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Review

Research Status and Development Prospects of *Sea buckthorn* (*Hippophae rhamnoides* L.) Resources in China

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Abstract: *Sea buckthorn* (*Hippophae rhamnoides* L.), as an economically and ecologically valuable plant with rich nutritional and bioactive compounds, has garnered significant interest. The demand for *Sea buckthorn* has explosive growth, highlighting the urgent need for the cultivation of fast-growing, high-quality *Sea buckthorn* seedlings. However, there are still some controversies in *Sea buckthorn* germplasm resource research. This review provides a comprehensive summary of the recent research findings on *Sea buckthorn* plants, encompassing their classification, distribution, propagation methods, medical functions, and valorization. It aims to offer strong support for the industrial utilization of the *Sea buckthorn* and explores the prospects for molecular breeding in *Sea buckthorn*.

Keywords: *Sea buckthorn*; propagation; flavonoid; carotenoid; vitamin; valorization

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1. Introduction

Sea buckthorn (*Hippophae rhamnoides* L.) is a shrub or small tree belonging to the Elaeagnaceae family and is known for its inducible rooting characteristics [1,2]. It is also commonly referred to as vinegar willow, sour thorn, and blackthorn. Every part of this plant, including its fruits, leaves, stems, branches, roots, and thorns, has traditional uses in traditional medicine, nutritional supplements, soil and water conservation, and the establishment of wildlife habitats. In recent years, it has played a significant role in afforestation in the Tibet region; however, *Sea buckthorn* still holds untapped potential that requires further development [3]. *Sea buckthorn* exhibits a wide distribution, primarily in temperate, cold-temperate, and subalpine regions of the Eurasian continent [4]. In China, *Sea buckthorn* is extensively found in provinces and autonomous regions such as Qinghai, Tibet, Gansu, Ningxia, Inner Mongolia, Xinjiang, Sichuan, Yunnan, Guizhou, Liaoning, Jilin, and Heilongjiang. Tibet and Qinghai are the primary distribution areas. *Sea buckthorn* is a highly stress-resistant and ecologically adaptable plant, and it has found extensive applications in the fields of soil and water conservation and ecological construction [5]. The fundamental plan for *Sea buckthorn* resource development should be based on existing natural and artificial resources, actively utilizing the excellent *Sea buckthorn* resource varieties available in China, establishing high-quality *Sea buckthorn* industry parks, and rationally optimizing the layout of enterprises.

With the increasing awareness of the value of *Sea buckthorn*, the demand for *Sea buckthorn* has also been on the rise. An increasing number of scholars are researching and exploring the physiological characteristics of *Sea buckthorn* and cultivating excellent varieties with economic, medicinal, and ecological significance. Anonymous et al. [6] analyzed the diversity of endophytic bacteria in the root nodules of Tibetan *Sea buckthorn* using Illumina MiSeq high-throughput sequencing technology. In addition to the Frankia bacteria that form nitrogen-fixing symbiotic relationships with *Sea buckthorn*, other microbial communities are present in the root nodules of Tibetan *Sea buckthorn*. These findings imply the existence of potentially valuable endophytic bacterial resources. The root nodule function of *Sea*

buckthorn is achieved through symbiosis with rhizobia, facilitating nitrogen fixation to convert atmospheric nitrogen into plant-accessible ammonia, providing a nitrogen source for growth. Adverse conditions can induce changes in photosynthesis, metabolic processes, and growth and development in plants of the *Sea buckthorn* genus, leading to alterations in morphological structures. The research into the resistance physiology of *Sea buckthorn* plants can provide a theoretical basis for the conservation and development of germplasm resources within this genus [7]. Ghendov-Mosanu et al. [8] observed that the addition of 1% *Sea buckthorn* berry powder to wheat bread resulted in a product rich in health-promoting bioactive molecules, improved sensory and antioxidant properties, and an extended shelf life. Furthermore, *Sea buckthorn* fruits are rich in various nutritional and active components, such as vitamins C, E, and K, carotenoids, flavonoids, phenolic acids, and flavones, which exhibit potent antioxidant and anti-inflammatory effects. According to modern ethnobotanical records, *Sea buckthorn* fruit can effectively treat various allergy symptoms. To obtain pharmacological evidence for this observation, the anti-inflammatory activity of the fruit was studied using in vivo animal models.

2. Overview of *Sea buckthorn* Plant Resources

2.1. Species of Sea buckthorn

Sea buckthorn is a dioecious, deciduous perennial small tree or shrub, and it is an emerging fruit-bearing tree. Depending on the classification system used, *Sea buckthorn* plants have different classification methods, and the results obtained from different classification methods are not entirely consistent. Moreover, there are limitations to the classification methods. In 1996, according to the latest classification system by Chinese *Sea buckthorn* botanist Lian Yongshan [9], the *Sea buckthorn* genus was divided into 6 species and 12 subspecies based on different morphological characteristics of *Sea buckthorn* plants, categorized into two groups: those with skin and those without skin. In China, there are 6 species and 8 subspecies, earning it the title of the "Kingdom of *Sea Buckthorn*". In 2003, based on the different morphological characteristics of *Sea buckthorn* plants, Chen Xuelin, Ma Ruijun, and others [10] classified the *Sea buckthorn* genus into 7 species and 11 subspecies, with China having 7 species and 7 subspecies. *Sea buckthorn* is an ideal crop for regions south of the Indian Himalayas and other marginal areas with extreme weather conditions. Additionally, cultivated varieties of *Sea buckthorn* are found throughout the country. The majority of *Sea buckthorn* taxa are concentrated in the Himalayas and adjacent regions [11]. Based on the convergence of several key factors, it is concluded that the Himalayan region and its vicinity are not only the center of distribution for *Sea buckthorn* genus plants but also the center of differentiation and the origin of the primitive groups within this genus. Therefore, it can be inferred that *Sea buckthorn* plants likely originated in this region [11]. Chinese scientist Hu updated and improved the classification system, revising the *Sea buckthorn* genus to include 6 species and 17 subspecies [12]. Currently, apart from the Caucasian *Sea buckthorn*, Karbaq Thousand Mountain *Sea buckthorn*, Streamside *Sea buckthorn*, and Coastal *Sea buckthorn*, the other 6 species and 13 subspecies are distributed in China, with the discovery of the Wolong *Sea buckthorn* as a new subspecies in the year 2000, as shown in Table 1.

Table 1. Classification of *Sea Buckthorn* (*Hippophae rhamnoides* L.) distributed in China.

Genus	Group	Species	Subspecies
Hippophae L.	Skinless group	*H. salicifolia*	
		H. rhamnoides	*subsp.sinenis* *subsp.yunnanensis* *subsp.wolongensis* *subsp.turkestanica* *subsp.mongolica*

Table 1. *Cont.*

Genus	Group	Species	Subspecies
Hippophae L.	Skinned group	*H. goniocarpa*	*subsp.litangensis* *subsp.goniocarpa*
		H. gyantsensis	*subsp.linearifolia* *subsp.gyantsensis*
		H. neurocarpa	*subsp.stellatopilosa* *subsp.neurocarpa*
		H. tibetana	*subsp.yadongensis* *subsp.tibetana*

2.2. Habitat and Geographical Distribution of Sea buckthorn

Sea buckthorn has a very wide distribution range and is primarily found in Asia, Europe, and North America. According to the statistical data, as of December 2020, *Sea buckthorn* fruits have been distributed in 52 countries worldwide, covering a total area of 2.33 million hectares. China accounts for approximately 2.1 million hectares, with the remaining area distributed across other countries [13]. As shown in Figure 1, in China, *Sea buckthorn* is primarily distributed in the northern regions, including Liaoning, Inner Mongolia, Hebei, Shanxi, Shaanxi, Ningxia, Qinghai, Gansu, Xinjiang, and other provinces and autonomous regions. Additionally, it can be found in high-altitude areas such as Tibet, Sichuan, and Yunnan. Due to its ability to thrive in adverse environments, *Sea buckthorn* has an extensive distribution range, particularly flourishing in arid, cold, and high-altitude areas. Furthermore, *Sea buckthorn* exhibits some unique growth environments and distribution patterns.

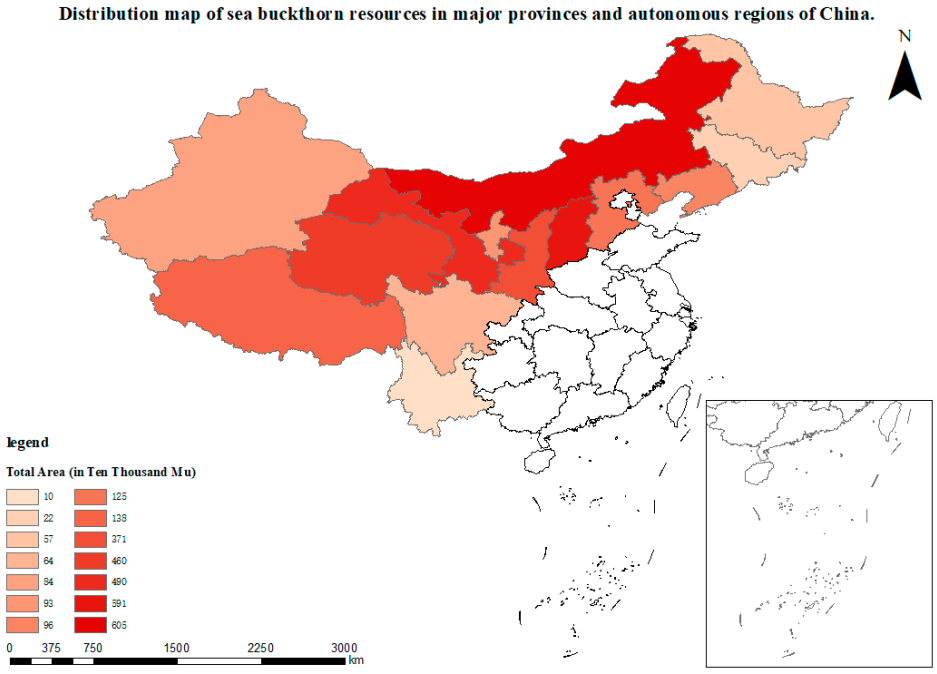

Figure 1. Distribution map of *Sea Buckthorn* (*Hippophae rhamnoides* L.) in various provinces (autonomous regions) of China.

- Desert and Semi-Desert Regions: *Sea buckthorn* exhibits strong salt and drought resistance, making it well suited for arid environments such as deserts and semideserts. It can assist in soil improvement and prevent land degradation. Therefore, it is widely distributed in desert regions in China, such as Inner Mongolia and Xinjiang. Under drought stress conditions, there is a decelerated response observed in the changes in

abscisic acid and flavonoid content, as well as their respective gene expressions [14]. These characteristics are crucial for *Sea buckthorn* survival in arid conditions.

- High-Altitude Areas: *Sea buckthorn* can also adapt to high-altitude and cold environments, possessing strong cold tolerance. It can thrive in high-altitude regions, such as the Qinghai–Tibet Plateau and the Himalayas in China. In these areas, *Sea buckthorn* faces extremely harsh conditions with low temperatures, strong winds, and intense radiation. However, its cold resistance and wind tolerance enable it to grow and reproduce in these environments. Xu Di [15] and others found that *Sea buckthorn* seeds still exhibit high vitality and germination rates at 10 °C when studying the impact of different temperature conditions on seed germination in Tibetan *Sea buckthorn*. This indicates that the Tibetan *Sea buckthorn* demonstrates strong environmental adaptability to the unique high-altitude and cold plateau environment of Tibet during the seed germination stage. In summary, *Sea buckthorn* possesses strong adaptability and vitality, allowing it to thrive in various extreme environments. This is of significant importance for local ecological environments and economic development. Its highly nutritious fruits hold significant economic and medicinal value.

3. Propagation System in *Sea buckthorn*

With the discovery of *Sea buckthorn*'s nutritional and economic value, the demand for it has been steadily increasing. It is widely used in the fields of medicine, food, cosmetics, beverages, water conservation, and soil protection as part of afforestation efforts. Simultaneously, it has expedited the development of local agriculture. Therefore, there is a need for a detailed analysis of *Sea buckthorn* seedlings and afforestation techniques to enhance their survival rate. This is crucial for cultivating high-quality *Sea buckthorn* with high survival rates and for maximizing its ecological and economic value. Due to *Sea buckthorn*'s strong adaptability, conventional tree propagation methods can be applied to *Sea buckthorn*. Currently, there are two main methods of *Sea buckthorn* propagation: sexual reproduction and asexual reproduction. Each propagation method comes with unique advantages and disadvantages, as shown in Figure 2.

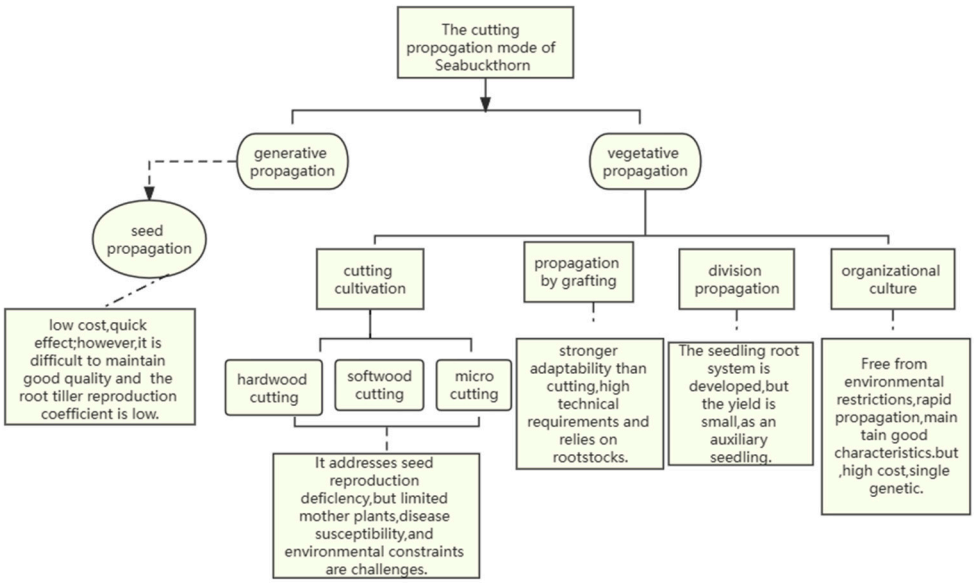

Figure 2. The main reproduction method of *Sea buckthorn*.

3.1. Sexual Reproduction

Sexual reproduction, also known as seed propagation, is suitable for large-scale expansion and is a commonly used method for propagating *Sea buckthorn*. It involves the use of seeds to germinate and develop into mature *Sea buckthorn* plants. Seed propagation is characterized by its low cost, minimal labor input, well-developed root systems, and strong

adaptability. However, due to the predominantly male population of *Sea buckthorn*, which affects fruit production, it is not suitable for economic and artificial forest plantations. *Sea buckthorn* seeds are small, with thick and hard skins, and are coated with an oily adhesive film, which hinders water absorption [16]. The following are the steps involved in *Sea buckthorn* seed propagation:

- Harvesting: *Sea buckthorn* has many thorns, so during collection, it is advisable to either knock the fruits off during the winter or prune the branches before processing [17]. After harvesting the ripe *Sea buckthorn* fruits, they are soaked in clean water for approximately half an hour to remove surface dust and impurities. The fruits are then placed in a well-ventilated area to air dry until the surface is free of moisture.
- Removal of fruit skins: The dried *Sea buckthorn* fruits are processed to remove the fruit skins, and the seeds are extracted. The seeds are then cleaned and subjected to disinfection to eliminate surface bacteria and viruses, improving the germination rate.
- Soaking: Typically, the cleaned seeds are soaked in warm water for 24 h to promote germination.
- Sowing: The soaked seeds are sown in various containers, such as seedling trays, nursery boxes, or flowerpots. The seeds should be evenly sown to avoid overcrowding and competition among seeds. A layer of well-draining soil or leaf mold can be used as a covering.
- Placement and care: The sown containers are placed in direct sunlight, maintaining suitable temperature and humidity. Regular watering and ventilation are necessary. *Sea buckthorn* seeds take a relatively long time to germinate, typically requiring 2–3 weeks or even longer.
- Transplantation and cultivation: Once *Sea buckthorn* seedlings reach a certain stage of growth, they can be transplanted and cultivated until they become mature plants.

Seed propagation is a simple and cost-effective method with quick results. It is widely utilized for *Sea buckthorn* development and utilization in most regions of China [18]. In summary, *Sea buckthorn* seed propagation requires the selection of mature fruits, seed treatment, and disinfection to ensure high germination rates and survival rates. Additionally, providing a suitable environment and proper management, including regular watering, ventilation, and appropriate fertilization, are crucial for the growth and development of *Sea buckthorn* seedlings. It is reported that the application of bioapatite and biolan in the fertilization experiment led to an increase in stem diameters when compared to the control treatment [2]. Through scientific techniques, the survival rate and quality of *Sea buckthorn* seedlings can be improved, promoting the development of the *Sea buckthorn* industry. However, relying solely on seed propagation may make it challenging to maintain the characteristics of excellent varieties in production. The rhizome propagation coefficient is low, and the currently used cutting propagation in production has a low survival rate and is susceptible to disease transmission. Therefore, for large-scale production with quality assurance, specific propagation techniques must be chosen [19].

3.2. Asexual Reproduction

The ways of asexual reproduction for *Sea buckthorn* include cutting, layering, division, grafting, and tissue culture. Among these, cutting and layering have relatively lower success rates and are typically used for specialized seedling production and research purposes. Division propagation is suitable for mature *Sea buckthorn* plants and involves cutting the root system of mature plants into several parts for transplantation and reproduction. Grafting propagation allows for the combination of *Sea buckthorn*'s resilience and salt tolerance with other tree species, creating new varieties with significant practical value. By controlling the nutrient components, hormones, and other environmental conditions of the growing medium, tissue growth and differentiation can be stimulated to produce new plants.

3.2.1. Cutting Propagation

Cutting propagation is one of the most widely researched and applied methods in *Sea buckthorn* seedling cultivation. It includes two methods: hardwood cutting and softwood cutting. Through cutting propagation, it is possible to quickly obtain excellent asexual seedlings identical to the parent plants, thereby compensating for the shortcomings of seed propagation. Cutting propagation offers advantages such as high rooting rates and relatively high seedling survival rates. Importantly, for the propagation of rare and valuable varieties, asexual reproduction is necessary. However, as cutting propagation becomes more widespread, its disadvantages also become evident. These include limitations on the number of parent plants available for cutting, restrictions on the age of the parent plants to be harvested, and the potential environmental impact of cutting, all of which can affect *Sea buckthorn* survival and rooting rates [20].

Currently, the research reports indicate that there are three methods of cutting propagation: hardwood cutting, softwood cutting, and softwood micro cutting, each with its unique characteristics, as detailed in Table 2. Hardwood cutting involves the use of fully woody branches for propagation. After trimming, these branches are bundled into groups of 50–100 and soaked in water for approximately 36 h, with the base of the cutting submerged to a depth of approximately 4 cm. The cuttings should be uniform in length, with a flat cut and two buds remaining. To prevent desiccation and promote rooting, these cuttings should be buried in moist sand or water containing rooting hormone powder [21]. Softwood cutting involves using semi-woody branch cuttings with leaves during the growing season. Softwood cutting in *Sea buckthorn* is best performed early in the growing season, with late-season cutting reserved for propagating valuable varieties or varieties from natural forests. Late cuttings may result in damage to cuttings with roots during the winter [22]. Wang Yunli [23] broke through this bottleneck by researching micro cuttings of *Sea buckthorn* using 2–3 cm branches and pointed out that "*Sea buckthorn* axillary bud seedlings are an easy-to-root and effective new technology." Yao Jingyu concluded that within a certain range, longer cuttings are better as they retain more leaves, which helps the healthy growth of the above-ground portion after cutting.

Table 2. Comparison of Different Propagation Methods in *Sea buckthorn*.

Cutting Propagation	Hardwood Cutting	Softwood Cutting	Softwood Micro Cutting
branch selection	Vigorous, straight, stress-resistant and fully woody, 15–20 cm length with 3–4 fully buds	Semi-woody with leaves	2–3 cm branches [24]
optimal time	Late winter to early spring [25]	July [26]	June [27]
advantages	Less stringent conditions	High survival rates and high efficiency [28]	Overcomes drawbacks of hardwood cutting; sufficient propagation
disadvantages	Lower rooting rate, Once-a-year operation Limited pruning and lower propagation coefficient [13]	Risk of rot with improper handling [19]	Unable to store large amounts of nutrients [21]
rooting enhancement	1:1 river sand and peat [29] Cold storage and GGR6 [30]; GGR rooting powder [31] greenhouse [32,33] 3:1 river sand and humus [34,35]	Indole butyric acid [26,36,37]; temperature 26–32 °C and humidity 70%–80% [38]; density between 400 plants/m^2 and 600 plants/m^2 [39,40]; NAA at 200 mg/L [22,41]	*Sea buckthorn* axillary bud seedlings [24]; Sand cultivation [1,42,43]
considerations	High-quality material, well-drained sandy loam [13]; seedling height [28]; different hormone [44]; Mother tree age [34]	Thickness of sand bed, depth of planting [45]; hormones [38]; Mother tree age [22]; substrates [46,47]	Longer cuttings with a range [24,48]

For these three cutting methods, there are various factors influencing the success of hardwood cutting. To minimize disease and pest issues during the propagation period, the seedbed should be thoroughly disinfected with fungicides or potassium permanganate solution [49]. Simultaneously, when plants are damaged by herbivores, they release volatile

organic compounds that attract the natural enemies of the herbivores to protect themselves. The larvae of *Holcocerus hippophagous* primarily infest the nitrogen-fixing roots of *Sea buckthorn* plants, aiding in the absorption of water and nutrients from the soil through symbiotic relationships with mycorrhizal fungi and rhizobacteria [50]. Studies showed that the *Sea buckthorn* fruit fly causes severe damage to *Sea buckthorn* berries, while Brassinosteroid (BR)enhances *Sea buckthorn* resistance to *Rhagoletis batava obseuriosa* Kol. (RBO) [51].

3.2.2. Grafting Propagation

Grafting propagation is even more advantageous than stem-cutting propagation because it is based on the root system of plants, thereby giving the plant greater adaptability. The grafting process is not limited by the compatibility of male and female plants, allowing for the control of the male-to-female ratio in *Sea buckthorn* plants [19].

3.2.3. Propagation of Ramets

The ramets have a strong ability to use *Sea buckthorn* sprouting, and the tillering roots are vigorous. In spring and autumn, healthy tillering seedlings are cut off from the ramets together with fibrous roots [23]. Although this method can promote the root development of seedlings, its yield is small, so it is regarded as an auxiliary seedling-raising method in actual production, and the application range is relatively limited [52].

3.2.4. Tissue Culture

With the accelerated pace of development in the western regions, there is an increasing demand for a large quantity of *Sea buckthorn* seedlings for afforestation and ecological agriculture. The traditional methods of division propagation and softwood stem-cutting propagation are no longer sufficient to meet this demand. In contrast, tissue culture propagation is not limited by season or geography, and it offers the advantages of rapid breeding and the preservation of desirable characteristics. In particular, tissue culture propagation holds great potential for breeding *Sea buckthorn* from male and female plants with separate sexes [53]. Currently, softwood stem-cutting propagation is more commonly used in production, but it is susceptible to diseases. In comparison, using tissue culture for seedling propagation can significantly accelerate the breeding process and maintain the quality of resources, making it the primary method for scaling up seedling production [54]. There have been numerous studies on tissue culture in this regard. In the research conducted by Liu Hongtao [54], it was shown that the optimal conditions for *Sea buckthorn* stem segment differentiation include using the following culture medium: B5 + 6-BA 0.5 mg/L + IAA 0.3 mg/L. The best culture medium for proliferation and inducing seedling growth was B5 + 0.5 mg/L 6-BA + 0.5 mg/L IAA, and the best rooting culture medium was 1/2 B5 + 0.5 mg/L IAA + 0.5 mg/L IBA.

4. Research on the Functions of *Sea buckthorn*

The functional research on *Sea buckthorn* has yielded promising results, covering multiple areas of application, as shown in Figure 3. In the medicinal field, *Sea buckthorn* has been extensively studied for its fruit, which is rich in vitamin C, vitamin E, beta-carotene, polyphenolic compounds, and catechins, among other antioxidant substances. These components provide it with various biological activities, such as antioxidant, anti-inflammatory, antimicrobial, and antitumor properties. These qualities make *Sea buckthorn* a potential complementary treatment option for various chronic diseases, including cardiovascular diseases, cancer, and inflammatory conditions. In the beauty industry, *Sea buckthorn* oil has garnered attention due to its high content of antioxidants and fatty acids. It is widely used in skin care products and contributes to reducing skin inflammation, accelerating wound healing, and improving skin elasticity and hydration, thereby reducing wrinkles and dryness. *Sea buckthorn* oil has already made a mark in the beauty industry, offering a natural and effective solution for skin care. Furthermore, *Sea buckthorn* has extensive applications in the food industry. Its berries are used to make juices, jams, wines, and

health foods, enjoying popularity due to their unique sweet–sour taste and rich vitamin content. *Sea buckthorn* juice is rich in nutrients, providing people with a healthy dietary choice. The functional research on *Sea buckthorn* has provided a solid scientific foundation for its applications in various fields, including medicine, beauty, and juice production. With a deeper understanding of its benefits and ongoing research, we can expect to see more innovative *Sea-buckthorn*-related products and therapies to meet people's health and beauty needs.

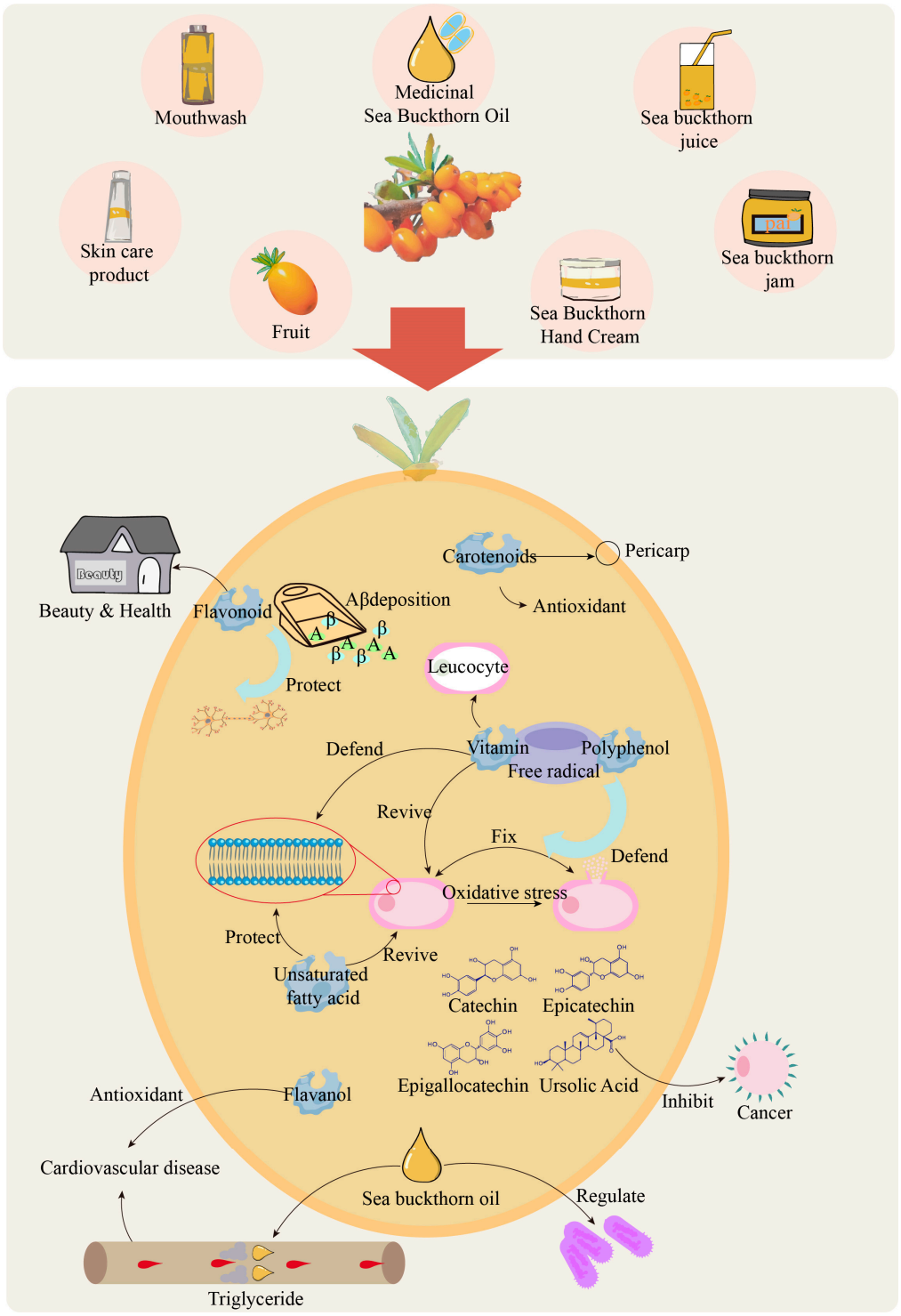

Figure 3. The functional applications of *Sea buckthorn*.

4.1. Medical Functions of Sea buckthorn

Sea buckthorn has many characteristics that are beneficial to human health, and its roots, stems, leaves, flowers, and fruits have good medicinal value potential. China has a long history of the medicinal use of *Sea buckthorn*, which has been widely used in the field of national medicine. It is a commonly used medicinal material for Tibetan medicine and Mongolian medicine. Many famous medical classics also record the medicinal efficacy of *Sea buckthorn*. It is a guiding theory of medication accumulated by ancient working people and medical experts through a large number of clinical practices for a long time, which plays an important guiding role in the mining of *Sea buckthorn* efficacy and product development. There are many metabolic pathways in the whole life cycle of *Sea buckthorn*. These metabolic pathways lead to the production of many secondary metabolites, which have certain medicinal value, such as flavonoids and phenolic acids. Studies have found that these components have a wide range of health benefits by exerting antioxidant, anticancer, anti-inflammatory, antibacterial, and antiviral effects, as well as protective effects on the cardiovascular system, skin, nerves, and liver. The extensive research by many scholars has focused on these bioactive compounds, which primarily function by neutralizing free radicals, inhibiting lipid peroxidation reactions, and activating antioxidant systems [55]. The nutritional and bioactive content of *Sea buckthorn* fruit influences its health value [56].

4.1.1. Flavonoids

Flavonoid compounds may have potential roles in preventing chronic diseases such as diabetes, cardiovascular diseases, and cancer [57]. Guo et al. [57] found that total phenols and flavonoid alcohols in *Sea buckthorn* extracts exhibited antioxidant and anti-proliferative activities. To date, 95 flavonoid compounds have been identified in *Sea buckthorn*, including 75 flavonol alcohols, 2 dihydroflavonols, 6 catechins, 1 resveratrol, 9 anthocyanins, 1 proanthocyanidin, and 1 flavone [58]. Resveratrol is a phenolic phytoalexin exhibiting antifungal properties within the realm of plant secondary metabolites. The research has indicated its beneficial impact on human health, in conjunction with other categorized compounds. Investigations highlight that diverse technical approaches during the processing of plant materials can exert an influence on the presence of these phenolic compounds in the ultimate product. The conclusions drawn from the research report authored by Aleksander V. et al. [59] underscore that the initial processing and brewing methodology can impact and augment the resveratrol content. The concentration of resveratrol tends to escalate with prolonged soaking and fermentation times. Notably, red grape wine manifests a higher resveratrol content compared to white grape wine. The thermal vinification process, involving heating to 60 °C with a 1-h incubation, proves to be more efficacious in extracting phenolic substances than traditional methods. Additionally, the judicious selection of suitable yeast strains and enzyme formulations can further elevate the content of resveratrol and phenolic constituents in grape wine. *Sea buckthorn* serves as a source of natural antioxidants for the prevention and treatment of oxidative stress-related diseases. This finding aligns with the antioxidant properties found in many fruits and plants. *Sea buckthorn* is capable of clearing Aβ deposits within cells, with the most significant effect observed at a *Sea buckthorn* berry powder concentration of 1.5 g/mL. This discovery may be attributed to the higher levels of antioxidants present in *Sea buckthorn* berry powder. Antioxidants exert neuroprotective effects by inhibiting Aβ-induced toxicity and preventing cell death. *Sea buckthorn* holds promise as a potential treatment for Alzheimer's disease [60]. Another study demonstrated that *Sea buckthorn* flavonoids promoted the activation of insulin receptor substrate (IRS)/AKT, reduced the expression of protein-tyrosine phosphatase 1B (PTP1B), and restored insulin signaling pathways, neurogenic damage, and the ERK/CREB/BDNF signaling pathway. It inhibited insulin resistance and neuroinflammation, alleviated high-fat diet-induced cognitive impairment, and effectively prevented memory loss [61]. However, these conclusions are based on scientific research and should be approached with caution, especially before further research supports clinical treatment. Additionally, *Sea buckthorn* improved iron-induced epilepsy-like activity in the cerebral

cortex and hippocampus of rats, reduced anxiety-like behavior, and improved memory impairment and tissue damage in rats [61]. In summary, *Sea buckthorn* has been shown to have neuroprotective effects. These effects may be attributed to the presence of flavonoids and other antioxidant compounds in *Sea buckthorn*. Future clinical trials are necessary to investigate the neuroprotective effects of *Sea buckthorn* in humans. The richest flavonoids in *Sea buckthorn* fruits and leaves are isorhamnetin and quercetin [62], indicating the historical and practical use of *Sea buckthorn* in herbal medicine and beauty and health care.

The studies have also investigated the cytotoxic effects of *Sea buckthorn* flavonoids on human liver cancer cells (BE2-7402) [63] and observed cytotoxic effects due to the accumulation of isorhamnetin within the cells. After 48 h of treatment, BE2-7402 tumor cells exhibited isorhamnetin-induced chromatin condensation and fragmentation, indicating that *Sea buckthorn* extracts have antitumor and growth-inhibiting effects on cancer cells. Another study by Kim et al. [64] explored whether *Sea buckthorn* leaf extracts inhibit the proliferation and promote apoptosis of rat glioma C6 cells. They found that treatment with *Sea buckthorn* leaf extracts significantly inhibited the proliferation of rat C6 glioma cells in a dose-dependent manner and reduced the generation of reactive oxygen species (ROS), which are crucial for tumor cell proliferation. Additionally, *Sea buckthorn* treatment significantly upregulated the proapoptotic protein Bax and promoted its nuclear localization. *Sea buckthorn* extracts also contain β-sitosterol, which is reported to possess antitumor activity [65,66]. It is important to note that despite these favorable research findings, *Sea buckthorn* as a standalone treatment for cancer is not sufficient to replace traditional cancer treatments such as radiation, chemotherapy, and surgery. *Sea buckthorn* can serve as a healthy dietary supplement to support the immune system and overall health. However, in the context of cancer treatment, more research is still needed to determine its exact efficacy and usage.

4.1.2. Phenolic Acid Compounds

Polyphenols are the main compounds in *Sea buckthorn* responsible for its antioxidant activity. They are a class of compounds with multiple phenolic ring structures, including flavonoids, flavonols, and phenolic acids. Polyphenols possess strong antioxidant properties, neutralizing and stabilizing free radicals and reducing cell damage induced by oxidative stress. The reported polyphenol content in *Sea buckthorn* fruit ranges from 12.36 to 34.6 milligrams of gallic acid equivalents (GAEs) per gram, which is higher than that in oranges (1.27 mg GAE/g), citrus fruits (1.16 mg GAE/g), blueberries (2.19 mg GAE/g), sour cherries (2.56 mg GAE/g), and strawberries (1.12 mg GAE/g) [67,68]. A recent review indicated that nearly 100 polyphenolic compounds have been identified and isolated from *Sea buckthorn* [69], including 17 phenolic acids found in *Sea buckthorn* berries. Salicylic acid is the primary phenolic acid in berries, comprising 55%–74.3% of the total phenolic acids [70]. However, another study reported that ellagic acid is the main phenolic acid in *Sea buckthorn* fruits and leaves [69].

Sea buckthorn fruit and its seed oil are rich in beneficial unsaturated fatty acids, including omega-3, omega-6, and omega-7, along with natural antioxidants, vitamins such as vitamin E and vitamin K, carotenoids, and plant sterols [71]. The combined action of these chemicals helps protect cell membranes and promote cell regeneration. Furthermore, palmitoleic acid in *Sea buckthorn* oil has been used to treat burns and promote wound healing. Reported potential uses for *Sea buckthorn* oil include preventing and treating various types of gastric ulcers, chronic cervicitis, and atopic dermatitis [72,73]. In a study conducted by Edraki et al. [74], *Sea buckthorn* oil, olive oil, and their mixtures were used to treat burns in rats.

4.1.3. Vitamins

The quality of *Sea buckthorn* fruit is often evaluated based on its abundant nutritional value [67]. *Sea buckthorn* is renowned as a "natural treasure trove of vitamins" due to its high vitamin content. The vitamin C content in *Sea buckthorn* fruits varies between

52.86 mg and 896 mg per 100 g [56,67]. The vitamin C content in 100 g of *Sea buckthorn* berries can reach as high as 275 mg, far surpassing the same quantity of other fruits, such as mangoes (27.7 mg), apricots (10 mg), bananas (8.7 mg), oranges (50 mg), and peaches (6.6 mg). Hence, owing to its elevated vitamin C content, *Sea buckthorn* products are capable of retaining substantial vitamin C levels even post-processing. This is crucial, as many products encounter challenges in preserving adequate vitamin C levels throughout processing. Nevertheless, certain studies indicate that subjecting *Sea buckthorn* to high-temperature processing may result in a reduction in vitamin C content. This juice can be effectively harnessed for the production of nutritionally rich fruit juice powder through the utilization of the spray drying process. Alterations in spray drying conditions, such as the inlet air temperature, are observed to impact the vitamin C content of the fruit juice powder. It was noted that a significant increase in the vitamin C content of the juice powder could be achieved by adjusting the spray drying conditions, specifically by reducing the inlet air temperature [75].

Vitamin C is crucial for maintaining the normal function of the immune system. It helps promote the generation of white blood cells, which play a critical role in combating infections. *Sea buckthorn* is rich in antioxidants such as vitamin C, vitamin E, and flavonoids. These antioxidants can neutralize free radicals, reduce oxidative stress, and thereby help protect the immune system from damage. Moreover, certain components in *Sea buckthorn* exhibit anti-inflammatory properties, which can alleviate chronic inflammation and contribute to maintaining the balance of the immune system. The research also suggests that beta-carotene in *Sea buckthorn* can influence human immune function by regulating the expression of specific genes. It is important to note that while *Sea buckthorn* can provide support to the immune system, the health of the immune system is influenced by various factors, including overall diet, lifestyle, and genetics. Maintaining a balanced diet, moderate exercise, sufficient sleep, and stress management are also essential factors in preserving immune system health. Additionally, *Sea buckthorn* shows significant antiviral activity. *Sea buckthorn* may serve as a potential source of antiviral medication against HSV-2, providing an alternative drug candidate for patients infected with acyclovir- and penciclovir-resistant strains [76]. The research has found that immunization using *Sea buckthorn* leaf extract and inactivated rabies virus antigen (SBTE + Rb) can increase rabies virus neutralizing antibody (RVNA) titers and cytotoxic T lymphocyte (CTL) responses. Compared to the Rb-immunized group, the SBTE + Rb-immunized group showed a significant increase of 5.5% in memory T cells and 1.9% in plasma cells. The components of *Sea buckthorn* leaf extract that may have immune-adjuvant activity include quercetin and other flavonoids [77]. Studies have found that *Sea buckthorn* proteins can increase the quantities of Bifidobacterium, Lactobacillus, and Bacteroides while decreasing Clostridium.

4.2. Commercial Values and Valorization of Sea Buckthorn

As quality of life improves, people become more concerned about health and wellness. Due to its rich nutritional components and medicinal value, Sea buckthorn has been extensively developed into various functional foods.

4.2.1. Development of *Sea buckthorn* Functional Foods

Sea buckthorn has significant importance in the food industry, particularly as a raw material for functional foods or dietary supplements. While all parts of the *Sea buckthorn* plant have diverse applications, the fruit, especially the pulp (used for making *Sea buckthorn* juice) and the fruit seeds (used for oil extraction), are the most valuable components [78,79]. Various products derived from *Sea buckthorn* fruit have been developed, similar to common products obtained from other fruits, and there were over 200 different products derived from *Sea buckthorn* species in 2018 [69]. *Sea buckthorn* low-temperature freeze-dried powder, prepared through low-temperature freeze-drying technology, can actively impact the composition and structure of the gut microbiota and help combat high-fat diet-induced obesity [80]. Adding 3% *Sea buckthorn* fruit juice extract to pork sausages effectively in-

hibited lipid oxidation and reduced the total bacterial count by approximately 7 times, thereby enhancing the microbial content of the sausages [81]. In Finland, *Sea buckthorn* is used as a functional ingredient in baby food products [82]. Additionally, the market offers *Sea buckthorn* products without additives that have unique flavors and high nutritional value and exhibit outstanding antioxidant properties, making them a preferable choice for promoting health [69].

4.2.2. Extraction of *Sea buckthorn* Oil

Sea buckthorn oil can be categorized into fruit oil, seed oil, and blended oil. Product types include capsules, oral liquid, and bottled oil, among others. In the food market, *Sea buckthorn* products containing added *Sea buckthorn* oil hold an important and distinct position. *Sea buckthorn* oil can be found as an ingredient in certain dietary supplements, such as those aimed at improving mucous membrane conditions. These supplements are highly appealing to consumers because they are sourced naturally and offer health benefits [83] *Sea buckthorn* fruits contain two different oil components: one obtained from the seeds and the other retained in the pulp. The primary compounds in these oil fractions are unsaturated fatty acids and tocopherols, but their concentrations vary significantly. Seed oil contains higher concentrations of tocopherols and α-linolenic acid, while pulp oil has higher concentrations of palmitoleic acid. Smida et al. [84] reported an experimental oral mouthwash based on *Sea buckthorn* fruit oil that exhibited bactericidal effects against certain periodontal bacteria and could inhibit the formation of single and multistrain biofilms. Palmitoleic acid is a skin component used in burn treatment and wound healing. *Sea buckthorn* oil is reported to have preventive and therapeutic effects on various conditions, such as gastric ulcers, chronic cervicitis, and atopic dermatitis [85,86]. Furthermore, a randomized triple-blind clinical trial demonstrated that patients treated with 40% *Sea buckthorn* cream for second-degree burns had a shorter healing time by approximately 5 days compared to patients treated with 1% silver sulfadiazine cream dressings. *Sea buckthorn* cream exhibited superior clinical efficacy and accelerated the healing of second-degree burns [87]. The research has revealed that *Sea buckthorn* seed oil facilitates wound contraction and enhances the healing of full-thickness burn wounds by increasing hydroxyproline, hexosamine, DNA, and total protein content. The wound-healing potential of *Sea buckthorn* seed oil depends on the presence of ω-3 and ω-6 fatty acids, tocopherols, and carotenoids [88]. Additionally, a fraction enriched with palmitic acid purified from *Sea buckthorn* seed oil exhibited cell-proliferative properties by promoting the growth of keratinocytes and dermal fibroblasts, making it suitable for developing skincare formulations and products [89]. Moreover, *Sea buckthorn* oil has been tested for its potential to alleviate menopausal symptoms such as vaginal atrophy and thinning and drying of the vaginal mucosa. It is suitable for women who cannot tolerate estrogen therapy. A study included over 90 women who took oral *Sea buckthorn* oil supplements [90]. After three months, these women exhibited improved vaginal health conditions, including a significant improvement in vaginal epithelial integrity. Therefore, *Sea buckthorn* oil therapy can offer an alternative to estrogen treatment for vaginal atrophy.

Considering the known positive effects of *Sea buckthorn* oil on the skin and mucous membranes, researchers have investigated its potential impact on dry eye syndrome. A group of men and women suffering from dry eye syndrome orally consumed *Sea buckthorn* oil for three months during the autumn and winter. *Sea buckthorn* oil reduced the increase in tear film osmolarity during the cold season and had a positive effect on dry eye symptoms [91]. Despite the long history of *Sea buckthorn*'s nutritional and medicinal use, information regarding its toxicity and safety remains relatively limited. Wen et al. [92] reported that *Sea buckthorn* oil is not a mutagenic or teratogenic substance. They found that *Sea buckthorn* oil had no mutagenic activity against tryptophan-dependent strains of Salmonella typhimurium within the exposure concentration range of 8 to 5000 μg/plate. Even at a dosage of up to 9.36 g/kg body weight, *Sea buckthorn* oil did not significantly affect sperm morphology or the micronucleus rate of polychromatic erythrocytes in mice. More-

over, a dosage of 4.68 g/kg *Sea buckthorn* oil did not induce maternal or embryonic toxicity in pregnant mice. The no observed adverse effect level (NOAEL) in rats was determined to be 4.68 g per kilogram of body weight. A 90-day safety study in rats demonstrated that the NOAEL was 100 mg of *Sea buckthorn* fruit water extract per kilogram of body weight [93]. Furthermore, Zhao et al. [94] reported that the maximum tolerated dose of *Sea buckthorn* fruit oil in acute toxicity studies in mice was greater than 18.72 g/kg. In a 90-day repeated oral toxicity test in rats, the NOAEL was 9.36 g per kilogram of body weight. *Sea buckthorn* fruit is healthy and nontoxic, and it can be used for human consumption, medicinal purposes, or dietary supplements.

4.2.3. Making *Sea buckthorn* Juice Beverages

Sea buckthorn has a wide range of applications in food, providing not only a delicious taste and color to dishes but also a rich nutritional content and antioxidants for the human body. These applications not only enrich food choices but also contribute to promoting health and creating delicious meals. Some of the most popular and ancient *Sea buckthorn* products are juices and refreshing beverages. These nutrient-rich drinks are abundant in vitamin C and carotenoids and are highly popular in China, Germany, the Scandinavian Peninsula, and other Nordic countries. *Sea buckthorn* beverages served as the official drink for Chinese athletes during the 1988 Seoul Olympics [95]. They are also used in the diets of Indian soldiers working in extremely cold conditions [96]. Furthermore, *Sea buckthorn* berries, despite their tartness, are used for making jams and jellies. Their rich aroma can be balanced by blending *Sea buckthorn* juice or sauce with other milder-flavored fruits in various proportions [97]. The research indicates that *Sea buckthorn* fruits are valuable for jam production due to their high content of bioactive compounds. In a study by Rafalska et al. [98], various jams with different flavors and colors were prepared by mixing *Sea buckthorn* fruit with other fruits, such as apples, currants, raspberries, and strawberries. A sensory analysis showed that *Sea buckthorn* jam with the addition of strawberries and raspberries was most appreciated by the evaluators [98]. Attri and Goel [99] used an in vitro simulated gut model to study the impact of polyphenol-rich *Sea buckthorn* berry juice on colon microbial composition and diversity. The study showed that *Sea buckthorn* juice had a stimulating effect on beneficial microbial populations, such as the Lactobacillus, Bifidobacterium, and Prevotella species. The existing research suggests that the addition of *Sea buckthorn* pulp significantly increases the antioxidant properties of fermented beverage products and increases their acidity [98]. However, some studies have confirmed that the content of bioactive compounds, especially polyphenols, has changed significantly after the application of fermentation in fruit processing. A study has concluded that the presence of Botrytis cinerea in grapes has an impact on the content of selected phenolic compounds in wine, exhibiting differences compared to wine produced from healthy grapes [100]. A research investigation demonstrated an increased quercetin content in macerated fruit pulp (FP) compared to pomace, which had not undergone maceration [101]. Reduced maceration times resulted in significantly lower phenolic content compared to the extended maceration used in red wine production [102]. *Sea buckthorn* berries are also used in the production of sheep cheese, where they form a biodegradable framework. Beneficial probiotic strains such as Lactobacillus casei ATCC 393 can grow on this framework. Additionally, the incorporation of *Sea buckthorn* was found to reduce the number of pathogenic microorganisms and improve the sensory properties of cheese [103]. Wen et al. [92], in their exposure studies of *Sea buckthorn* berries (SB) at different concentrations, found no mutagenic activity on histidine-dependent strains of Salmonella Typhimurium in mice, as well as no impact on mouse sperm and micronucleus rate of polychromatic erythrocytes. These results support the safe use of *Sea buckthorn* berry oil as a potential dietary consumption or dietary supplement in food products. *Sea buckthorn* serves as an excellent source of functional and therapeutic foods. An analysis of the published studies on *Sea buckthorn* toxicity and safety reveals that the majority of the reported research results are either beneficial or show no significant adverse effects. No

study has deemed its consumption harmful to humans. However, it is noteworthy that safety assessments are in their initial stages, and further experimentation is required to validate its safety.

5. Conclusions and Prospects

Sea buckthorn offers rich nutritional value; however, there is still room for ongoing improvements in various aspects, including genetic enhancement and adaptability to diverse environments. As a nutrient-rich fruit, *Sea buckthorn* has a wide range of applications and prospects, but future development should encompass factors such as variety improvement, agricultural practices, food safety, market promotion, sustainable production, clinical research, and international cooperation. Through continued research and ongoing improvement in practices, *Sea buckthorn* is poised to become an integral component of healthy food and sustainable agriculture.

- Breeding of New Varieties: *Sea buckthorn* has multiple varieties, and variations in nutritional content and taste may exist among different varieties. The future research should focus on breeding *Sea buckthorn* varieties with higher yields, drought resistance, and enhanced nutritional value to meet market demands. This will contribute to improving the sustainable production and commercial potential of *Sea buckthorn.*
- Genetic Enhancement of *Sea buckthorn*: While *Sea buckthorn* exhibits strong adaptability to the environment, the regions suitable for its growth may change with climate change and rising temperatures. The research indicates that global warming in recent decades has led to changes in the distribution range of *Sea buckthorn*. For instance, the population of *Sea buckthorn* in some high-latitude areas has decreased, while *Sea buckthorn* in some low-latitude regions is gradually expanding northward. Furthermore, climate change may also affect the quality and yield of *Sea buckthorn* berries. As *Sea buckthorn* has high requirements for sunlight and water, climate change may lead to drought and excessively high temperatures, affecting *Sea buckthorn* growth and fruit yield. This matter requires attention, and therefore, more research is necessary to understand the genetic improvement of *Sea buckthorn* so that it can withstand adverse environmental changes and we can enable appropriate measures to protect and manage *Sea buckthorn* resources.
- Agricultural Practices and Sustainability: The cultivation and management techniques for *Sea buckthorn* need continuous improvement to enhance yield and quality while ensuring sustainable agricultural practices. Farmers need training to understand how to maximize the potential of this plant. *Sea buckthorn* is a highly adaptable and drought-resistant plant suitable for growth under various climatic conditions. Therefore, it has the potential to become a promising agricultural crop that can improve rural economies and increase farmers' income. Additionally, the root system of *Sea buckthorn* can be used to prevent soil erosion, contributing to sustainable land management. Sustainable methods of *Sea buckthorn* production and harvesting need to be considered to ensure that they do not harm the ecosystem. Planting and harvesting practices should take into account their environmental impact and resource management.
- Food Safety and Innovation: As the production and consumption of *Sea buckthorn* products increase, ensuring food safety is crucial. The research should focus on hygiene standards and food preservation techniques during the production process to prevent foodborne illnesses. There is still significant room for the use of *Sea buckthorn* in the food industry. Food producers can continue to develop a variety of new products, such as *Sea buckthorn* jams, cookies, ice creams, beverages, and dietary supplements, to meet consumer demands for natural and nutrient-rich foods.
- Clinical Research: The potential medicinal value of *Sea buckthorn* has yet to be thoroughly explored. Clinical trials can investigate its role in the treatment of chronic diseases, promoting skin health, improving eye health, and its potential applications in drug development.

- International Cooperation: With increasing global demand for *Sea buckthorn* products, international trade will become a vital area of growth. Simultaneously, there is substantial potential for international trade and cooperation involving *Sea buckthorn*. Countries can collaborate to conduct research, share best practices, and promote international trade of *Sea buckthorn* products, fostering sustainable growth of the global *Sea buckthorn* industry and advancing the international trade of *Sea buckthorn* and its products, promoting agricultural cooperation and economic development.

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