenological events.

Appendix S3. Taxonomic breakdown of studies and unique tests within them for effects of microbes on plants.

Appendix S4. Results reported in Figure 3 of the main text, but with 95% HPDI for determining different groups.

Appendix S5. Overlap of tests across microbial effect mechanism, taxonomy, and location.

Appendix S6. Summary of microbial effects on plant phenology for studies featuring different inoculum types, host life-forms (perennial vs. annual), and host mating strategies (predominantly selfing vs. outcrossing).

Appendix S7. Summary of the numbers of studies considering microbes residing in each plant organ.

Appendix S8. Summary of the numbers of studies considering microbes belonging to various taxonomic groups or categories.

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