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# Charophytes: drivers of carbonate sedimentation, carbon sequestration and aquatic health

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This review explores biomass production and  $\text{CaCO}_3$  precipitation by charophytes (Charophyta) and their environmental implications. A hypothesis was developed that charophytes play a substantial role in sedimentary processes and that the long-term deposition of  $\text{CaCO}_3$  in the sediments contributes significantly to the sequestration of excess carbon in bottom sediments. The study shows that, compared to angiosperms, many charophytes produce significantly greater dry mass. Tall and branchy species produce higher dry weight (DW) per individual but form sparser communities while smaller and slender charophytes can produce lower DW but tend to create very compact carpets that balance species-specific differences in dry mass production. While charophyte dry mass frequently exceeds  $1 \text{ kg DW m}^{-2}$  or even  $2 \text{ kg DW m}^{-2}$  in temperate climate, the study from Mediterranean climate reports charophyte DW can exceed  $4.1 \text{ kg m}^{-2}$  and in extreme cases be up to  $11.5 \text{ kg m}^{-2}$ . Compared to angiosperms some charophytes are highly efficient in utilizing bicarbonate as a carbon source for photosynthesis and precipitating calcium carbonate encrustation but it varies in space and time. This process contributes to water decalcification, impacting water chemistry and carbon cycling in aquatic ecosystems. Charophytes, particularly large species, play a significant role in carbon sequestration through the precipitation and deposition of  $\text{CaCO}_3$ , and this review shows that charophytes can capture and deposit in the bottom sediments up to  $>300 \text{ g C m}^{-2}$ . However, different species exhibit varying degrees of carbonate deposition and recirculation. Therefore, although the hypothesis adopted was supported by the results of this review, further study is needed to fully understand the long-term impact of charophytes on carbon sequestration and the influence of climate change on their growth and permanent  $\text{CaCO}_3$  deposition.

## KEYWORDS

Characeae, chara-lakes, calcite, inorganic carbon, recycling, ecosystem services, macrophytes

## Introduction

The presence of submerged aquatic vegetation (SAV) exerts direct and indirect influences on the biotic and abiotic components of lake ecosystems, shaping community structure and ecosystem function (e.g., Scheffer et al., 1993; Jeppesen et al., 1998; Kufel et al., 2016). Extensive SAV stands reduce nutrient concentrations in the water column, effectively competing with phytoplankton, stabilize bottom sediments, prevent their resuspension and facilitate the sedimentation of suspended particles. In addition, aquatic vegetation serves as a refuge for zooplankton, offering protection from predators, and creates complex habitats that are particularly well-suited for benthic invertebrates and

predatory fish (Blindow et al., 2014). In this way, submerged vegetation plays a crucial role in improving water quality, ultimately contributing to clearer waters.

Among the systematic groups that form SAV, angiosperms and charophytes, are considered crucial to the functioning of freshwater lakes. These groups exhibit different mechanisms in their ecological roles, as summarized by Blindow et al. (2014). In recent decades, charophytes, also known as stoneworts in North America and Europe, have gained increasing scientific attention as particularly effective ecosystem engineers (Pukacz et al., 2024). Charophytes represent an ancient lineage within the phylum Charophyta, with a fossil record dating back to the Upper Silurian (Apolinarska et al., 2011 and references therein), and are considered to be among the closest relatives of the first land plants (Karol et al., 2001). All extant charophytes are classified within the family Characeae, which constitutes the sole extant order Charales. Paleontological research indicates, however, that two other orders, Sycdiales and Moelleriales, occurred in the geological past, when there was a greater diversity of families and species (Martín-Closas et al., 2024).

Charophytes are often pioneer organisms in newly formed bodies of water (Pukacz et al., 2024). However, they can be found in a diverse range of aquatic environments worldwide, primarily in clear and mesotrophic freshwater lakes, where they coexist with angiosperms in submerged vegetation stands or, in less fertile and calcium-rich lakes, where charophytes form extensive, dense beds referred to as charophyte or underwater meadows (Hilt, 2015). These charophyte-dominated lakes (*Chara*-lakes), are considered valuable ecosystems which are susceptible to degradation. As such, they are protected under the European Natura 2000 program as Natura 2000 Habitat 3140: Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp. While some charophyte species can be considered somewhat cosmopolitan in their distribution, many exhibit limited geographical ranges and are classified as rare or threatened (Wood and Imahori, 1965; Korsch, 2018; Schubert et al., 2024). In addition, because they can be highly sensitive to water fertility, charophytes decline with increasing eutrophication of waters (Schneider et al., 2015). Consequently, they serve as sensitive bioindicators of water quality, finding widespread application in environmental monitoring (Doege et al., 2016; Pukacz et al., 2024).

A key feature distinguishing charophytes from angiosperms is the high degree of calcium carbonate encrustation of the charophyte thalli, indicating their potential in efficient  $\text{CaCO}_3$  deposition in lake sediments (Shaw and Rabenhorst, 1997; Pelechaty et al., 2013; Strzałek et al., 2024). This review article explores the dry mass production and  $\text{CaCO}_3$  precipitation by charophytes and their environmental implications. It is hypothesized that charophytes play a substantial role in sedimentary processes and the long-term deposition of  $\text{CaCO}_3$  in the sediments of charophyte-dominated lakes. In this way, charophytes might contribute significantly to the sequestration of carbon in bottom sediments.

This meta-analysis is based on an extensive literature review. Initially, articles were collected in order to compare the results of the author's previous studies with existing literature. In the next step, leading scientific literature databases, i.e., Web of Science and Scopus, were used to supplement this preliminary review

with the latest research. Various keyword combinations were used, including the terms “charophyte”, “Characeae”, “biomass”, “dry mass”, “dry weight”, “ $\text{CaCO}_3$ ”, “carbonate”, “precipitation”, “incrustation”, “encrustation”, “deposition”, and “sedimentation”, to select relevant articles. The search included articles published in these databases up to October 2024. It is worth mentioning that parallel participation in the development of selected chapters of the monograph “Charophytes of Europe” (Schubert et al., 2024) also helped in collecting literature and in assessing which data had not yet been published in synthetic review publications.

While working on this review article, it was assumed that the importance of charophytes in lakes extends beyond inducing and maintaining clear water conditions, and also includes a vital role in forming  $\text{CaCO}_3$  deposits in lake sediments across various species, lake water properties, depths, and climatic conditions. However, this literature review showed that the available data concern mainly lakes located in the temperate climate zone, primarily in Europe. This bias should be acknowledged, but in the author's opinion it should not be seen solely as a limitation, but also as a suggestion for the direction in which future research should proceed.

## The unique morphological structure of charophytes

Charophytes are structurally simple organisms characterized by large, multinucleate internodal cells and smaller nodal cells (Beilby and Casanova, 2014). Many species, particularly within the *Chara* genus, are further differentiated by an additional layer of cells known as the cortex. Unlike plants with tissues and organs, charophytes exhibit a thallus morphology, resembling the structure of *Equisetum*. The thallus consists of a main axis with whorls of branchlets and side branches, further segmented into nodes and internodes (Figure 1). In many species, these structures are heavily encrusted with calcium carbonate ( $\text{CaCO}_3$ ) (Figures 1B, D); therefore the terms dry mass, dry matter, or dry weight seem more appropriate for charophytes than the term biomass. Charophytes are attached to the bottom by delicate rhizoids and can grow from a few centimeters to over 1 m high, with the most complex morphology being found in the genera *Chara* and *Lychnothamnus* (Krause, 1997; Martin et al., 2003). Therefore, the dry mass produced by charophytes likely depends on their structure and size, which are reflected in their genus- and species-specific life forms, and individuals of bigger, thicker and more branchy species produce higher dry mass compared to small charophytes (Pukacz et al., 2016b).

However, charophytes can grow sparsely or form extensive communities of SAV which can be mirrored in their dry mass expressed as dry weight per unit bottom area, i.e.,  $\text{g DW m}^{-2}$  or  $\text{kg DW m}^{-2}$ . In clear-water, calcium- and bicarbonate-rich, alkaline mesotrophic lakes, charophytes tend to form very compact beds (Hilt, 2015; Pelechata et al., 2020). Tall and branchy species (e.g., *Chara tomentosa* L.) form thick but sparser communities while slender charophytes (e.g., *Nitellopsis obtusa* (Desvaux) J. Groves) tend to create very compact carpets. It is, thus, plausible that species-specific differences in biomass production can be

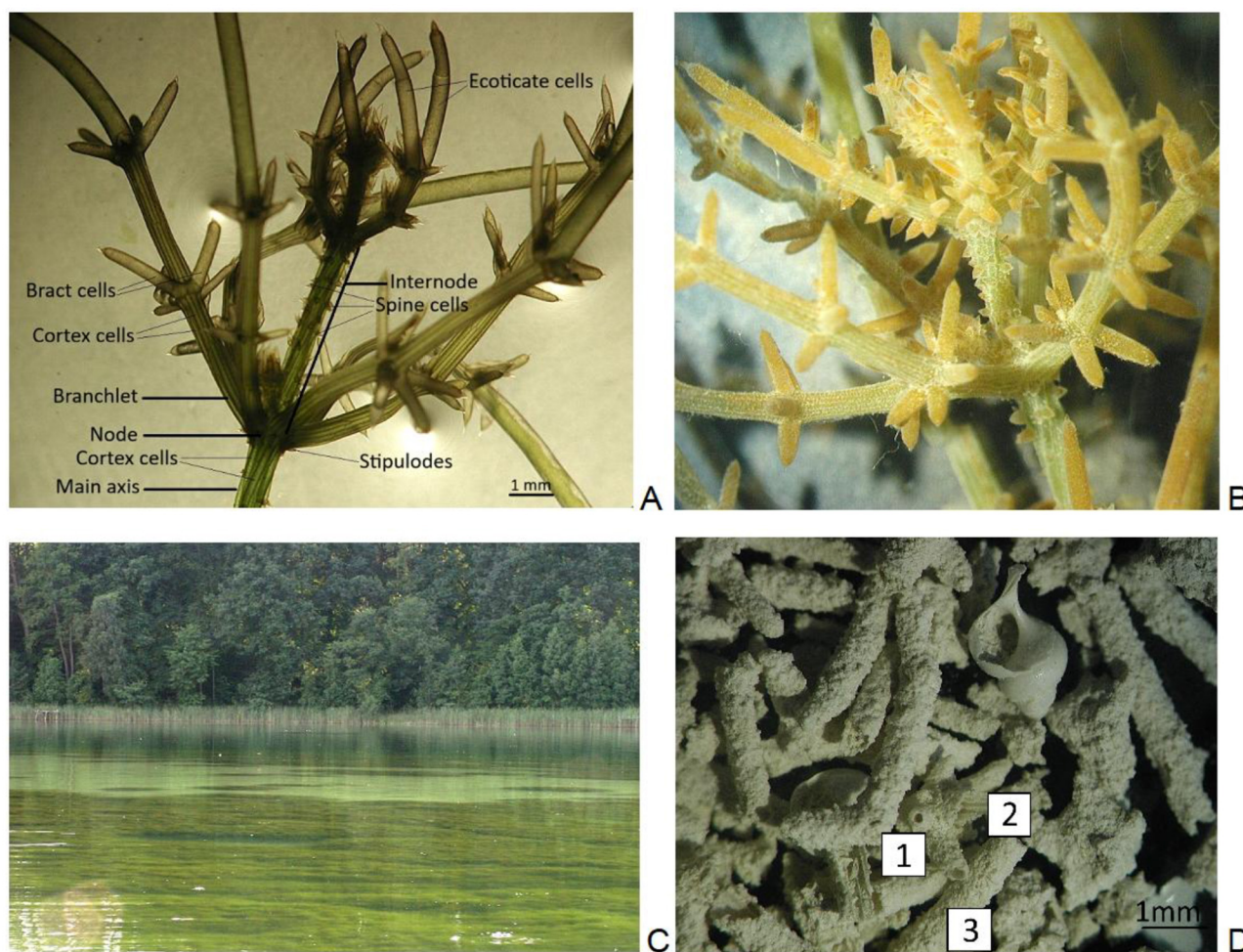


FIGURE 1

Morphological features and carbonate encrustation of charophytes (A, B, D) illustrated by *Chara tomentosa* L. and the charophyte underwater meadows exemplified by *Chara tomentosa* and *Chara aculeolata* Kütz. in Rchb. beds (C). A and B - the upper part of *Chara tomentosa* thallus showing (A) the corticate main axis with two fully developed nodes with whorls of branchlets and (B) the calcium carbonate deposited on the surface of the axis and branchlets; (C) - extensive charophyte beds in the lake littoral zone; (D) - remains of heavy charophyte encrustations stored in a marl lake sediments, 1 - charophyte node with a whorl of branchlets, 2 - cortex imprint in carbonate crust, 3 - fragments of branchlets/axis internode.

generalized when the dry weight of a charophyte community per unit of bottom surface area is taken into account.

## Dry matter production by charophytes: patterns of variation

Data from the literature shows that, compared to angiosperms, charophytes produce larger dry masses (Blindow, 1992; Kufel and Kufel, 2002; Brzozowski and Pelechaty, 2022; Pelechata et al., 2023). In the study by Kufel and Kufel (2002), the average dry mass of angiosperms reached  $73 \text{ g DW m}^{-2}$  (*Stuckenia pectinata* (L.) Börner; syn. *Potamogeton pectinatus* L.). The average dry weight of various *Chara* species and *Nitellopsis obtusa* were higher compared to angiosperms and ranged from  $36 \text{ g DW m}^{-2}$  to  $500 \text{ g DW m}^{-2}$  (cf. Kufel and Kufel, 2002; Table 2). The authors emphasized that the maximum value of charophyte dry weight in the data they analyzed was significantly higher, and reached  $1,200 \text{ g m}^{-2}$ .

Compared to these data, higher mean summer DW values of charophyte beds, ranging from  $319$  to  $813 \text{ g m}^{-2}$ , were reported by Andersen et al. (2017) while Sand-Jensen et al. (2021) reported charophyte summer dry mass values which maximally exceeded  $1,500 \text{ g DW m}^{-2}$ ; both reports from Sweden. In a hard-water mesotrophic lake in north-eastern Poland, extensive charophyte beds were characterized by a mean DW of  $623 \text{ g m}^{-2}$  and a maximum DW exceeding  $1,000 \text{ g m}^{-2}$  (Pelechaty et al., 2013). The above data indicate that the maximum dry mass values of charophytes can exceed  $1,000 \text{ g m}^{-2}$ , as documented in Table 1. Maximum values of charophyte dry mass up to twice as high as this were found in a mesotrophic, hard-water charophyte-dominated lake in western Poland (Pukacz et al., 2014a). It is noteworthy that the average DW of charophyte beds in this lake also exceeded  $1,000 \text{ g m}^{-2}$  and reached as much as  $1,166 \text{ g m}^{-2}$ .

Another study of the same lake (Pukacz et al., 2016a), conducted monthly from spring to autumn, provided evidence of a decrease in dry mass values with increasing depth of a charophyte

TABLE 1 Comparison of the dry weight of charophyte species per 1 m<sup>2</sup> of lake bottom based on published literature data.

| Species                                                                       | Dry weight (g m <sup>-2</sup> ) | Reference                                       | Climate, country     |
|-------------------------------------------------------------------------------|---------------------------------|-------------------------------------------------|----------------------|
| <i>Chara aculeolata</i> Kütz. in Rchb (syn. <i>C. polyacantha</i> A. Braun)   | 2,076.0                         | <a href="#">Pukacz et al. (2014a)</a>           | Temperate, Poland    |
| <i>Chara aspera</i> Willd.                                                    | 220.6*                          | <a href="#">Królikowska (1997)</a>              | Temperate, Poland    |
| <i>Chara contraria</i> A. Braun ex Kütz                                       | 172.3*                          | <a href="#">Królikowska (1997)</a>              | Temperate, Poland    |
|                                                                               | 1,059.0                         | <a href="#">Pelechaty et al. (2013)</a>         |                      |
| <i>Chara globularis</i> Thuill. (syn. <i>C. fragilis</i> Desv.)               | 10.3*                           | <a href="#">Królikowska (1997)</a>              | Temperate, Poland    |
| <i>Chara hispida</i> L.                                                       | 2,300.0                         | <a href="#">Rodrigo et al. (2015)</a>           | Mediterranean, Spain |
|                                                                               | 4,168.0                         | <a href="#">Puche et al. (2024)</a>             | Mediterranean, Spain |
| <i>Chara papillosa</i> Kütz. (syn. <i>Chara intermedia</i> A. Braun ex Lange) | 1,030.0 (231.3*)                | <a href="#">Królikowska (1997)</a>              | Temperate, Poland    |
| <i>Chara tomentosa</i> L.                                                     | 465.0*; 478.0*                  | <a href="#">Blindow (1992)</a>                  | Temperate, Sweden    |
|                                                                               | 1,200.0 (383.5*)                | <a href="#">Królikowska (1997)</a>              | Temperate, Poland    |
|                                                                               | 700.0; 800.0                    | <a href="#">Blindow et al. (2002)</a>           | Temperate, Sweden    |
| <i>Lychnothamnus barbatus</i> (Meyen) Leonh.                                  | 1,368.0                         | <a href="#">Brzozowski and Pelechaty (2022)</a> | Temperate, Poland    |
| <i>Nitella flexilis</i> (L.) C. Agardh                                        | 2.1*                            | <a href="#">Królikowska (1997)</a>              | Temperate, Poland    |
| <i>Nitellopsis obtusa</i> (Desvaux) J. Groves                                 | 118.5*                          | <a href="#">Królikowska (1997)</a>              | Temperate, Poland    |
|                                                                               | 335.0*                          | <a href="#">Blindow (1992)</a>                  | Temperate, Sweden    |
|                                                                               | 140.7                           | <a href="#">Brainard and Schulz (2017)</a>      | Temperate, USA       |
|                                                                               | 203.0                           | <a href="#">Carver et al. (2024)</a>            |                      |
|                                                                               | 417.0                           | <a href="#">Pukacz et al. (2014a)</a>           | Temperate, Poland    |
|                                                                               | 457.0                           | <a href="#">Brzozowski and Pelechaty (2022)</a> |                      |

\*Maximum and/or average values are included.

bed and showed that the highest charophyte DW occurred in August and September. While the same trend of decreasing biomass with depth was demonstrated by [Brzozowski and Pelechaty \(2022\)](#) for *Nitellopsis obtusa*, a trend of increasing biomass with depth was found for *Lychnothamnus barbatus* (Meyen) Leonh., a species morphologically similar to *Nitellopsis obtusa*, but producing a much higher dry mass.

In summary, the dry mass of charophytes seems species- and site-specific as shown in [Table 1](#), and tends to decrease with increasing depth.

### Dry mass production by charophytes: does climate matter?

Previous studies on charophyte biomass have focused primarily on temperate regions, specifically on water bodies located in central and northern Europe. While the articles reviewed here emphasize a strong link between abundant charophyte communities and clear, calcium-rich, alkaline waters with a low trophic level, the role of climate can only be inferred indirectly and to a considerably limited degree, which results from the above-mentioned biased focus of the research on the temperate climate zone.

The relationship between climatic conditions and the dry mass production was included in the study of two groups of lakes dominated by either charophytes or angiosperms in

two distant (>500 km) regions of Poland, western—warmer and north-eastern—colder ([Pelechata et al., 2023](#)). The two regions are characterized by clearly different climatic features and the temperature differences range between 1.5 and 1.9°C. The obtained results revealed differentiation in the dry mass produced by both groups of macrophytes. Charophyte beds produced higher biomass in the warmer western region than in the colder north-eastern lakes, with maximum DW reaching 2,144.2 g m<sup>-2</sup> vs. 1,182.1 g DW m<sup>-2</sup>, respectively ([Pelechata et al., 2023](#)). In both regions, charophytes also determined the maximum values of the total dry mass of macrophytes. The average values of charophyte DW were 415.6 g m<sup>-2</sup> in the lakes of the warmer region and 250.8 g DW m<sup>-2</sup> in the colder region. The study also showed that charophytes reached significantly higher maximum (2,144.2 g m<sup>-2</sup> as mentioned above vs. 319.2 g m<sup>-2</sup>) and average (661 g m<sup>-2</sup> vs. 115.6 g m<sup>-2</sup>) dry weights than angiosperms, corroborating conclusions drawn by [Kufel and Kufel \(2002\)](#). The study took into account all seasons in the annual cycle; the maximum values, however, were determined at the peak of growing season ([Pelechata et al., 2023](#)).

Although the above-presented charophyte biomass values are among the highest reported to date from temperate regions, higher values were reported from a Mediterranean climate zone ([Table 1](#)). In a newly created Mediterranean pond located in the Albufera de València Natural Park in Spain, [Rodrigo et al. \(2015\)](#) estimated maximum charophyte (*Chara hispida* L.) dry mass values higher

than 2 kg DW m<sup>-2</sup> (note the change of units!). Extremely high biomass of 11.5 kg DW m<sup>-2</sup> was reported by Puche et al. (2024) from a small lake belonging to the group of lakes of The Lagunas de Ruidera Natural Park in Spain with submerged vegetation dominated by charophytes. Excluding the above extreme value, the mean submerged vegetation dry mass was 1.0 kg DW m<sup>-2</sup>, and the highest dry mass that the authors determined exceeded 4.1 kg DW m<sup>-2</sup> and was accumulated by *Chara hispida*. The study also corroborated a decrease in biomass values with increasing depth, from an average value of 1.4 kg DW m<sup>-2</sup> at a depth of 4 m to 0.9 kg DW m<sup>-2</sup> at a depth of 8 m.

Although the values of charophyte dry matter reported from the Mediterranean climate are clearly higher than those from central and northern Europe and North America (Table 1), it is difficult to unequivocally state whether or not a warmer climate promotes higher values of charophyte biomass, as this requires further research across climatic zones.

## CaCO<sub>3</sub> precipitation by charophytes

A distinctive characteristic of some charophytes is the photosynthetically-mediated precipitation of mineral crusts on the surface of their thalli. These crusts, commonly referred to as encrustations or incrustations, consist of calcium carbonate, predominantly calcite (Anadón et al., 2002). Charophytes are known for their efficient utilization of bicarbonate ions as a source of carbon for photosynthesis (McConnaughey, 1991; McConnaughey and Whelan, 1997; van den Berg et al., 2002; Sand-Jensen et al., 2018, 2021), which leads to heavy CaCO<sub>3</sub> encrustations. The encrustations, forming distinct bands or deposited layer by layer across the entire cell wall (Kawahata et al., 2013), are tightly attached to the charophyte thalli, preventing CaCO<sub>3</sub> detachment and dispersion under the influence of water movement (Raven et al., 1986; Coletta et al., 2001).

Data from literature suggest that the highest photosynthetic production and thus the most intensive dry mass increase in charophytes occurs between June and July in the Northern Hemisphere. This temporal pattern has been consistently observed in several studies (Hough and Putt, 1988; Blindow et al., 2002; Torn et al., 2006). Accordingly, the greatest increase in the proportion of carbonates in the charophyte dry mass has been reported during the summer months. Pelechaty et al. (2010) found a significant increase in encrustation content in the photosynthetically most active apical parts of *Chara subspinosus* Ruprecht (syn. *Chara rudis* (A. Braun) Leonhardt) from June to July, followed by a decrease in early autumn. The proportion of carbonate encrustation ranged between 13.92 and 53.93% of the dry weight. Similar patterns of increasing encrustation toward summer have been observed in other studies (Pukacz et al., 2016a; Herbst et al., 2018). Herbst et al. (2018) demonstrated that CaCO<sub>3</sub> precipitation in charophytes is species- and lake-specific. Beyond central and northern Europe, similar seasonal trend was reported from Spanish lakes by Rodrigo et al. (2015) who found an increase in CaCO<sub>3</sub> encrustation from the cool to the warm season, reaching up to 55% of the charophyte dry weight.

In addition to sunlight, a critical factor influencing calcium carbonate precipitation in charophytes is the physicochemical composition of water. As a result, the carbonate content in the dry mass of charophytes typically exceeds 50% in calcium-rich freshwater environments. In Swedish ponds, Sand-Jensen et al. (2021) found that extensive CaCO<sub>3</sub> encrustations contributed an average of 72% to the charophyte dry mass. In general, as Sand-Jensen et al. (2021 and references therein) calculated for 79 charophyte stands studied in central and northern European lakes, the average CaCO<sub>3</sub> content can reach 64%. One of the key drivers of the carbonate precipitation is the pH of water, which directly affects the degree of dissociation and the proportions of carbon dioxide (CO<sub>2</sub>), and bicarbonate (HCO<sub>3</sub><sup>-</sup>) and carbonate (CO<sub>3</sub><sup>2-</sup>) ions. The state of bicarbonate supersaturation also plays an important role (Pelechaty et al., 2013 and references therein) as in alkaline waters preferred by charophytes the availability of CO<sub>2</sub> is limited and bicarbonate becomes an alternative source of carbon needed for photosynthesis (van den Berg et al., 2002). For some species, however, bicarbonate supersaturation is not necessarily required for efficient photosynthesis and CaCO<sub>3</sub> precipitation. A quintessential example is *Chara virgata* Kütz., which can form extensive beds in soft-water lakes and precipitate CaCO<sub>3</sub>, constituting an average of 46.1 % of the charophyte dry mass (Kufel et al., 2016). Those authors studied 6 species (five *Chara* species plus *Nitellopsis obtusa*) in 10 lakes of eastern Poland and showed that CaCO<sub>3</sub> precipitation was species- and lake-specific. Calcium and phosphate concentrations were responsible for 72% of the observed variability of carbonate encrustation but the saturation with bicarbonates had no significant effect. While Kufel et al. (2016) reported positive effect of calcium and negative effects of phosphate concentrations in water, the proportion of CaCO<sub>3</sub> in the dry mass of charophytes was positively correlated with pH, but negatively correlated with Ca<sup>2+</sup> and total inorganic carbon concentrations in the study by Herbst et al. (2018).

The study by Kawahata et al. (2013) suggests that corticate species can be more heavily encrusted than ecorticate ones. However, data from the literature indicates that this relationship is not always so unequivocal. Blindow (1992) showed similar average contribution of CaCO<sub>3</sub> to charophyte dry mass for corticate *Chara tomentosa* and ecorticate *Nitellopsis obtusa* (Table 2). Similar to the above study by Blindow (1992), the highest carbonate contents found by Herbst et al. (2018) did not differ between *Chara contraria* and *Nitellopsis obtusa*. A minor difference was reported from Spain by Rodrigo et al. (2015) between annual mean CaCO<sub>3</sub> precipitation, which was slightly higher for corticate *Chara hispida* than for ecorticate *Nitella hyalina* (De Candolle) Agardh (Table 2).

The genus-, species- and habitat-specific architecture of the charophyte thallus can also influence the proportion of carbonate encrustation in the dry mass of individuals. Pukacz et al. (2014b) found correlations between the CaCO<sub>3</sub> content in DW and morphological features of *Chara aculeolata* and *Chara subspinosus* individuals, forming separate extensive beds in a shallow mesotrophic lake. The calcite content in DW did not differ significantly between the species and reached 70% in summer (Table 2). The percentage of carbonate in *Chara aculeolata* showed a positive correlation with the length of the axis and internodes. The carbonate content in *Chara subspinosus*, however, was negatively

TABLE 2 Examples of studies providing data on the content of encrustation in the dry mass of charophyte species and/or CaCO<sub>3</sub> precipitation per 1 m<sup>2</sup> of lake bottom enabling calculation of C sequestered in charophyte carbonates.

| Species                                                                      | CaCO <sub>3</sub> (% DW) | CaCO <sub>3</sub> (g m <sup>-2</sup> ) | C (g m <sup>-2</sup> ) | Reference               |
|------------------------------------------------------------------------------|--------------------------|----------------------------------------|------------------------|-------------------------|
| <i>Chara aculeolata</i> Kütz. in Rchb (syn. <i>C. polyacantha</i> A. Braun)  | 76.0; 82.3               | 1,696.0                                | 203.5 <sup>1</sup>     | Pukacz et al. (2014a,b) |
| <i>Chara contraria</i> A. Braun ex Kütz                                      | 76.0                     | 685.5                                  | 82.3 <sup>1</sup>      | Pelechaty et al. (2013) |
|                                                                              | 74.8                     | -                                      | -                      | Herbst et al. (2018)    |
|                                                                              | -                        | 776.1                                  | 93.1 <sup>1</sup>      | Strzałek et al. (2024)  |
| <i>Chara globularis</i> Thuill. (syn. <i>C. fragilis</i> Desv.)              | 86.0                     | 280.0                                  | 33.6 <sup>1</sup>      | Pentecost (1984)        |
|                                                                              | 68.3                     | -                                      | -                      | Pukacz et al. (2016b)   |
| <i>Chara hispida</i> L.                                                      | 30.0*                    | -                                      | -                      | Rodrigo et al. (2015)   |
|                                                                              | 63.0                     | 2,625.8 <sup>1</sup>                   | 315.1 <sup>1</sup>     | Puche et al. (2024)     |
| <i>Chara subspinoso</i> Ruprecht (syn. <i>C. rudis</i> (A. Braun) Leonhardi) | 69.0                     | -                                      | -                      | Pukacz et al. (2014b)   |
|                                                                              | -                        | 1,053.7                                | 126.4 <sup>1</sup>     | Strzałek et al. (2024)  |
| <i>Chara tomentosa</i> L.                                                    | 70.0*                    | -                                      | -                      | Blindow (1992)          |
|                                                                              | 70.9                     | -                                      | -                      | Pukacz et al. (2016b)   |
|                                                                              | -                        | 1,517.6                                | 182.1 <sup>1</sup>     | Strzałek et al. (2024)  |
| <i>Nitella hyalina</i> (De Candolle) Agardh                                  | 21.0*                    | -                                      | -                      | Rodrigo et al. (2015)   |
| <i>Nitellopsis obtusa</i> (Desvaux) J. Groves                                | 68.0*                    | -                                      | -                      | Blindow (1992)          |
|                                                                              | 74.9                     | -                                      | -                      | Herbst et al. (2018)    |
|                                                                              | -                        | 405.3                                  | 48.6 <sup>1</sup>      | Strzałek et al. (2024)  |

\*Maximum and/or average values are included.  
<sup>1</sup>Values calculated based on available published data.

correlated with the number of main branches and the number of branchlets. The above correlations were also found for the dry mass of the studied species, both in terms of the strength and direction of the relationship (Pukacz et al., 2014b).

The close relationship between carbonate precipitation and habitat conditions might significantly mask the influence of species-specific morphological features, e.g., the size of individuals. In the study by Pukacz et al. (2016b), carried out in five lakes with abundant charophyte vegetation in western Poland, the CaCO<sub>3</sub> content in DW was only slightly higher in bigger *Chara tomentosa* than in relatively smaller and slender *Chara globularis* Thuiller, exceeding maximally ca. 70% (Table 2). This finding emphasized lake-specificity in carbonate precipitation. This is particularly evident in light of a study on the dry mass per individual and the proportion of encrustation of two morphologically different charophyte species occurring in the same habitat conditions (Pukacz et al., 2014b). Individuals of much thicker and more branched *Chara subspinoso* produced a much higher dry weight per individual than slender but longer individuals of *Chara aculeolata*. Despite this, however, both species had a similar proportion of CaCO<sub>3</sub> in the dry mass of individuals.

### CaCO<sub>3</sub> deposition by charophytes

Bicarbonate is the main external inorganic carbon source for charophytes (Sand-Jensen et al., 2018), and their efficiency in utilizing this form of dissolved inorganic carbon (DIC) is greater compared to angiosperms (van den Berg et al., 2002). This indicates

that charophytes contribute to water decalcification and the higher the share of charophytes in submerged vegetation, the lower the calcium and bicarbonate concentrations in lake water (van den Berg et al., 1998; Pelechaty et al., 2015; Pukacz et al., 2016b). In the dense *Chara aspera* Willd. bed, DIC concentration decreased to 0.2 mM in summer compared to 0.5 mM in the *Stuckenia pectinata* community and 1.2 mM in the vegetation-free open water of a shallow, alkaline lake (van den Berg et al., 2002). Up to half of the calcium and DIC pools can be used for photosynthetic calcification during a single daylight period by dense charophyte vegetation (Andersen et al., 2017). As a consequence of photosynthetic activity and encrustation, charophytes can significantly participate in the deposition of CaCO<sub>3</sub> in the lake bottom sediments (Pelechaty et al., 2013 and references therein; Sand-Jensen et al., 2021).

For *Chara globularis*, the maximal CaCO<sub>3</sub> content exceeding 80% (with an average of 63.5%), and the annual CaCO<sub>3</sub> deposition of 280 g CaCO<sub>3</sub> m<sup>-2</sup> were reported by Pentecost (1984, Table 2). Similarly, in the study by Pelechaty et al. (2013), the contribution of carbonates in *Chara contraria* dry mass exceeded 70% plus the contribution of mineral substances other than CaCO<sub>3</sub>, which did not exceed 6%. *Chara contraria* is, similar to *Chara globularis*, a slender charophyte, which formed compact beds in the studied lake. The maximum precipitation of carbonate per unit area of bottom exceeded 685 g CaCO<sub>3</sub> m<sup>-2</sup> (Table 2). The distribution of the amount of precipitated carbonate at particular depths was consistent with the distribution of the charophyte dry mass, which means that the greatest amount of carbonate was determined at an intermediate depth (2 m, 589 g CaCO<sub>3</sub> m<sup>-2</sup> on average). Considering all the studied depths (1, 2 and 3 m), *Chara contraria*

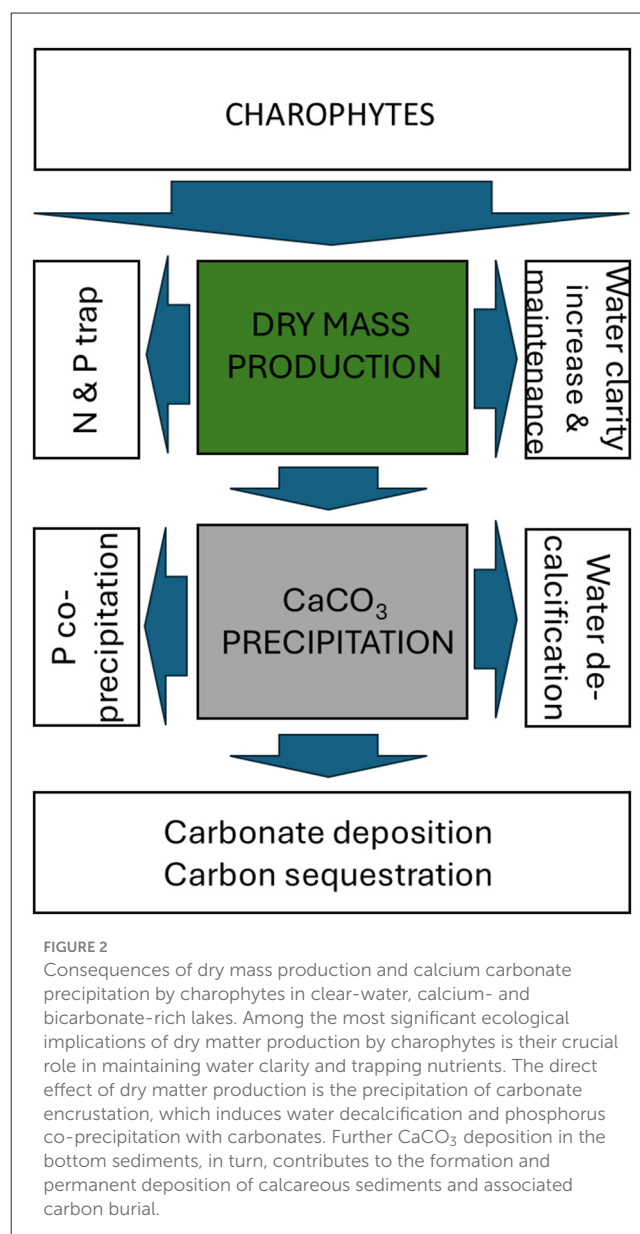
precipitated an average of  $438 \text{ g CaCO}_3 \text{ m}^{-2}$  at the peak of the growing season.

Based on the study conducted in charophyte-dominated lakes of western and northeastern Poland, [Strzałek et al. \(2024\)](#) reported summer  $\text{CaCO}_3$  precipitation differing significantly between *Nitellopsis obtusa* and *Chara tomentosa* (Table 2). The authors found inter- and intra-specific variation, depending on the lake, site and region. Higher  $\text{CaCO}_3$  precipitation values were found in lakes of western Poland compared to northeastern Poland, which seems to be a function of higher dry matter production in western lakes. Compared to the study in Poland, in Spanish lakes of the Lagunas de Ruidera Natural Park, carbonate encrustations of charophytes ranged from 40 to 63% of dry weight (50% on average; [Puche et al., 2024](#)). Interestingly, unlike charophyte dry mass, the authors observed no significant differences in the proportion of carbonate encrustation in DW between shallower (4 m) and deeper (8 m) sites. Assuming an average dry mass of  $1,000 \text{ g DW m}^{-2}$  found by the authors in the studied lakes and 50% as the average  $\text{CaCO}_3$  content in DW, charophytes could deposit an average of  $500 \text{ g CaCO}_3 \text{ m}^{-2}$ . In shallower sites, where the biomass was higher,  $\text{CaCO}_3$  deposition could reach  $700 \text{ g m}^{-2}$ , while in deeper sites it was  $450 \text{ g m}^{-2}$ .

Higher maximum  $\text{CaCO}_3$  deposition reaching  $2 \text{ kg m}^{-2}$  was found in a small mesotrophic lake in western Poland ([Pukacz et al., 2014a, Table 2](#)). The authors found a significant decrease in  $\text{CaCO}_3$  deposition with increasing depth. The average  $\text{CaCO}_3$  precipitation reached  $891 \text{ g m}^{-2}$ . The first two depths (1 and 3 m) were overgrown by *Chara aculeolata*, whereas at 5 m *Nitellopsis obtusa* dominated. The highest carbonate content in the charophyte dry mass was found at an intermediate depth of 3 m and reached 82.3%. The average carbonate content was similar at depths of 1 and 3 m and was 81.0 and 80.0%, respectively. At a depth of 5 m the values were significantly lower and amounted to 41.3%.

Among aquatic plants, photosynthesis based on bicarbonates is known in charophytes and half of the angiosperms ([Madsen and Sand-Jensen, 1991](#); [Sand-Jensen et al., 2021](#)). However, the content of precipitated carbonate crusts differs significantly between the two groups of macrophytes. While for *Chara* spp. and *Nitellopsis obtusa* up to >70% or even >80% of encrustation in DW was reported as shown above, it is far below the threshold of 50% in angiosperms. In the study by [Blindow \(1992\)](#) the  $\text{CaCO}_3$  content was only 17% for *Myriophyllum spicatum* and 19% for *Stuckenia pectinata*. The difference between charophytes and angiosperms is related to the specificity of their adaptation to carbon acquisition for photosynthesis. While charophytes, especially *Chara* spp. and *Nitellopsis obtusa*, are covered with thick crusts, most angiosperms have carbonate deposits restricted to the upper leaf surface, leaving the lower leaf surface freely available for  $\text{CO}_2$  uptake, in which they are more efficient compared to charophytes primarily adapted to use bicarbonates ([Sand-Jensen et al., 2018](#)).

In conclusion, charophytes are more efficient in the bicarbonate utilization and photosynthetically mediated  $\text{CaCO}_3$  precipitation than angiosperms. The proportion of carbonate encrustation in the dry mass of charophytes varies significantly depending on water chemistry and habitat conditions and reveals inter- and intraspecific variation, as well as lake- or site-dependency. Species-specific morphological features, such as the presence or absence of a cortex and the architecture of the thallus, can also influence



carbonate encrustation. In a result of carbonate precipitation, charophytes contribute to water decalcification, which can impact the overall water chemistry and the biogeochemical cycling of carbon in aquatic ecosystems (Figure 2).

## Charophytes as carbon sink: a closer look at $\text{CaCO}_3$ deposition and recirculation

Recent studies suggest that water reoligotrophication ([Richter and Gross, 2013](#); [Brzozowski et al., 2021](#)) and warming temperatures ([Brzozowski et al., 2022](#)) may favor the recovery of at least some charophyte species that declined in the second half of the 20<sup>th</sup> century due to eutrophication. The globally rare charophyte, *Lychnothamnus barbatus*, has re-established its populations,

becoming a beneficiary of climate warming (Brzozowski et al., 2021, 2022). In addition, climate warming may favor the expansion of some species beyond their native ranges. A known example is *Nitellopsis obtusa*, a species native to Eurasia but considered alien and invasive in North America (Larkin et al., 2018). Also, the ability of charophytes to overwinter in increasingly milder winters (Brzozowski and Pelechaty, 2022) combined with intrabiocenotic relationships, in which they often play a central role (Blindow et al., 2014), gives them an advantage over other primary producers and promotes their stabilization in lakes (Pelechata et al., 2015, 2023). It must be emphasized, however, that climate warming-related eutrophication could trigger conflicting responses in charophytes. Consequently, while some charophyte species emerge as winners, others could decline as the climate warms (Auderset Joye and Rey-Boissezon, 2015).

Due to the recent study by Pelechata et al. (2023), it is plausible that the climate warming-related increase in water temperature can benefit charophyte photosynthesis and, consequently, biomass production, which will further promote the sedimentation of calcium carbonate and the sequestration of excess atmospheric carbon in the sediments. Since extensive charophyte communities occur in alkaline waters where bicarbonate supersaturation aids  $\text{CaCO}_3$  precipitation, carbonate dissolution is assumed to occur exclusively in sediments. While organic matter deposited in the sediments can undergo biological degradation, returning organic carbon to the cycle, charophyte carbonate encrustations can be deposited permanently, constituting a significant carbon sink. However, as suggested by Sand-Jensen et al. (2021), in dense charophyte stands, pH may decrease to levels that induce partial dissolution of  $\text{CaCO}_3$  encrustations deposited on the basal parts of charophyte thalli, which are shaded by the charophyte stand, and, during the night, also on the apical parts due to nocturnal respiration. Consequently, the amount of calcium carbonate deposited in the sediments may differ, or more specifically, be lower than values determined based on studies of summer charophyte standing crop. Therefore, understanding the actual proportion of  $\text{CaCO}_3$  produced through charophyte photosynthesis that is stored in the bottom sediments is crucial for assessing their role in calcareous sediments deposition and carbon sequestration.

Studies on the amount of  $\text{CaCO}_3$  precipitated per unit of the bottom surface are rarely undertaken, and even more sporadic studies concern the further fate of calcium carbonate deposited in the sediments. In charophyte-dominated lakes of north-eastern and western Poland, Strzałek et al. (2024) conducted quantitative analyses of  $\text{CaCO}_3$  precipitation by charophytes and its dissolution and recirculation into the water or deposition in bottom sediments. Based on the study of seasonal trajectories of changes in organic matter and  $\text{CaCO}_3$  contents in charophyte dry matter, the authors attempted to determine seasonal rates of  $\text{CaCO}_3$  encrustation loss from the summer standing crop till autumn and then from autumn till spring of the following year. Two different patterns of  $\text{CaCO}_3$  loss were identified, with the proportion between recirculation and deposition being dependent on species characteristics (species-specific) and habitat conditions (site-specific). Despite interspecific and site-related variations, no significant regional differences were observed in  $\text{CaCO}_3$  dissolution or burial. However, the ultimate fate of  $\text{CaCO}_3$  appears to be influenced not only by species

characteristics and water properties but also by the frequency of charophyte overwintering, which is more prevalent in western (warmer) Polish lakes (Pelechata et al., 2023).

The cited study provides a framework for quantifying the magnitude of actual permanent deposition of  $\text{CaCO}_3$  in lake sediments and the corresponding sequestration of C by charophytes. The authors demonstrated that solely during the interval between summer and autumn, charophytes permanently deposited in the bottom sediments up to 88.7% of  $\text{CaCO}_3$  precipitated in summer. Considering the loss of  $\text{CaCO}_3$  between summer and the following spring, it can be calculated from the data presented by the authors (see Table 3 in Strzałek et al., 2024), that the maximum percentage of  $\text{CaCO}_3$  deposition by charophytes reached 98.3%. This efficiency was mediated by *Chara contraria*, which was also characterized by a negligible recirculation of  $\text{CaCO}_3$  into the water column. Considering the values of  $\text{CaCO}_3$  precipitation for the same species in a large *Chara*-lake (Pelechaty et al., 2013) and the median calculated by Strzałek et al. (2024) for the permanent deposition of  $\text{CaCO}_3$  in the sediments for the summer-autumn period, it can be calculated roughly that *Chara contraria*, which on average precipitated  $438 \text{ g CaCO}_3 \text{ m}^{-2}$  at the peak of summer, permanently deposited  $>300 \text{ g CaCO}_3 \text{ m}^{-2}$  into the sediments. Taking into account the entire range of precipitation ( $71.3$  to  $685.5 \text{ g CaCO}_3 \text{ m}^{-2}$ ), this species deposited between  $51.2$  and  $492.2 \text{ g CaCO}_3 \text{ m}^{-2}$  of the summer precipitation. Based on these values, the amount of carbon deposited can be calculated to be  $6.1$ – $59.1 \text{ g C m}^{-2}$ . The amount of carbon precipitated as  $\text{CaCO}_3$  by various charophyte species is calculated in Table 2. Depending on the species, these values range from  $<34$  to  $>300 \text{ g C m}^{-2}$ .

In general, large, branched, corticate charophyte species (represented by *Chara tomentosa* and *Chara subspinososa*) were in the study by Strzałek et al. (2024) less efficient in carbonate deposition in lake sediments during the summer-autumn period (see Table 4 in Strzałek et al., 2024) than slender and less corticate (*Chara contraria*) or ecorticate (*Nitellopsis obtusa*) species. However, the species of the first group proved to be more efficient in  $\text{CaCO}_3$  deposition between autumn and spring compared to the species of the second group. The ranges of  $\text{CaCO}_3$  deposition were broad and the interspecific differences in  $\text{CaCO}_3$  recycling or permanent deposition demonstrated by Strzałek et al. (2024) require further consideration. Namely, the largest mass of  $\text{CaCO}_3$  in the summer period was in the cited study mediated by *Chara tomentosa*, i.e.  $1,517.6 \text{ g m}^{-2}$ , of which only 18.9% was permanently deposited in the sediments by the following spring. This translates into a value of  $286.8 \text{ g m}^{-2}$  of deposited  $\text{CaCO}_3$  and  $34.5 \text{ g m}^{-2}$  of carbon buried in the sediments. The remaining mass of  $\text{CaCO}_3$  was dissolved and recycled. On the other hand, the highest efficiency in the permanent deposition of  $\text{CaCO}_3$  in the first group was evidenced for *Chara subspinososa*, which from the precipitated summer value of  $1,053.7 \text{ g CaCO}_3 \text{ m}^{-2}$  deposited 97.5% in the sediments. Without losses due to dissolution and recycling, this species deposited  $1,027.4 \text{ g CaCO}_3 \text{ m}^{-2}$  and trapped  $123.3 \text{ g C m}^{-2}$  from summer to the following spring. This is the highest deposition value that can be calculated from the data presented by Strzałek et al. (2024). In the second group, the maximum deposition percentage, i.e., 98.3%, and simultaneously the highest as previously mentioned for all studied species and sites, was found for *Chara contraria*.

This species also deposited the largest mass of carbonate in the sediments in the second group, i.e., 776.1 g  $\text{CaCO}_3 \text{ m}^{-2}$ , which translates into 93.1 g C  $\text{m}^{-2}$ . On average, large corticate species permanently deposited a greater mass of  $\text{CaCO}_3$  per unit area of the bottom from the peak of summer to the following spring compared to smaller and less corticate or ecorticate species (336.0 vs. 231.9 g  $\text{CaCO}_3 \text{ m}^{-2}$ , respectively, which gives accordingly 40.3 vs. 27.8 g C  $\text{m}^{-2}$ ).

Given that the above considerations pertain solely to additional carbon deposited as  $\text{CaCO}_3$  and not to organic carbon fixed through photosynthesis, the cited and calculated values suggest a significant role of charophytes as an important sediment-forming factor, as well as a carbon sink. This is an important component of the ecosystem services which, in addition to intrabiocoenotic feedbacks, charophytes provide to clear- and hardwater charophyte-dominated lakes (Figure 2). However, further research is required to understand the significance of phenological changes occurring under a warming climate and the increasingly frequent overwintering of charophytes in milder winters and the degree to which carbon is permanently sequestered from the atmosphere.

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