

# *Research progress on algal biokarst and its implications for carbonate rock dissolution and weathering*

Jiawei Zhao<sup>1,2</sup>, Kangning Xiong<sup>1,2,\*</sup>, Ni Yan<sup>1,2</sup>

<sup>1</sup>School of Karst Science, Guizhou Normal University, Guiyang, 550001, China

<sup>2</sup>State Engineering Technology Institute for Karst Desertification Control, Guiyang, 550001, China

\*Corresponding author

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**Abstract:** In the fragile ecological environment of karst rocky desertification, exposed bedrock, vegetation such as forests and grasses are difficult to grow on a large scale, and regional ecological problems are difficult to continuously improve, seriously restricting the sustainable development of regional economy. Therefore, the governance of rocky desertification in karst areas is urgent. Karst biogenic algae can directly act on carbonate rocks and produce strong dissolution, accelerating soil formation. Therefore, studying the dissolution effect of algae on carbonate rocks is beneficial for further understanding the soil formation and vegetation restoration succession in karst areas, and provides a theoretical basis for controlling the fragile ecological environment in karst rocky desertification areas. At present, the research status and progress on the ecological restoration and weathering effects of algae on fragile karst ecosystems are not clear, and the summary of research results and problems is insufficient. On the basis of 71 relevant literature, this article focuses on sorting out the karst mechanism and ecological restoration potential of algae, revealing the achievements and shortcomings of current research on algae karst and ecological restoration.

## 1. Introduction

Biokarst refers to the phenomenon and products of karstification caused by organisms, which destroy soluble rocks and sediments, form secondary chemical sediments and their remaining or formed forms (Viles, 1984[1]), and play a huge role in the formation and evolution of karst, accelerating the dissolution or deposition of soluble rocks. At the biosphere lithosphere interface, organisms colonize carbonate rocks through biophysical and biochemical processes and rely on them for survival. The metabolic processes of organisms activate the carbonate rock lithosphere (Cao, 2001[2]). Biocrust is an organic complex formed by bacteria, fungi, algae, lichens, mosses, and soil particles. It is a special ground cover in arid and semi-arid areas (Zhang et al., 2015[3]), which can regulate biogeochemical element cycling, fix soil, and improve soil fertility.

It is an engineer of ecosystems. In desert areas, algae play an irreplaceable role in the early formation and strength maintenance of biological crusts. In karst areas, algal organisms reproduce and grow with their unique physiological and ecological characteristics, and deeply affect the

formation and development of karst (Wang et al., 1995[4]). Especially, blue-green algae in algal plants can promote soil formation, fix nitrogen and carbon, and retain water and soil, And become a pioneer species in ecological restoration in rocky desertification areas (Kidron et al., 2014[5]). Therefore, understanding and mastering the functional characteristics of lithophytic algae, the mechanism of karst action, and the interaction mechanism with the environment are of great significance for studying biodiversity, ecological restoration of rocky desertification, karst carbon sink, and enriching the theory of biological karst in karst areas. However, the study of algal plant karst processes has not yet entered the systematic research stage due to its involvement in numerous disciplines and complex issues. In order to break down barriers between different disciplines and promote further development of research on algal plant karst, this article reviews the research progress of algal plant karst from the following aspects based on recent literature on algal plant karst.

## 2. Method

We conducted a Chinese literature search using the China National Knowledge Infrastructure (CNKI) Information Resource Database to scientifically and quantitatively analyze the research trends of algal karst processes; Use Web of Science and other tools to search for foreign literature. Chinese literature search is conducted in the full text database of China National Knowledge Infrastructure, with "theme and keywords" as the search options, "biological weathering and biological karst" as the first search term, and "weathering effects of blue-green algae dissolution and weathering" as the second search term; Simultaneously using "Biokarst", "Biological Weathering" "Bioedibility", "Cyanobacterium" The keywords are searched in foreign language databases as of December 30, 2023.

## 3. Result

### 3.1. Functional characteristics and environmental adaptability of rock algae

1) The unique cellular structure and carbon dioxide concentration mechanism of algae are their adaptation strategies to extreme and stressful environments

The karst ecosystem is an ecosystem constrained by the karst environment, characterized by a karst geochemical background rich in calcium and slightly alkaline, and a double layered structure of karst hydrogeology. Therefore, the vegetation in the karst area has characteristics such as lithophytic, xerophytic, and calcium loving (Zhou et al., 2003[6]). Cao et al.(1999) found through indoor evaporation experiments and active water absorption experiments that compared with rocks without biological cover, rocks with algae biological cover had a surface water loss and water absorption increase of 18.8 and 1.6 times, respectively, and a water holding capacity increase of 16.6 times [7]. Algae in karst areas are small in size and evenly distributed on the surface of rocks (Zhang, 1993[8]). According to the contact relationship between algae and carbonate rocks, they can be divided into three types: surface type, cave type, and endophytic type (Wang et al., 1995[4]). Some scholars have studied the basic structure of rock algae and found that their unique cell structure and CCM (CO<sub>2</sub> Concentrating Mechanism) make them have the ability to fix carbon and nitrogen, retain water and moisture, resist strong light, and withstand high temperatures The ecological functions of drought resistance make it a pioneer species for ecological restoration in karst rocky desertification areas. Another major advantage of algae participating in karst processes is that the heterotypic cells within nitrogen fixing cyanobacteria contain nitrogenase, which can fix free N<sub>2</sub> in the atmosphere into nitrogen compounds. However, their nitrogen fixing activity is closely related to the number, location, shape of heterotypic cells, differences in algal species, and

the environment. The unique CCM of blue-green algae can promote their photosynthesis rate under low CO<sub>2</sub> environmental conditions by increasing the internal CO<sub>2</sub> concentration of carboxylation sites (Price et al., 2002[9]). These research results indicate that algae can improve soil chemical properties by transporting available organic matter to the soil through their own carbon and nitrogen metabolism processes, which is of great significance for the ecological restoration and reconstruction of exposed carbonate rock surfaces in rocky desertification areas.

2) Algae's water storage and moisturizing ability, as well as their photosynthetic rehydration characteristics, not only increase the interaction time between water and rock, but also give algae strong photochemical ability, making them a pioneer species in desert areas

In arid environments, the key to biological survival is the ability to reactivate metabolism and growth in a short period of time with water, as well as the ability to delay metabolism during dehydration. However, algae living in such extremely harsh environments can still maintain their photosynthetic oxygen release and carbon fixation abilities, and can quickly recover some chlorophyll fluorescence and photochemical activity after re wetting (Nie et al., 2012[10]). At the same time, the changes in algae between the dry and wet states drive the binding particles on the rock surface, making the rock surface loose and accelerating the soil formation rate of carbonate rocks.

3) Algae colonize the rock surface, enrich nutrients, promote the weathering of carbonate rocks into soil, lay a material foundation for the growth and colonization of other plants, and promote the succession of vegetation communities on the rock surface.

The algae that inhabit the surface of inland carbonate rocks are mainly calcium loving cyanobacteria. The common algae genera in karst areas of southwestern China include *Microcystis sp*, *Gloeocapsa sp*, *Chlorococcus sp*, *Stigonema sp*, *Topothrix sp*, *Scytonema sp*, and *Nostoc sp* (Wang et al., 1993[11]). Algae can maintain a water film on the surface of rocks after precipitation, greatly increasing their water holding capacity and prolonging the time of water rock interaction. Cao et al. (1999) found that compared with rocks without biological cover, rocks with algae biological cover have a surface water loss and water absorption increase of 18.8 and 1.6 times, respectively[7]. The time for evaporative water loss and active water absorption is extended by 48% and 57%, respectively, and the water holding capacity is increased by 16.6 times. At the same time, the improvement of water conditions also stimulates the metabolic activity of lithophytes, promotes the secretion of biological acids, and accelerates the exchange rate and amount of CO<sub>2</sub> between the rock surface and the atmosphere. However, there are differences in the intensity of life activities among different algae plants, which inevitably leads to differences in metabolic production and quantity, resulting in changes in the physical and chemical properties of the surrounding micro water environment (such as pH value, conductivity, HCO<sub>3</sub><sup>-</sup> level, etc.), and ultimately affecting changes in the intensity of biological dissolution. However, there is currently little attention paid to the effects of algae colonization on the surface of carbonate rocks on their CO<sub>2</sub> and hydrological dynamics, which in turn affect karst. Algae can not only dissolve rocks through biochemical means, but also damage bedrock through physical and mechanical actions. For example, the dissolution effect of algae drilling causes the shallow surface of the rock to loosen by 0-2cm, reducing the surface hardness of the rock. The improvement of rock surface conditions has also promoted the proliferation of lichens, mosses and other plants on the rock surface, and covered the rock surface. After the colonization of moss, the water holding capacity of rocks is further increased. At the same time, with the growth of moss, moss pseudoroots often adhere to a large amount of brown black fine-grained soil, alleviating the harsh conditions of rock habitats, gathering nutrients, and providing a material basis for the direct germination and growth of higher plant seeds on the rock surface (Cao et al., 1999[7]), further promoting the positive succession of vegetation in rocky desertification areas.

## 3.2 The dissolution of algae and plants

### 3.2.1 The principle and process of algal plant dissolution

The principle and process of dissolution of rocks by algae plants are essentially the interaction between minerals in rocks and algae plants. The microenvironment on the surface of rocks usually determines the algae and their distribution patterns that grow on the rock surface, and during the growth process, algae change their surrounding microenvironment through their own metabolism. The magnitude of this karst driving force varies due to changes in plant morphology, rock properties, and living environment. Algae release CO<sub>2</sub> through respiration, which generates carbonic acid upon contact with water and can cause dissolution in the microenvironment. It also releases acidic substances and chelating metabolites, promoting the dissolution of calcite (Golubic, 1973[12]). Algae can form 1.1cm deep algal dissolution pores on hard limestone statues after 620a, with a dissolution rate of 20% of the comprehensive chemical dissolution rate (Cao, 1993[13]). At the same time, the secretions of algae contain acetic acid, and their dead bodies can be oxidized and decomposed into oxalic acid, which has a dissolution effect, under the action of microorganisms (Wang, 1993[11]). The loose structure of extracellular polysaccharide microfilaments produced during the growth and metabolism of algae often fills the gap between the algal filaments and the substrate, which may lead to the disintegration of carbonate rocks. The controlling role of algal organisms is also very important. On the one hand, it makes the rock surface rough and uneven, increases the dissolution surface area, and greatly accelerates the dissolution rate. Especially on rock surfaces with more water flow such as depressions or dissolution channels, algae growth is more vigorous and their dissolution rate is faster. On the other hand, the control and promotion effects of algal organisms jointly constitute algal dissolution, which greatly destroys the rock particle cementation on the surface of carbonate rocks, making the rock surface loose and significantly reducing the hardness value of the carbonate rock surface (Tian et al., 2004[14]). Aerial algae have a positive biological dissolution effect in stone forest areas, which can affect the formation of stone forest morphology and even landscape. This impact can be divided into direct and indirect. The direct impact refers to the active control of algal morphology over dissolution morphology, that is, the algal biological control effect; Indirect impact refers to the role of algae in indirectly participating in and strengthening the formation of dissolution morphology through their own life activities and physiological and biochemical processes, promoting the formation of dissolution morphology appearance, that is, promoting effect (Tian et al., 2004[14]). Algal crusts can also drive the weathering and dissolution of soluble rocks through physical processes. Algae hyphae have extremely strong mechanical penetration, which can penetrate and grow within soil mineral particles, accelerating the fragmentation and disintegration of minerals.

### 3.2.2 Analysis of Algae Plant Corrosion Products

The soil in karst areas mainly has characteristics such as karst drought, high bicarbonate, low nutrition, and high pH, which limit the growth and development of plants (Zhao et al., 2011[15]). In the absence of soil nutrients, especially Fe, Zn, Mn, and Cu, many plant roots release more organic acids to cope with this situation (Neumann et al., 2007[16]). However, research on the dissolution of organic acids mainly focuses on the mineral weathering of microorganisms, mosses, and higher vascular plants. Alkali metals such as Na<sup>+</sup>, K<sup>+</sup>, and Ca<sup>2+</sup>, as well as alkaline earth metal cations, are easily exchanged with H<sup>+</sup> and dissolved in ores. Minerals dissolve under acidic conditions formed by microbial action. Some organic acids such as citric acid, oxalic acid, and tartaric acid are prone to form complexes with high valence metal ions in rocks (such as Fe, Al, Cu, Zn, and Mn) through complexation, thereby significantly increasing the dissolution of these elements. Dou et al. (2009)

found through leaching experiments of lithophytic fungi on calcite powder that fungi can significantly increase the leaching amount of  $\text{Ca}^{2+}$ , and the metabolic process of fungi can produce organic acids that dissolve carbonate rocks, thus proving the important role of lithophytic fungi in the weathering process of carbonate rocks[17]. Wang et al. (2015) studied the dissolution effect of extracellular organic acids on calcite by three common bacteria, namely silicate bacteria, *Staphylococcus aureus*, and *Escherichia coli*. They found that the main components of extracellular organic acids in these three bacteria are oxalic acid, lactic acid, citric acid, and succinic acid. Although different organic acids have different dissolution effects on calcite, they can all promote the release of Ca ions to varying degrees[18]. Cao et al. (2001) found that during the life activities of moss plants, essential nutrients are continuously absorbed from the outside, while sugars, amino acids, fatty acids, and their derivatives terpenoids and flavonoids, as well as  $\text{CO}_2$ , are released, which have a dissolution effect on carbonate rocks[2]. There is relatively little research on the secretion of organic acids by algae and plants. Therefore, in future research on the dissolution of organic acids secreted by algae, we should draw on the research methods of microorganisms and mosses on organic acids, and combine organic chemistry, gas chromatography-mass spectrometry (GC-MS), nuclear magnetic resonance (NMR), liquid chromatography (HPLC) and other technical means to deeply study the dissolution process and mechanism of algae plants.

Polysaccharides are the third type of macromolecules besides proteins and nucleic acids, mainly present in the forms of glycoproteins, glycolipids, and proteoglycans. Polysaccharide compounds exist in animals, higher plants, algae, and bacteria in nature, and are widely distributed, making them the most abundant biopolymers in nature. Usually, we refer to extracellular polysaccharides (EPS) as the polysaccharides released from bacterial and fungal sheaths, capsules, and mucilage, as well as water-soluble polysaccharides released from bacterial and fungal sheaths, capsules, and mucilage into the surrounding environment. Microbes can make microbial cells fix on the rock surface to form gel layer or biofilm by secreting extracellular polymer substance (EPS). Biofilm uses bacterial extracellular polymers as a contact medium, and forms a special microenvironment on the surface of minerals through the complexation of uronic acid and other residues, achieving mineral dissolution. Extracellular polymers contain a large number of hydroxyl groups with adsorption capacity, which have a significant adsorption effect on organic acids and some inorganic ions. Through the adsorption of large molecular groups such as extracellular polysaccharides, they directly break certain chemical bonds in the mineral lattice (Uroz et al., 2009), thereby promoting mineral weathering.

Carbonic anhydrase (CA) is a metal enzyme containing Zn, widely distributed in animals, plants, and prokaryotes. The research on algal plant CA mainly focuses on its catalytic effect on carbon dioxide water and reaction, CA content, activity, and its promoting effect on mineral element migration. For example, Wang et al. (2007) found that the CA secreted by diatoms can accelerate the catalytic hydration reaction of  $\text{CO}_2$ , reduce the pH of karst water, and promote the dissolution of carbonate rocks[19]. Wu et al. (2015) found that the carbonic anhydrase secreted by algae has a significant promoting effect on mineral weathering, mainly manifested in its enzymatic effect on  $\text{CO}_2$  conversion reactions[20]. Li et al. (2007) used microalgae (*Chlamydomonas reinhardtii*) as material and found a good correlation between the average activity of carbonic anhydrase in the leachate and the total amount of  $\text{Ca}^{2+}$  leaching through microalgae soil column leaching experiments, proving that microalgae and their carbonic anhydrase have a strong driving effect on the migration of Ca elements in limestone soil systems[21]. But existing research cannot quantify the contribution of CA in algal plants to karst processes? Is there a difference in CA activity between different algal species? The regulatory mechanisms and principles of CA metabolism in algae plants are still unknown.

### 3.3 The Sedimentary Mechanism of Algae Plants

The formation and development of soil in karst areas are the result of long-term dissolution, weathering, and biological enrichment of carbonate rocks. On the one hand, they are influenced by rock structure and properties, and on the other hand, they are closely related to vegetation. Research has shown that the soil formation rate of carbonate rocks is directly proportional to the rock dissolution rate, and is closely related to the content of acid insoluble substances. Another manifestation of algal plant sedimentation is limestone or calcareous deposits. The participation of algae makes the formation mechanism of calcareous deposits more complex, and the biological effects of algae are also influenced by many factors such as the hydrochemical composition, topography, water flow conditions, and other environmental factors of the calcareous sediment water. Different algal communities often form microbial mats or biofilm layers with a thickness of several hundred micrometers to 1-2 mm, which serve as important sites for calcium carbonate deposition, namely the active layer of calcium carbonate deposition. Moreover, within this active layer, the algae and their secreted extracellular polymers (EPS) can provide numerous nucleation sites and growth templates for the growth of calcium carbonate crystals, greatly promoting the deposition of calcium carbonate deposits. Shiraishi et al. (2008) found that surfaces covered with algal biofilms exhibit greater  $\text{Ca}^{2+}$  and  $\text{HCO}_3^-$  transport fluxes, indicating that algal mediation can overcome the energy barrier of calcium carbonate deposition[22]. Li et al. (2007) found that the layering and lateral extension accumulation of blue-green algae mats ultimately led to the formation of calcareous edge stone dams, while diatoms can grow in large quantities in fast flowing shoals, forming cotton like deposits with layered structures[21]. The biological sedimentation of algal calcareous deposits is complex and is influenced by many factors such as the hydrochemical composition of the sedimentary water, topography, water flow conditions, and other environmental factors. More research work is needed to accurately understand and quantify the role of algae in the formation of calcareous deposits, especially in the microscale aspects of the active layers of calcareous deposits controlled or influenced by algal growth. Multiple methods such as geochemistry, mineralogy, and microfacies should be comprehensively utilized to reveal the role of algae in the formation of calcareous deposits.

## 4. Conclusion and future research

The karst process of algae plants is a dynamic process of direct mutual utilization between algae plants and rocks. In recent years, significant research progress has been made on the karstification of algal plants, mainly focusing on the dissolution of metabolic products from algal growth, such as CA (carbonic anhydrase) accelerating the catalysis of atmospheric  $\text{CO}_2$  water and reaction, organic acids promoting the dissolution of calcite, extracellular polysaccharides increasing rock water holding capacity, algal calcification deposition, weathering and soil formation of algal plants and algal crusts, and migration of geochemical elements. But there are also shortcomings, with the following four aspects being the most prominent.

### 4.1 The intrinsic mechanism and process of algal plant karstification

At present, the karstification of algae and plants is mainly described qualitatively, while there are few quantitative descriptions about dissolution rate, sedimentation rate, etc. The comprehensive dissolution mechanism of algae on soluble rocks is not yet deeply studied. How algae can obtain the mineral nutrients they need through element migration caused by dissolution and physicochemical reactions on rocks. Meanwhile, with the growth, reproduction, aging, and death of algal organisms, what changes occur in the way and speed of algal control, and what are the differences in dissolution rates between biological dissolution and non-biological dissolution? What are the



metabolites of algae growth involved in dissolution? The reaction process between these substances and soluble rocks, the migration and consumption of mineral elements, the generation of new weathered minerals, the qualitative and quantitative analysis of products, as well as their dissolution rate and soil formation rate, and the differences in karstification between different algae species or algae with different growth characteristics, are still not clear enough in the research on the key basic issues of algal biokarstification. Therefore, in the future, efforts should be made to strengthen the research on the driving effects, driving mechanisms, and karst action rates of algae plants on karst dynamic systems.

#### **4.2 Karstification and weathering effects of algae and plants**

The research on the karstification of algal organisms is preliminary. The differences in the dissolution rate of carbonate rocks by algal organisms under different environmental conditions, as well as the synergistic relationship between algal action and soil formation, have not been thoroughly studied. Algae organisms vary in temperature, light, pH, and water conditions in different environments, affecting their growth and resulting in different biomass of algae. As a result, their water retention, drilling, and secretion of metabolic substances on the surface of carbonate rocks also vary, leading to differences in the dissolution rate of carbonate rocks. Therefore, in the future, the following three aspects of research work need to be carried out: (1) The colonization of algae plants and their effects on the dry and humid conditions, dissolution micro state, dissolution landform shaping, soil physicochemical properties, etc. in rock microenvironments. (2) The different natural geological backgrounds create rich climate types. Factors such as temperature, humidity, light intensity, pH, and bedrock lithology have an impact on the growth and reproduction, physiological regulation, and biomass of algae and algal crusts, resulting in differences in dissolution rate and mechanism of action. The direct synergistic relationship between these environmental factors and carbonate soil formation needs further research. (3) The research on the direct growth promotion relationship between algae and their symbiotic microorganisms, as well as the synergistic mechanism in dissolution, is not yet in-depth enough.

#### **4.3 The Physiological Metabolic Processes of Algae Plants and Their Relationship with Bioenzymes, Organic Matter, and Karstification**

The mechanisms by which algae and plants erode soluble rocks are physical and chemical. Biochemical dissolution is a common erosion mechanism in karst areas. The chemical dissolution of algae is caused by some chemical processes related to the physiological activities of algae. CA is widely present in plants and can accelerate the reaction between carbon dioxide and water, promoting karstification. Algae plants also produce a large amount of CA during their growth process, but differences between different plants and even within the same type of plant can also affect CA activity, thereby affecting the dissolution rate. Therefore, exploring how to regulate algal CA metabolism and improve its activity from a biological perspective is also a scientific issue that should be paid attention to in the future. The main component of the mucus secreted by the gel sheath of algae is polysaccharides. Polysaccharides can be converted into oxalic acid and produce carbon dioxide gas through microbial action in aerobic environments, further becoming the driving force for eroding soluble rocks. Algae produce CO<sub>2</sub> through respiration during their growth process, which reacts with water to produce carbonic acid. Further research is needed to investigate the differences and interrelationships between this dissolution effect and the dissolution effect of metabolic secretions.

#### 4.4 Adaptation characteristics of algal plants in karst areas and their mechanisms for maintaining biodiversity

Shallow soil layer, poor soil quality, and high calcium content are typical characteristics of karst ecosystems. Algae plants growing in karst areas have developed drought resistance and calcium loving characteristics during their long-term evolution. However, the understanding of the environmental adaptability characteristics of algae and plants in karst areas and their relationship with ecosystem processes and functions is still very limited, making it difficult to reveal the mechanisms of biodiversity maintenance in karst ecosystems. In future research, it is necessary to strengthen the analysis of the interaction mechanism between the composition characteristics, reproductive succession mechanisms, physiological regulatory functions (metabolic processes, carbon and nitrogen fixation, photosynthetic respiration, etc.), genetics and species diversity of biological algae plant populations in karst areas, and the types, functional structures, and biodiversity of karst ecosystem components.

In addition, scientific issues such as insufficient research on the dissolution mechanism and weathering effect of algae in karst rocky desertification areas should be addressed to explore the effects of algae CA, organic acids, extracellular polysaccharides, and their changes in conductivity and acid-base during the dissolution process of carbonate rocks. Dominant algae species should be screened to elucidate the dissolution mechanism of algae on carbonate rocks. Therefore, future research should reveal the synergistic relationship between environmental factors and algal dissolution to promote carbonate rock weathering and soil formation by investigating the effects of temperature, light and different water conditions on the rate of algal dissolution, which will provide a new theoretical basis for future rock desertification management. Meanwhile, with the utilization of H<sub>2</sub>O and CO<sub>2</sub> by algae as the central link, studying the differences in HCO<sub>3</sub><sup>-</sup> levels can help to understand the relationship between the physiological functions of algae and the intensity of biological karst. However, research in this area is still blank both domestically and internationally. Due to the prominent role of HCO<sub>3</sub><sup>-</sup> in photosynthesis and biological erosion, it has become a key core hub connecting the life processes of algae with their biological dissolution effects. By studying the differences in HCO<sub>3</sub><sup>-</sup> levels of algae in different niches, groups, and ecological factors, important information can be provided to understand the relationship between the physiological functions of algae and the intensity of biokarst.

#### Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

#### Author contributions

JZ and KX conceived the work, conducted data sorting, and analysis. JZ, NY collected the biocrust samples and rock samples. JZ performed the microscopic study for cyanobacteria phenotypic characterization. JZ conducted a shaking bottle simulation experiment. JZ wrote the manuscript and NY revised it. KX provided financial support and summarized manuscripts. All authors contributed to the article and approved the submitted version.

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