

Anabaena: A New Chassis for Space Exploration

The Biological Toolkit of Anabaena for Extraterrestrial Environments

The genus *Anabaena*, a member of the filamentous, heterocyst-forming cyanobacteria, represents a compelling biological chassis for space exploration due to its unique combination of metabolic capabilities and environmental resilience. These organisms are fundamentally suited for extraterrestrial life support systems because they perform oxygenic photosynthesis, fixing atmospheric carbon dioxide into organic matter while producing molecular oxygen as a byproduct^{14 39}. This dual function is critical for any closed-loop system designed to sustain human life. Beyond this core process, *Anabaena* possesses a suite of specialized biological traits that enhance its potential utility in the challenging environments of space. Perhaps most notably, it can fix atmospheric dinitrogen (N₂) into biologically available ammonia through specialized cells called heterocysts^{39 43}. This capability is of paramount importance for missions to Mars, where the surface soil contains abundant N₂ but lacks accessible fixed nitrogen, a major limiting factor for terrestrial agriculture^{15 44}. The ability to convert an inert atmospheric gas directly into a nutrient source could drastically reduce the need for resupply from Earth and enable the establishment of self-sufficient food production systems on the Red Planet.

Further bolstering its credentials, *Anabaena* demonstrates remarkable metabolic versatility. It is capable of synthesizing a diverse array of secondary metabolites, including bioactive compounds with potential pharmaceutical applications, such as terpenoids, carotenoids like β -carotene, and non-ribosomal peptides^{34 39}. These molecules often play roles in stress defense, such as UV protection, which is a significant concern outside Earth's protective atmosphere³⁴. The genus also produces essential biomolecules like vitamin C and K1 at levels that surpass those found in common leafy vegetables, suggesting a potential role not only in air revitalization and biomass generation but also in providing supplemental nutrition³⁴. Furthermore, *Anabaena* contributes to ecosystem engineering through its capacity for bio-weathering. Studies have shown that species like *Anabaena cylindrica* can effectively leach nutrients from basaltic rocks, releasing essential elements such as calcium, iron, potassium, and magnesium¹³⁷. This ability to "mine" nutrients from inorganic substrates is a key prerequisite for in-situ resource utilization (ISRU), allowing the organism to transform barren regolith into a viable growth medium. This multifaceted biological toolkit—combining primary production, atmospheric processing, and resource extraction—positions *Anabaena* as a uniquely powerful candidate for a wide range of space biotechnology applications.

The physiological architecture of *Anabaena* is intrinsically linked to its survival strategies. Its filamentous morphology allows for cellular differentiation, creating a division of labor within a single organism. Vegetative cells handle photosynthesis, while specialized heterocysts manage nitrogen fixation in an oxygen-sensitive environment, all within a connected network^{39 43}. This organization

maximizes efficiency and provides a buffer against localized damage. In addition to heterocysts, *Anabaena* produces akinetes, which are thick-walled resting cells that confer extreme resistance to desiccation, freezing, and other harsh conditions¹⁴³. These akinetes serve as a natural form of stasis, enabling the organism to survive periods of environmental stress or transit between celestial bodies. The formation of biofilms, mediated by complex regulatory networks involving exopolysaccharides (EPS), further enhances its resilience by protecting cells from desiccation, radiation, and predation^{40 43}. While this biofilm-forming tendency can be advantageous for robust colonization of surfaces, it may present challenges for certain photobioreactor designs; however, some strains like *Anabaena* sp. PCC 7938 exhibit less aggregation, making them more suitable for fluid-based cultivation systems^{8 30}. This inherent physiological complexity, combining efficient metabolism with sophisticated survival mechanisms, forms the foundation of *Anabaena*'s potential as a cornerstone organism for future space exploration endeavors.

Resilience and Performance Under Martian Analog Conditions

The viability of *Anabaena* as a foundational organism for Martian exploration hinges on its demonstrated resilience to the planet's most hostile abiotic conditions. Extensive research has subjected various strains to simulated Martian environments, revealing a remarkable capacity for survival and even vigorous growth under conditions that would be lethal to most other known life forms. One of the most critical factors is the low-pressure, CO₂-rich atmosphere. Experiments using the MDA-1 atmosphere—a mixture of 96% N₂ and 4% CO₂ at a total pressure of 100 hPa—showed no statistically significant differences in the biomass production of *Anabaena* sp. PCC 7938 compared to ambient air controls after ten days of cultivation^{10 12 13}. Similarly, another study reported that *Anabaena* sp. maintained diazotrophic growth under these low-pressure conditions, confirming its tolerance to Mars' thin atmosphere¹³. However, the same study noted that chlorophyll *a* levels were significantly lower when grown in water supplemented with MGS-1 regolith simulant under MDA-1, indicating that while the organism can survive the atmospheric pressure, the interaction with regolith may impose additional stressors¹².

Temperature extremes on Mars pose another significant challenge, with surface temperatures ranging from -140° C at night to 20° C during the day¹⁵. Research has shown that *Anabaena* possesses exceptional cold tolerance. Akinetes of *Anabaena cylindrica* survived 28 days in ground-based simulations of Martian conditions, which included a temperature of -28° C, with a notable 35.3% viability¹. Further studies confirmed survival at even lower temperatures, with viability being maintained down to -80° C¹. Conversely, exposure to high temperatures proved fatal, as no survival was observed at 40° C or above¹. When exposed to a full diurnal cycle in a planetary simulator, *Anabaena* sp. showed low-level positive survival, evidenced by detectable chlorophyll content and esterase activity, although critical functions like nitrate reduction were absent post-exposure²⁹. This suggests that while the organism can withstand severe cold and temperature cycling, its functional integrity may be compromised by prolonged exposure to suboptimal thermal conditions.

Perhaps the most significant test of its suitability for Martian ISRU is its performance in simulated regolith. *Anabaena* sp. PCC 7938 has been identified as a superior performer, exhibiting the highest

biomass productivity on Martian Global Simulant (MGS-1), achieving over double the biomass of other tested strains^{8 30}. Its growth dynamics in this medium followed a Monod equation, with phosphorus identified as the primary limiting nutrient; supplementing phosphorus increased biomass by 67%, highlighting the need for targeted nutrient management⁴. The organism also shows moderate resistance to perchlorates, a highly oxidizing compound present in Martian soil. PCC 7938 maintained >62% of its control biomass when exposed to 12 mM calcium perchlorate, demonstrating a level of chemical tolerance crucial for direct use of Martian resources^{6 30}. A critical consideration for photobioreactors is light availability. High concentrations of regolith simulant cause significant shading; a concentration of 20 kg m⁻³ was found to reduce photosynthetically active radiation (PAR) below detection levels, indicating that either dilute cultures or engineered light delivery systems would be necessary for effective photosynthesis in a solid-medium reactor⁴. Despite this limitation, the overall body of evidence strongly supports *Anabaena*'s potential as a pioneer organism for ecopoiesis and ISRU on Mars, capable of surviving and growing under a wide range of simulated Martian stresses.

Stress Factor	Condition	Strain(s)	Outcome	Citation
Atmospheric Pressure	100 hPa, 96% N ₂ , 4% CO ₂	<i>Anabaena</i> sp. PCC 7938	No significant difference in biomass vs. ambient air. Chlorophyll a levels reduced in regolith media.	10 12
Temperature	-28° C (simulated Mars)	<i>Anabaena cylindrica</i>	35.3% viability of akinetes after 28 days.	1
Temperature	-80° C to +26° C (diurnal cycle)	<i>Anabaena</i> sp.	Low-level positive survival based on esterase activity and chlorophyll content.	29
High Temperature	≥40° C	<i>Anabaena</i> sp.	No survival after extended periods.	1
Perchlorate	12 mM Ca-perchlorate	<i>Anabaena</i> sp. PCC 7938	Maintained >62% of control biomass.	30
Regolith Concentration	20 kg m ⁻³ MGS-1 simulant	<i>Anabaena</i> sp.	Reduced PAR below detection levels, causing shading.	4

Physiological Responses and Systemic Challenges in Microgravity

While *Anabaena* demonstrates impressive resilience to static abiotic stressors, its behavior in the dynamic physical environment of microgravity remains a critical area of investigation for space application. The effects of microgravity on microbial physiology are complex and not yet fully understood, with responses varying significantly across species and experimental conditions⁵. For many organisms, the primary driver of change is not a direct effect on the cell itself, but rather the profound alteration of the surrounding fluid dynamics. On Earth, gravity-driven sedimentation and

convection are dominant forces for nutrient transport and waste removal. In microgravity, these processes are eliminated, replaced by diffusion-limited transport, which can dramatically alter mass transfer rates and create steep chemical gradients around individual cells or colonies ⁵. This shift is believed to be a key factor behind the inconsistent results seen in different ground-based simulation facilities, such as clinostats and random positioning machines (RPMs), which attempt to replicate microgravity by continuously reorienting samples ⁵.

Studies on other photosynthetic organisms provide cautionary insights into the potential challenges. For instance, experiments on the European Space Agency's MELiSSA program involved growing the microalga *Limnospira indica* in an RPM setup under continuous illumination. The results showed a significant reduction in growth rate and an increase in the doubling time compared to 1g controls ⁹. Proteomic analysis revealed that this was likely due to a thicker stagnant fluid boundary layer around the cells, which impeded the release of oxygen produced during photosynthesis. This accumulation of oxygen inhibited the key enzyme RuBisCO, leading to carbon limitation despite ample light ⁹. This finding highlights a critical design consideration for any photobioreactor intended for space: passive oxygen stripping will be insufficient, and active methods for maintaining mass transfer will be essential to prevent inhibition of photosynthesis. Although specific data on *Anabaena* in microgravity is limited in the provided sources, these findings from *L. indica* suggest that similar challenges related to fluid dynamics and gas exchange are likely to be relevant.

In contrast to these negative impacts, some studies suggest that certain cyanobacteria may be inherently well-suited to microgravity. Research on *Anabaena siamensis* indicated that microgravity did not impair its photosynthesis or nitrogen fixation capabilities ⁴³. Furthermore, its filamentous nature and motility via hormogonia (shortened, motile filaments) could potentially allow it to navigate fluid layers more effectively than unicellular organisms, mitigating some of the negative effects of diffusion limitation ⁴³. Another study highlighted the suitability of algae like *Anabaena* for Controlled Ecological Life Support Systems (CELSS) specifically because of their adaptation to weightless conditions ²⁵. This apparent contradiction underscores the current knowledge gap regarding how different strains of *Anabaena* respond to microgravity. It is possible that certain physiological adaptations, such as robust biofilm formation or motility, could provide a competitive advantage in a microgravity environment, but this requires direct experimental validation. Without comprehensive data from actual spaceflight or long-duration ground simulations, the net effect of microgravity on *Anabaena* remains an open question. Addressing this uncertainty is paramount, as the success of any BLSS deployed in orbit or beyond will depend on its ability to function reliably in the unique fluid environment of space.

Harnessing Metabolic Potential Through Genetic Engineering

To transition *Anabaena* from a promising natural organism to a predictable and controllable synthetic biology chassis, it must be equipped with a sophisticated genetic toolkit for precise and efficient genome editing. Recent breakthroughs have established *Anabaena* sp. PCC 7120 as a model organism with proven genetic tractability, opening the door to the metabolic engineering required for advanced space applications ^{17 24}. The cornerstone of this progress is the successful adoption of CRISPR-Cas12a (Cpf1) systems, which offer several advantages over older technologies like

CRISPR-Cas9. Early work demonstrated that Cas9 was toxic in *Anabaena* PCC 7120, necessitating the search for alternative systems³¹. The *Francisella novicida* Cas12a (FnCas12a) system proved to be highly effective, enabling markerless gene knockouts, point mutations, knock-ins, and gene replacements with high efficiency^{17 21 23}. Subsequent optimization efforts have refined these tools, achieving near 100% editing success rates and enabling rapid multiplex editing of multiple genes simultaneously^{18 20}.

Building on this foundation, researchers have developed even more advanced genetic tools. A landmark achievement was the development of a CRISPR-associated transposase (CAST) system for *Anabaena*. This technology allows for the targeted integration of DNA cargo at specific genomic locations without requiring homology-directed repair or creating double-strand breaks, which can be error-prone and cytotoxic^{27 28}. The CAST system, derived from *Scytonema hofmannii*, uses an RNA-guided mechanism to insert a transposon carrying a desired genetic payload precisely 63 base pairs downstream of a protospacer adjacent motif (PAM)^{28 32}. This "cut-and-paste" mechanism ensures unidirectional insertion of the cargo without integrating the entire donor plasmid, minimizing off-target effects and simplifying strain construction^{27 28}. The development of modular Golden Gate vectors (CASTGATE) has further streamlined this process, making it highly efficient and scalable^{27 28}. These tools collectively represent a paradigm shift, transforming *Anabaena* from a recalcitrant organism into a versatile platform for synthetic biology.

The practical application of these tools has already begun to yield engineered strains with enhanced properties. The SEVA-Cpf1 vector system, for example, has enabled the deletion of the *nblA* gene in *Synechocystis* 6803, a proof-of-concept experiment that validates the system's functionality in other cyanobacteria¹⁶. More directly, CRISPR interference (CRISPRi) has been successfully implemented in *Anabaena* sp. PCC 7120 to repress the expression of key genes like *glnA* (encoding glutamine synthetase) and *devH*, allowing for inducible control over ammonium production²¹. Furthermore, conditional mutagenesis of essential genes, such as *polA* encoding DNA polymerase I, has been achieved using a theophylline-induced riboswitch, demonstrating the ability to create tunable, auxotrophic strains that are safer for containment^{17 21}. The existence of stable integrative vectors like pFPN, which integrate into the genome and do not rely on antibiotic selection markers, also provides an important tool for creating genetically stable strains suitable for industrial or long-term space applications²⁴. Together, this expanding arsenal of genetic tools provides the necessary framework to systematically optimize *Anabaena* for the specific demands of space exploration.

Comparative Analysis: *Anabaena* Versus Other Cyanobacterial Chassis

While *Anabaena* is emerging as a premier candidate for space biotechnology, it exists within a broader context of cyanobacterial chassis that are also being explored for similar applications. A comparative analysis reveals distinct strengths and weaknesses, helping to define the ideal niche for each organism. The most prominent competitor in this arena is the unicellular model cyanobacterium *Synechocystis* sp. PCC 6803. *Synechocystis* benefits from decades of intensive research and a vast repository of pre-existing genetic tools, making it a well-understood chassis for basic research and

foundational synthetic biology. Indeed, many of the advanced genetic tools now being applied to *Anabaena*, such as the optimized CRISPR-Cas12a systems, were first developed and refined in *Synechocystis*¹⁸. However, *Anabaena* holds several key advantages that make it particularly attractive for the complex, multi-functional tasks required for space exploration.

First and foremost is the presence of heterocysts, which enables simultaneous oxygenic photosynthesis and anaerobic nitrogen fixation within the same organism^{39 43}. This unique metabolic compartmentalization is a game-changing feature for Mars applications, where establishing a sustainable nitrogen cycle is a primary goal. While nitrogen-fixing *Synechocystis* strains exist, they typically require separate, dedicated bioreactors or mixed-culture systems, adding complexity and mass to a life support system. *Anabaena*'s intrinsic ability to perform both functions co-locally offers a much simpler and potentially more robust solution. Second, *Anabaena* exhibits greater morphological diversity, including the formation of akinetes and biofilms, which confer exceptional environmental resilience and colonization capabilities^{1 40}. This makes it better suited for pioneering applications like bioweathering of regolith or establishing permanent bio-films on habitat surfaces. Third, recent comparative studies have definitively identified specific *Anabaena* strains, such as PCC 7938, as superior performers in terms of biomass productivity when grown on Martian regolith simulants, outperforming other tested strains, including PCC 7122 and PCC 7120^{8 30}.

Other cyanobacteria also contribute to the landscape of potential chassis. *Spirulina platensis*, for example, is used in the European Space Agency's MELiSSA pilot plant for Phase 1, where it converts organic wastes and CO₂ into biomass^{36 38}. Its value lies in its high protein content and established role within the MELiSSA loop. However, it lacks the nitrogen-fixing capability of *Anabaena*. *Chroococcidiopsis*, another extremophile, is renowned for its tolerance to desiccation and high radiation, having survived for years in outer space^{2 11}. While incredibly resilient, it is a unicellular rock-dweller and does not possess the metabolic versatility of a nitrogen fixer. Finally, symbiotic partners like *Anabaena azollae*, which lives in association with the aquatic fern *Azolla*, demonstrate the potential for integrated systems where the cyanobacterium fixes nitrogen to benefit a higher plant host, a model relevant for combined food production systems³⁵. The following table summarizes the key characteristics of these comparative chassis.

Feature	<i>Anabaena</i> sp. PCC 7938	<i>Synechocystis</i> sp. PCC 6803	<i>Spirulina</i> <i>platensis</i>	<i>Chroococcidiopsis</i> spp.
Nitrogen Fixation	Yes (via heterocysts)	Yes (requires separate reactor/culture)	No	Information not available in provided sources.
Genetic Tools	Advanced (Cpf1, CAST, CRISPRi)	Very advanced, foundational	Less developed	Information not available in provided sources.
Filamentous/Morphology	Filamentous, akinetes, biofilms	Unicellular	Unicellular	Unicellular

Feature	Anabaena sp. PCC 7938	Synechocystis sp. PCC 6803	Spirulina platensis	Chroococcidiopsis spp.
Performance in MGS-1	Highest biomass productivity	Not specified	Not specified	Survived in community but not cultured alone
Key Advantage	Integrated N ₂ fixation & O ₂ evolution	Foundational chassis, extensive toolset	Biomass/O ₂ production in MELiSSA	Extreme radiation/ desiccation tolerance
Known Weakness	Potential for aggregation in reactors	Lower biomass in regolith	Information not available in provided sources.	Slower growth rate

Ultimately, the choice of chassis depends on the specific mission objective. For a simple oxygen generator, *Synechocystis* might suffice. For a nitrogen-recycling system on Mars, *Anabaena* appears to be the clear frontrunner due to its unique combination of metabolic power, genetic accessibility, and superior performance in Martian regolith.

Future Directions and Knowledge Gaps for an *Anabaena*-Based Biotechnology Platform

The trajectory of *Anabaena* research points towards the creation of a sophisticated, engineered biotechnology platform for space exploration. Over the next five to ten years, the field is expected to advance from characterizing the natural capabilities of wild-type strains to designing and optimizing synthetic strains tailored for specific, high-stakes applications. The immediate priority is to address the remaining knowledge gaps that currently hinder the deployment of *Anabaena* in space. The most pressing of these is the lack of direct, quantitative data on its performance in true microgravity. While analogues and simulations are invaluable, a definitive assessment of how *Anabaena*'s growth, physiology, and fluid dynamics are affected aboard platforms like the International Space Station (ISS) or in new facilities like GraviSat³ is essential. Such experiments are needed to validate computational models and inform the design of scalable, reliable photobioreactors for long-duration missions.

Another critical knowledge gap lies in understanding the long-term stability and interactions of *Anabaena* in a closed-loop system. Questions remain about how it will interact with other microbes in a mixed culture, how it will cope with the elevated CO₂ and trace organics that build up over time, and whether its engineered traits will be retained across generations in a space environment^{26 33}. Research must focus on developing robust monitoring systems for genetic stability and on designing kill switches or other containment strategies to prevent unintended release. Furthermore, while *Anabaena* has been shown to produce valuable compounds, the pathways for high-yield production of specific molecules (e.g., pharmaceuticals, polymers, or advanced biofuels) have yet to be fully unlocked. Applying the mature genetic tools to heterologous pathway expression and metabolic flux redirection will be the next frontier of research.

The future of *Anabaena* as a space chassis will also involve moving beyond single-function organisms to integrated, multi-component systems. This includes coupling *Anabaena*-based photobioreactors with advanced bioreactors containing nitrifying bacteria, as exemplified by the MELiSSA project^{36,38}, to create a complete, cascading nutrient cycle. It also involves exploring symbiotic relationships, such as inoculating Martian regolith with *Anabaena* to create a living soil that can then support higher plants, mirroring the natural partnership between *Anabaena* and *Azolla*^{35,43}. The development of quorum-quenching genes to mitigate inhibitory signaling in closed loops is another innovative strategy that could improve system stability³⁷. To summarize, the path forward involves a synergistic effort combining fundamental research on microgravity effects, deep dives into long-term system integration, and aggressive application of synthetic biology to engineer ever-more-sophisticated and resilient *Anabaena* strains. By bridging these knowledge gaps, *Anabaena* has the potential to become a cornerstone of sustainable human presence beyond Earth.

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