Trends in Plant Science

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Forum

A Chemical Perspective on Microalgal–Microbial Interactions

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The exchange of chemical compounds is central to the interactions of microalgae with other microorganisms. Although foundational for many food webs, these interactions have been poorly studied compared with higher plant–microbe interactions. Emerging insights have begun to reveal how these interactions and the participating chemical compounds shape microbial communities and broadly impact biogeochemical processes.

Microalgal–Microbial Partnerships

Aquatic photosynthetic organisms primarily comprise eukaryotic microalgae and cyanobacteria and account for approximately half of the carbon fixation on Earth [1]. As primary producers, these photoautotrophs form the basis of aquatic food webs. For example, oceanic phytoplankton serve as the primary food source for zooplankton and thus is at the base of the food pyramid for all marine animals. Algae are also responsible for toxic blooms that negatively impact ecosystems, fishery resources, and human well-being and can lead to economic losses in the millions of dollars [2]. Biotechnologically, algae are being exploited for the production of biofuels and high-value products [3,4]; while this work has often focused on the use of pure cultures, an appreciation of the importance of studying and pursuing mixed cultivation in industrial settings will likely grow. Natural associations between eukaryotic algae and other microbes have been known for decades [5] and in many cases attempts to remove bacteria and fungi from microalgal cultures have failed, suggesting a dependence or close association of these organisms in their natural environment. To date, our understanding about the breadth, ecological significance, and chemical complexity of these partnerships has been limited, but new tools and strategies are being developed to shed more light on these multifaceted interactions (Figure 1A).

Emerging Concepts

Modes of Interaction

Nutritional interdependence provides a basis for understanding many microalgal–microbial associations (Figure 1B). As with some land plants, marine diatoms can derive their source of nitrogen by associating with diazotrophic cyanobacteria [6]. Haptophytes (prymnesiophytes) can also derive fixed nitrogen in association with a unicellular diazotrophic cyanobacterium, UCYN-A, that cannot fix CO_2 [7]. In return for fixed nitrogen, the haptophyte partner provides an as-yet-unidentified source of fixed carbon. Such symbioses between microalgae and nitrogen-fixing cyanobacteria are likely to be major determinants of marine productivity in oligotrophic waters [7].

Many microalgae depend on vitamin B_{12} from heterotrophic bacteria in exchange for fixed organic carbon (Figure 1B), which may affect the composition and productivity of microalgae-containing communities [8]. A mixed culture comprising a B_{12}-auxotrophic green alga, *Lobomonas rostrata*, and a B_{12}-providing bacterium, *Mesorhizobium loti*, was found to equilibrate at a cell ratio of approximately 1:30, although this ratio could be altered by the addition of external carbon or vitamin B_{12} [9]. In addition to a direct exchange of beneficial nutrients, cooperative interactions may occur indirectly via protection from detrimental factors or inhibition relief (e.g., defense against stress or the degradation of noxious waste products and toxins; Figure 1C).

In the past several years, a different type of microalgal–microbial interaction has come into focus: the production of and response to signaling chemicals and toxins. For example, some microalgae produce negative allelochemicals to compete with other microalgae or cyanobacteria within biofilms [10]. Other microalgae produce quorum-sensing mimics, probably as a means to interfere with bacterial communication [11]. The bloom-forming haptophyte *Emiliania huxleyi* collaborates with α-proteobacteria of the Roseobacter clade to provide organic carbon and sulfur in the form of dimethylsulfoniopropionate (DMSP) in return for antibiotics effective against other bacteria [12]. This mutualistic phase is terminated by a pathogenic phase involving the bacterial production of algicidal toxins. Such biphasic patterns may also govern the interactions of Roseobacter with dinoflagellates and may explain natural patterns of algal bloom formation and collapse [13].

Other antagonistic interactions include the encapsulation of haptophytes (*Phaeocystis* spp.) by *Acantharia*, a group of grazing zooplankton, in exchange for dimethylated sulfur compounds [14]. Physical association may also help to ensure generational persistence of partnerships (Figure 1C). To discern the types of interaction involved, a careful molecular characterization of microalgal–microbial associations is critical.

Division of Labor: Metabolic Complementation and Cooperative Biosynthesis

In laboratory co-culture experiments, the *Chlamydomonas* genus of green algae was found to trade nitrogen for carbon with a broad range of free-living ascomycetous fungi, including several genetically tractable model species (e.g., *Saccharomyces cerevisiae*, *Aspergillus nidulans*, *Neurospora crassa*) (Figure 1B) [15]. Although induced by artificial conditions, the phylogenetic breadth of this mutualism and the physical associations of alga with filamentous fungi (that resemble those

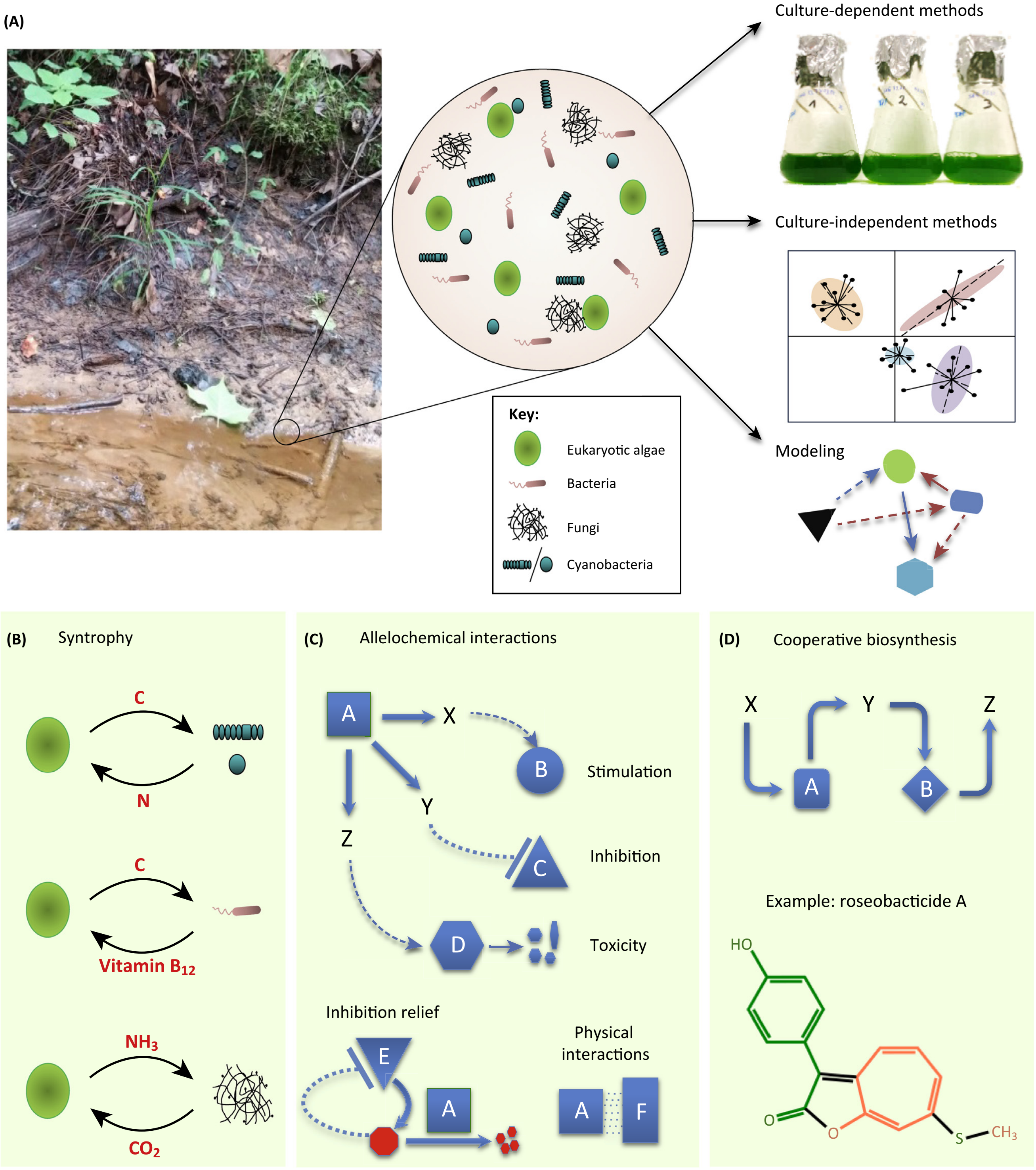

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Figure 1. The Interactions between Microalgae and Other Microorganisms Can Be Studied by Various Approaches and Comprise Various Types. (A) Analysis of microbial communities. Microalgae are present in bustling microbial communities with a multitude of interactions. A traditional approach to understanding these interactions would be to co-culture microalgae with a specific microbe of interest and to compare the growth and physiological parameters in axenic versus mixed cultures. Culture-independent methods like metagenomics and metabolomics can be employed to survey the complexity of microorganisms and their interactions in the wild, especially when the microbes are difficult to culture. Combining experimental observations, bioinformatics, and modeling tools are important for making sense of