

Warmer Autumn Temperatures Affect Wetland Plants

By

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Abstract

Temperature is an important driver of many plant developmental processes including seasonal activities; therefore, many studies have been conducted on the effect of increased temperatures on plants. These studies show delays in autumnal phenological events and advancements of spring events however often only look at leaf unfolding and senescence of trees. Therefore, in this study, whole-plant responses to increased temperature in autumn were studied for four common Northern Ontario wetland plants: *Carex lasiocarpa*, *Sparganium emersum*, *Dulichium arundinaceum* and *Rhynchospora alba*. Root and shoot growth in autumn and spring, autumn senescence along with the production of over-wintering structures was observed. The increased autumn temperature treatment was covered with transparent vinyl closed-top chambers while the ambient autumn temperature treatment consisted of open-top chambers. The treatments were applied from August 21st until November 5th. The results show an interspecific difference in responses specifically delayed senescence and increased growth in autumn and spring for two species: *C. lasiocarpa* and *R. alba*.

Keywords: *Carex lasiocarpa*, *Sparganium emersum*, *Dulichium arundinaceum*, *Rhynchospora alba*, warmer temperatures, wetland and species-specific

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Chapter 1: Introduction

Global warming due to climate change has already reached 1°C above pre-industrial levels in 2017 (Aragón-Duran et al., 2018). However, if all human-induced emissions were to be reduced to zero, further warming would likely be less than 0.5°C in the future (Aragón-Duran et al., 2018). This would affect many ecosystems and their plant life. This is the case for carbon cycling in ecosystems (Yvon-Durocher et al., 2010). The changes to the carbon cycle that are associated with climate change and therefore global warming are changes in productivity and resource quality along with precipitation patterns (Yvon-Durocher et al., 2010). Increased temperatures due to global warming change the relationship between net ecosystem productivity and gross primary productivity (Li et al., 2017). The change in net ecosystem productivity and gross primary productivity is due to increased temperatures increasing nutrient mineralization rates and fuelling plant phenological development such as spring growth (Kang et al., 2016). The phenological events that are important to determine spring growth are spring budburst and flowering date (Badeck et al., 2004; Kang et al., 2016). Badeck *et al.* (2004) show advancement of spring budburst and flowering date consistent with the global warming trend. In contrast, Pope *et al.* (2013) detected a nonlinear response of spring phenology to climate change by Bayesian analysis. They evaluated if species react more to a lack of winter chill than increased spring heat. They determined that species with earlier bud break responded to warmer spring temperatures then shift to respond to lack of enough chilling as warming continued (Pope et al., 2013). This also changes the start of the growing season which plays an important role in determining the length of the growing season (Liu et al., 2016). An important effect that climate change has on plant life is the shifting of ranges of certain species (Guan et al., 2020). A range to higher latitudes or elevations has been shown for trees (Zhu et al., 2012). In Guan *et al.* (2020), the northward expansion of eleven invasive species in China was investigated. They determined that these species due to climate change may have continued to expand northward (Guan et al., 2020). As for the higher elevations, Liang *et al.* (2018) found out that the montane plants shifted their ranges upward. Specifically, they determined that many montane trees, shrubs and

herbaceous plants in the Hengduan mountains in the Qinghai-Tibet region of China shifted their ranges upslope due to climate change (Liang et al., 2018).

Most research has been done on spring season effects in environments with very short seasons such as tundra and alpine environments. In tundra environments, the growing season is increasing because of warmer temperatures and earlier spring snowmelt (Ernakovich et al., 2014). In these environments, the change in the timing of spring phenological events could increase plant nutrient uptake and production of low shrubs, herbaceous plants and graminoids (Ernakovich et al., 2014). This has an opposite effect in alpine environments where the plant response to the photoperiod will be more important since the plants are adapted to using photoperiod as a cue to start growing which will limit spring phenology ultimately limiting the increase in the growing season (Ernakovich et al., 2014). But if there is a decrease in water availability along with the increase in temperature senescence will happen earlier (Ernakovich et al., 2014). This could result in a shorter growing season along with a decrease in production and an increase in nutrient loss (Ernakovich et al., 2014). Phenology can be altered by earlier leaf emergence, an earlier date that leaf area maximum is reached and the active growth period extended (Mäkiranta et al., 2018) since the temperature is an important driver of many plant developmental processes (Khanduri et al., 2008). Also, increased temperatures can cause allocation patterns to change (Mäkiranta et al., 2018). Shen *et al.* (2019) investigated the spatiotemporal change of the start date of the growing season and the possible effects of climate change on the start of the growing season in freshwater marshes in Northeast China. Their findings were that precipitation was the dominant factor affecting the start of the growing season in certain areas while the temperature was more important in other areas (Shen et al., 2019).

The effects of increasing autumn temperatures on plant growth are less studied. Even though less is known about the autumn season, here are some of what is currently known. Gallinat *et al.* (2015) outlined the complexity of studying autumn phenology and climate change which could be the reason why autumn is the neglected season in climate change research. They determined that it is the combination of many drivers that lead to the complexity of autumn phenology, including the prolonged nature of autumn events (Gallinat et al., 2015). These authors further state that a reason for the dominance

of spring studies is possible the attractivity of spring flowers. Gill *et al.* (2015) focus on the timing of leaf senescence in boreal and temperate deciduous forests with an emphasis on the magnitude, direction and spatial extent. They determined that leaf senescence had been delayed over time due to increasing temperatures, but at high latitudes, the delay has been less marked because the photoperiod had a stronger effect on the time of senescence (Gill *et al.*, 2015). Also, Li *et al.* (2003) found out that in Northern Europe daylength is more important than temperatures in triggering autumn phenology in birch. Contrastingly, Fu *et al.* (2017) focus on determining what environmental factors drive leaf senescence. They discovered that autumn leaf senescence had a larger response to the increased temperature than spring leaf-out which proposes a possible larger contribution of autumn senescence to extending the growing season under future climate change (Fu *et al.*, 2018). Schwieger *et al.* (2018) compared below- and aboveground phenology along with the ending of the growing season in heath and meadow vegetation and their response to warming in autumn. They determined that other factors than temperature controls root growth in autumn (Schwieger *et al.*, 2018).

Overall, many studies show that increased temperatures delay autumnal phenological events and advance spring events (Peñuelas & Filella, 2001). However, most of these studies have focused only on leaf senescence and leaf unfolding or the flowering date of trees, but not on whole-plant responses of other growth forms such as herbaceous plants (Peñuelas *et al.*, 2002). Also, the effects of the altered phenology have been only studied for spring, but not for autumn (Archetti *et al.*, 2013) even though these effects aren't clear-cut. Furthermore, there also is an interaction between autumn and spring phenology. Earlier spring growth due to increased temperature has been shown to cause autumn senescence to be advanced (Zani *et al.*, 2020). The authors of this study used experimental, observational and modelling methods that were based on European forest trees. But it has not been investigated if herbaceous plants respond to increased temperatures differently than trees.

Therefore, the aim of the present study is to investigate how increased autumn temperatures affect the growth of herbaceous plants in autumn and the timing of autumn senescence along with its effect on spring plant growth. The study will be conducted with perennial herbaceous wetland plants of Northern

Ontario. The growing season in the wetlands of northern Ontario can be very short, five months or less, as wetlands warm up later in spring than many upland habitats, due to the thermal effects of water, but in autumn cold air prevents a corresponding extension of the growing season. Herbaceous wetland monocots are known to have two contrasting root overwintering strategies – autumn senescence and overwintering – leading to markedly different phenologies (Nieman et al. 2018; Courchesne et al. 2020). Hence, in the present study, a focus was on how species with different root overwintering strategies, long-lived and short-lived, respond to the increased autumn temperatures. Many species have internal genetic constraints which can limit their response to a lengthened growing season (Starr et al., 2000). Nevertheless, warmer autumn prior to senescence may give an advantage and enhance growth even of species that senesce after a given period regardless of temperature. *R. alba* may be a species that does this (Byne & Ryser, 2020).

This study studies the whole-plant response of four common northern Ontario wetland plant species to increased autumn temperatures. *Carex lasiocarpa* and *Dulichium arundinaceum* have roots that overwinter and hence are long-lived, whereas *Sparganium emersum* and *Rhynchospora alba* have roots that senesce every fall and consequently are short-lived (Nieman et al., 2018). Those species require a longer growing season and can be found only on sites that have warmer spring and autumn (Courchesne et al., 2020). I hypothesize that warmer autumn temperatures will cause a delay in autumn senescence and spring growth. I also hypothesize that species with different root overwintering strategies will respond differently. Specifically, species with roots that overwinter have functional roots all the time and can respond better to warm autumn temperatures, while senescence in species with annual roots is most likely triggered by short days, and hence they cannot show a strong response to warmer fall temperatures. I predict that *C. lasiocarpa* and *D. arundinaceum* will have a delay in their autumn senescence as a consequence of warmer temperatures, but *R. alba* and *S. emersum* will not have this delay.

The approach of the present study is to investigate the effect of warmer autumn temperatures on these wetland species under seminatural and semi-controlled conditions, in an outdoor mesocosm experiment over two years. Results of this study will help to predict how different wetland species, and hence, wetland communities in Northern Ontario will respond to a changing climate.

Chapter 2: Materials and Methods

2.1 Species Studied

The four studied species are all perennial graminoid wetland monocotyledons; *Carex lasiocarpa* Ehrh (Cyperaceae), *Dulichium arundinaceum* (L.) Britton (Cyperaceae), *Sparganium emersum* Rehmann (Typhaceae), and *Rhynchospora alba* (L.) Vahl (Cyperaceae) (Fig. 1). All species show a circumboreal distribution, but *D. arundinaceum* occurs only in North America (Ball et al., 2003). The species nomenclature is according to Integrated Taxonomic Information System (ITIS) (*Integrated Taxonomic Information System*, n.d.). In Canada, all species occur from the east coast to the west coast (Ball et al., 2003). In Ontario, the northern limit of all species is in Hudson Bay lowlands, but *D. arundinaceum* just barely reaches the southern tip of James Bay (Ball et al., 2003). In eastern North American, the southern limit of their main distribution is south of the Great Lakes with occasional occurrences further down south except for *D. arundinaceum* that is common southwards down to Florida (USA) (Ball et al., 2003).

2.1.1 *Carex lasiocarpa*

This species grows in sedge meadows fens, bogs, lakeshores and stream banks, and usually in sites that are very wet and sometimes even as floating mats. This species is dominant in boreal wetlands forming huge stands (Reznicek & Catling, 2020) since they have rhizomes. They can survive water-logged and oxygen-poor conditions (Schutz, 2000). Besides its rhizomes, it has an overwintering root system (Nieman et al., 2018).

2.1.2 *Dulichium arundinaceum*

This species can be found in marshes and marshy shores, hollows, ponds, ditches and river margins in water less than 6m deep. It can, also, be found in bogs and swamps where they often form large beds due to rhizomes (Reznicek et al., 2011). This species has an overwintering rhizome and root system (Nieman et al., 2018).

2.1.3 *Rhynchospora alba*

This species grows in acidic, sphagnous, boggy, open sites, and poor fens as well on floating mats or peaty intervening space at rocky shores (Vitt & Slack, 1975). This species develops one winter bud from a meristem behind the leaf sheaths and can produce two or three of these buds as the only overwintering organs (Ohlson & Malmer, 1990; Nieman et al., 2018). It is a solitary plant and isn't connected by rhizomes, but it does have shallow roots (Ohlson & Malmer, 1990). It prefers soft substrates where it is part of mud bottom communities that create competition for nutrients that are deposited onto the surface of the mud (Ohlson & Malmer, 1990).

2.1.4 *Sparganium emersum*

The species grows in still-to-flowing eutrophic and mesotrophic nearly neutral to somewhat basic waters and is sometimes abundant in this water (Kaul, n.d.). It is perennial rhizomatous and monoecious and it has a root system that senesces in the fall (Côté, 2017; Thieret, 1982). Species of this genus are ecologically important for waterfowl and mammals by providing food and shelter (Sulman et al., 2013). Also, they help to reduce erosion of river banks (Ito & Cota-Sánchez, 2014).

2.2 *Plants used in the experiment*

All plants used in the experiments originated from local populations. They were propagated vegetatively from plants grown in the experimental garden for a few years by either using rhizomes, bulbils, stolons or tillers. For the experiments, two cohorts of plants were used, one was planted in spring 2019 and measured in 2019 and 2020, while the other was planted in spring 2020 and measured in 2020 and 2021. Bulbils of *R. alba* were planted in 2L pots in May 2019 and 2020, whereas the other three species were initially planted in 1L pots and then transferred in the 2L pots in June 2019 and 2020.

2.3 Experimental Design

The investigation was conducted on two sets of plants started either in the early summer of 2019 or early summer of 2020. The plants were placed in six pools of about 240cm x 70cm x 26cm (L x W x D) filled with groundwater. The plants were grown in 2L pots, with the water level at the substrate surface, varying about 3-4cm during the summers. In 2019, all plants expected for *R. alba* had as a substrate sieved wetland soil from Bainbridge Construction, North Bay, ON, Canada (Fig. 2). *R. alba* grows in nutrient-poor wetlands and to match its natural substrate horticultural peat (Fafard et Freres, Saint-Bonaventure, Quebec, Canada) was used. But as this doesn't contain any nutrients, some were added as 0.375% (v/v) of composted manure (Fig. 2). The manure was thoroughly mixed into the peat. For plants started in 2020, the substrate for all species was sieved commercially obtained artificial blend of loam, peat, moss and compost (President's Choice Black Earth, President's Choice, Brampton, ON, Canada) (Fig. 2).

The effect of warmer autumn temperatures was investigated by comparing plants growing under ambient temperatures with plants growing under slightly elevated temperatures during the autumn. The elevated temperatures were achieved by closed-top chambers constructed with wooden frames covered with transparent vinyl (Fig. 3). The closed-top chambers were placed on the pools on August 21st, 2019 and August 20th, 2020. The frames were left in place until plants were covered with straw for the winter which happened on the 5th of November in 2019 and on the 17th of November in 2020. Straw was placed over the plants to prevent the roots and the water in the pools from freezing. The time of the covering with straw was determined by the weather when the temperatures fell consistently below zero and the pools started to freeze. The temperatures inside the pools, under the straw, were most of the winter between 0°C and 2°C, in spring raising to 5°C during the last week before the uncovering. Such soil temperatures over the winter are similar to those in natural wetlands, freezing of the soil being prevented by thermal properties of water, insulation by litter and snow (Courchesne et al., 2020).

There were three replicate pools with the treatment of closed-top chambers and three pools with open-top chambers, as controls. In 2019, in each pool 9 replicate pots of each species were placed,

amounting to 27 plants per species and treatment. 12 of these plants were harvested destructively in the fall of 2019. 15 replicates of these plants were kept until the end of the growing season in 2020. In spring 2020, 12 new replicate plants were planted per species and treatment.

2.4 Temperatures

During the fall treatment in 2019, the average air and water temperature for the closed-top chambers pools were 13.3°C and 14.4°C whereas, for the open-top chambers, the average air and water temperatures were 11.4°C and 12.9°C. The detailed temperature data can be seen in Fig. S2 and Table S1. Both air and water temperatures for the pools with the closed-top chambers and the control pools ranged from 21.4°C to 2.4°C and from 21.9°C to 0.1°C. The first frost in the control pools occurred on October 31st, 2019 which is when the average air temperature went below zero. Air temperatures in the covered pools never fell below 0°C. Water temperatures never fell below 0°C in either pool (Fig. S1 and Table S1). For the pools with open-top chambers, the average temperatures for the air and water during 2020 were 14.9°C and 14.8°C respectively, while in the open-top chambers these values were 13.0°C and 13.2°C respectively. Water temperatures in the pools with closed-top chambers, ranged from 21.7°C to 1.9°C while the temperatures for the open-top chambers ranged from 20.8°C to 1.3°C. During the 2020 treatments, no average temperature per day went below 0°C.

2.5 Overview of the measurements

Four destructive harvests were conducted between Sept. 17th, 2019 to Oct. 29th, 2019 every two weeks. At each harvest, three replicate plants were harvested from each species and treatment, one plant per species from each pool. Before each harvest in the fall of 2019, the degree of senescence was assessed for all plants. With the remaining plants (109 plants, 4 replicates with 13 per species and treatment), an assessment of plant spring growth was done in the spring of 2020. This assessment was done by image

analysis of the projected area from images taken from the side once every week from June 6th to June 20th, analyzed by using the computer software ImageJ version 1.52a. In spring 2020, 24 more plants of each species were planted. The remaining plants from 2019 and the newly planted ones from the spring were used in fall 2020 to assess their degree of senescence. The spring 2020 plants were used in the spring 2021 growth measurements. This measurement consists of collecting aboveground biomass of sixteen plants of each species, drying them and then weight them.

2.6 Destructive fall harvests

Three replicate plants of each species and treatment were randomly selected with one plant from each pool being harvested with two-week intervals for a total of four harvests, amounting to a total of twelve plants per species and treatment. These four harvests were conducted from September 17th, 2019 to October 29th, 2019. During these four harvests, the number of plant parts: shoots, bulbils, stolons, inflorescences were counted. The dry mass of all plant parts: shoots, bulbils, stolons, inflorescences, rhizomes, and roots, was determined by drying all plant parts in a drying oven set to 75°C for at least 24 hours. A 3% TTC solution was used to determine the percentage of root length that was still alive at the time of harvest. The roots were submerged in this solution after a vacuum treatment to remove air from the roots to enhance the penetration of TTC in the roots. The root samples were left in the TTC for at least 24 hours incubated in a 30°C water bath. TTC (2,3,5,- triphenyltetazolium chloride) is typically used to measure the liveliness of plant tissue (Comas et al., 2000). This compound is colourless until it is reduced to red formazan by dehydrogenase enzymes that are related to mitochondrial function (Comas et al., 2000).

2.7 Fall 2019 and 2020 leaf and shoot senescence

Leaf fall senescence was assessed in 2019 and 2020. For that purpose, one shoot of each plant was marked using a coloured, blue or red, wire. In 2019, observations were conducted from Sept. 10th to

Oct. 22nd with 2-week intervals alternating with the destructive harvests. The senescence observations were conducted on the marked shoot by either looking at how much of the shoot had turned brown or how much of the leaves of the shoot had turned brown. For *R. alba* and *D. arundinaceum*, the degree of senescence was assessed based on the number of leaves at the various stages of senescence, whereas for *S. emersum* and *C. lasiocarpa* this was done based on the numbers of leaves that make up the shoots. In 2020, the observations were conducted from September 2nd to October 21st once every week which was done the same way as in the previous year except for *D. arundinaceum*, in which each pot was divided into four quarters and the degree of senescence in each quarter was recorded on a scale from no brown to 1/4 brown to 2/4 brown to 3/4 brown to fully brown separately. This was done to better describe the senescence of *D. arundinaceum*, as this species had a large number of shoots of varying ages with different stages of senescence.

The progress of senescence was described using a senescence index, calculation of which was based on numbers of shoots or leaves at different stages of senescence. The methods for the senescence index were modified from Ryser *et al.* (2020) to the methods below. The index is calculated as follows:

$$\text{Senescence Index: } \frac{(0 \times \#G) + (1 \times \#T) + (2 \times \#Q) + (3 \times \#H) + (4 \times \#TQ) + (5 \times \#F)}{(\#G + \#T + \#Q + \#H + \#TQ + \#F)}$$

, where #G is the number of shoots or leaves that were green, #T is the number of shoots or leaves that has only the tip brown, #Q is the number of shoots or leaves that are one-quarter brown, #H is the number of shoots or leaves that are half brown, #TQ is the number of shoots or leaves that are three-quarters brown and #F is the number of shoots or leaves that are fully brown and the numbers 0, 1, 2, 3, 4, and 5 are the weight assigned to each amount of brown. The senescence index ranges from 0 for completely green plants to 5 for completely senesced plants then was divided by five to turn it into a percentage which ranged from 0-1%. This was also done with each of the pot quarters for *D. arundinaceum*.

2.8 Spring 2020 and 2021 Growth

In 2020 from June 6th to June 20th once every week, the spring growth rate was determined using digital images taken with white backlit acrylic glass as a background. The images were analyzed by using ImageJ (Padrón et al., 2016). The images were transformed to binary black and white, and using a scale, the projected area of each plant was assessed. In 2021, the spring growth determination was done by harvesting aboveground biomass on two occasions on June 4th and June 15th and weighing its dry mass. An exception was *R. alba* where two of the longest shoots in each pot were collected instead. This was done because birds destroyed some of the bulbils in the fall of 2020 making the total biomass an unreliable variable. For this determination, sixteen plants of each species were collected with eight being from the increased autumn temperature treatment and another eight being from the ambient autumn temperature treatment for each species and were dried in a drying oven set at 75°C for at least 24 hours.

2.9 Statistical Analysis

For the senescence count, the data were transformed using log and arcsine transformations. Then general linear models and repeated measures ANOVAs were performed. For the data collected during each harvest: mean total root length, mean total dry mass, mean plant count, and mean percentage of roots still alive, a regular ANOVA was conducted. For the mean total leaf area, repeated-measures ANOVA was performed.



Figure 1. Species for Experiment. From left to right: *Sparganium emersum*, *Rhynchospora alba*, *Dulichium arundinaceum*, and *Carex lasiocarpa*.



Figure 2. Substrates used in planting species in experiment: composted manure (a), black earth (b), and Sphagnum peat moss (c)



Figure 3. Experimental Setup. From far left to far right; Closed-Top Chamber 1, Open-Top Chamber 1, Closed-Top Chamber 2, Open-Top Chamber 2, Closed-Top Chamber 3, and Open-Top Chamber 3 with 4 ibuttons in each pool; 2 ibuttons in the water of each pool to measure air temperature and the other two hanging to measure the air temperature.

Chapter 3: Results

The results section has been broken up into four sections for each of the following species; *Carex lasiocarpa*, *Dulichium arundinaceum*, *Rhynchospora alba* and *Sparganium emersum*. These sections were then broken up into two paragraphs where the first paragraph is about the senescence and the other one is about the growth of the plants. A general overview of the results (Table 1) is given in the next paragraph.

For fall senescence in 2019, general linear models (GLMs) were conducted using the senescence index as the dependent variable, the treatment as an independent factor and week of observation as an independent continuous variable. For this senescence period, the data shows that for all four species the increased temperature treatment caused the senescence to be delayed slightly but the effect was significant only in the case of *R. alba* (Fig. 4; Table 2). For fall senescence in 2020, repeated measures ANOVAs were conducted with the cohort as an independent factor, expressing the planting year of the plants (2019 or 2020), along with treatment and treatment x cohort interaction as factors. Week of observation was included as a continuous independent variable. The plants that were remaining from 2019 (2nd-year plants) were graphed separately from the 2020 plants (1st-year plants). Senescence in 2020 was faster for the 2nd-year plants compared to the 1st-year plants and the magnitude of the difference varied among the species. Treatment slowed down the senescence for all species, but for *S. emersum* the effect was only a non-significant trend.

For growth data, the three periods where this was studied were fall 2019, the spring of 2020 and spring of 2021. For the fall 2019 period, the effects were mostly non-significant due to large scatter. For spring 2020, the mean projected plant area was larger in the plants with warm autumn, but the effect was not significant due to large scatter. For the mean total dry mass data in spring 2021, the increased autumn temperature treatment either resulted in a higher shoot dry mass in *C. lasiocarpa* and *D. arundinaceum*.

3.1 *Carex lasiocarpa*

For senescence in fall 2019, plants in the warm autumn treatment had delayed senescence, but this trend was not significant due to the large scatter of the data (Fig. 4a and Table 2). The senescence in the fall of 2020 for this species was significantly delayed by the closed-top chambers (Fig. 5a and b). There was a significant difference between the 2nd-year and 1st-year plants when it comes to this delay (Table 3), the younger plants senescing more slowly than the older plants. The time effect was also significant as the senescence increases over time (Table 3). The treatment effect increased over time with a significant week x treatment interaction (Table 3).

There is a decrease in the amount of aboveground dry mass over time for this species in the course of the autumn due to senescence (Fig. 7a and Table 4), while the below-ground biomass significantly increases over the same time (Fig. 8a). closed-top chambers increased the aboveground biomass. For below-ground biomass, there was no significant treatment effect (Table 4). The number of green shoots decreased over time, but there was no significant treatment effect (Fig. 10a and Table 4). Comparable to the count of green shoots, the number of total overwintering structures, i.e., shoots with arrested growth, increased over time (Fig. 13a and Table 4).

Growth in spring 2020, based on measurement of the projected plant area for this species was somewhat faster in the closed-top chambers, but the difference was not statistically significant even though there was an increase over time (Fig. 15a) and Table 6). In spring 2021, the average aboveground biomass was in the closed-top chambers 29% higher than in the open-top chambers (Tables 7 and 8).

3.2 *Dulichium arundinaceum*

In 2019, the senescence for this species rapidly increased over the observation period, but there was no significant difference between the treatments (Fig. 4b and Table 2). In 2020, the closed-top chambers delayed senescence (Fig. 5c and Table 3). Senescence was slower for the younger plants compared to the older plants (Fig. 5c and d; Table 3). The week effect was also significant (Table 3).

There is a non-significant decrease during fall 2019 for the aboveground biomass (Fig. 7b and Table 4), while the below-ground biomass shows a significant increase. The total belowground mass was decreased by the closed-top chambers, this trend increasing over time, the treatment x time interaction being close to significant ($p=0.087$) (Fig. 8b and Table 4). The number of green leaves decreases over time (Fig. 11a and Table 4). Similarly, the mass of the overwintering structures, i.e., shoot with arrested growth, increases over time (Fig. 13b and Table 4). While the percentage of living roots also decreases over time (Fig. 14b and Table 4).

In spring 2020, the projected plant area increased over time but showed no treatment effect (Fig. 15b and Table 6). In spring 2021, the aboveground biomass for this species had 24% more aboveground biomass closed-top chambers than in the open-top chambers (Tables 7 and 8).

3.3 *Rhynchospora alba*

In 2019, the senescence for *R. alba* showed a statistically significant response to the treatment, senescing more slowly in the closed-top chambers (Fig. 4c and Table 2). In 2020, the closed-top chambers delayed senescence, especially for the younger plants (Fig. 5f and Table 3). There is a significant difference between the two cohorts, senescence being especially fast for the older plants (Fig. 5e and 5f and Table 3).

The amount of above-ground and below-ground dry mass for this species decreased over time (Figures 7c and 8c and Table 4). The closed-top chambers increased the number of green shoots (Fig. 10c and Table 4). The number of total overwintering structures, i.e., bulbils, increases over time (Fig. 13c and Table 4). The percentage of living roots for this species decreases over time (Fig. 14c and Table 4).

Spring growth in 2020, based on the projected plant area showed no significant treatment effects for this species, but there was an increase in projected plant area over time (Fig. 15c and Table 6). In spring 2021, the average aboveground biomass shows a treatment effect with the open-top chambers having 11% more aboveground biomass than the closed-top chambers (Tables 7 and 8).

3.4 *Sparganium emersum*

For this species, the closed-top chambers did not affect the senescence during the 2019 period (Fig. 4d and Table 2). In 2020, senescence significantly increased over time, but there was no significant treatment effect (Fig. 5g, 5h and Table 3).

The amount of aboveground and below-ground biomass decreases over time (Fig. 7d, 8d and Table 4), but the treatment didn't have any effect. The number of green shoots decreased over time (Fig. 10d and Table 4). The dry mass of overwintering structures (stolons) increases over time (Fig. 12d and Table 4) while the percentage of living roots decreases (Fig. 14d and Table 4).

In spring 2021, the average aboveground biomass for this species had, in the closed-top chambers, 26% more aboveground biomass than in the open-top chambers. However, this was only a non-significant trend ($p=0.071$), nevertheless, the larger treatment effect in the first harvest led to an almost significant treatment x harvest interaction (Table 7 and Table 8).

Table 1. Overview of the treatment effects for the four studied species

	Overwintering Roots		Autumn-Senescing Roots	
Species	<i>Carex lasiocarpa</i>	<i>Dulichium arundinaceum</i>	<i>Rhynchospora alba</i>	<i>Sparganium emersum</i>
Time of Senescence	delayed	delayed, but not significant	delayed	no effect
Spring Growth	increased	increased	increased	no effect
Aboveground Biomass	increased	no effect	no effect	no effect
Belowground Biomass	no effect	decreased	no effect	no effect
Overwintering Structures Mass	no effect	slight decrease, but not significant	no effect	no effect

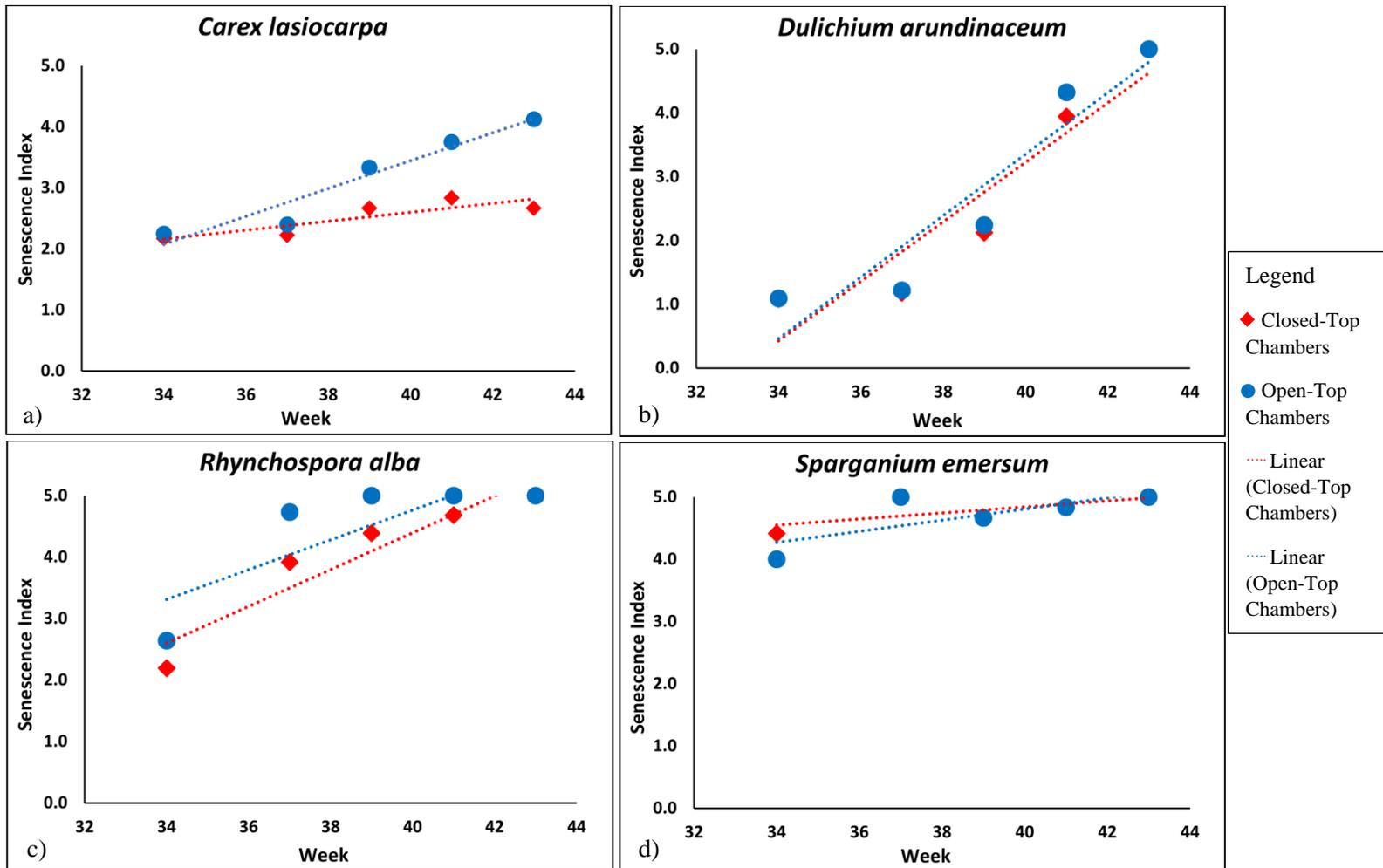


Table 2. General linear model of senescence index in fall 2019 for the four studied species

Species	N	R ²	Treatment		Week		Block	
			F	P	F	P	F	P
<i>Carex lasiocarpa</i>	12	0.763	5.219	0.071	2.377	0.186	0.064	0.939
<i>Dulichium arundinaeum</i>	12	0.998	1.969	0.220	729.110	0.000	62.834	0.001
<i>Rhynchospora alba</i>	12	0.947	6.725	0.049	20.236	0.003	0.931	0.379
<i>Sparganium emersum</i>	12	0.982	1.000	0.363	35.563	0.001	22.077	0.003

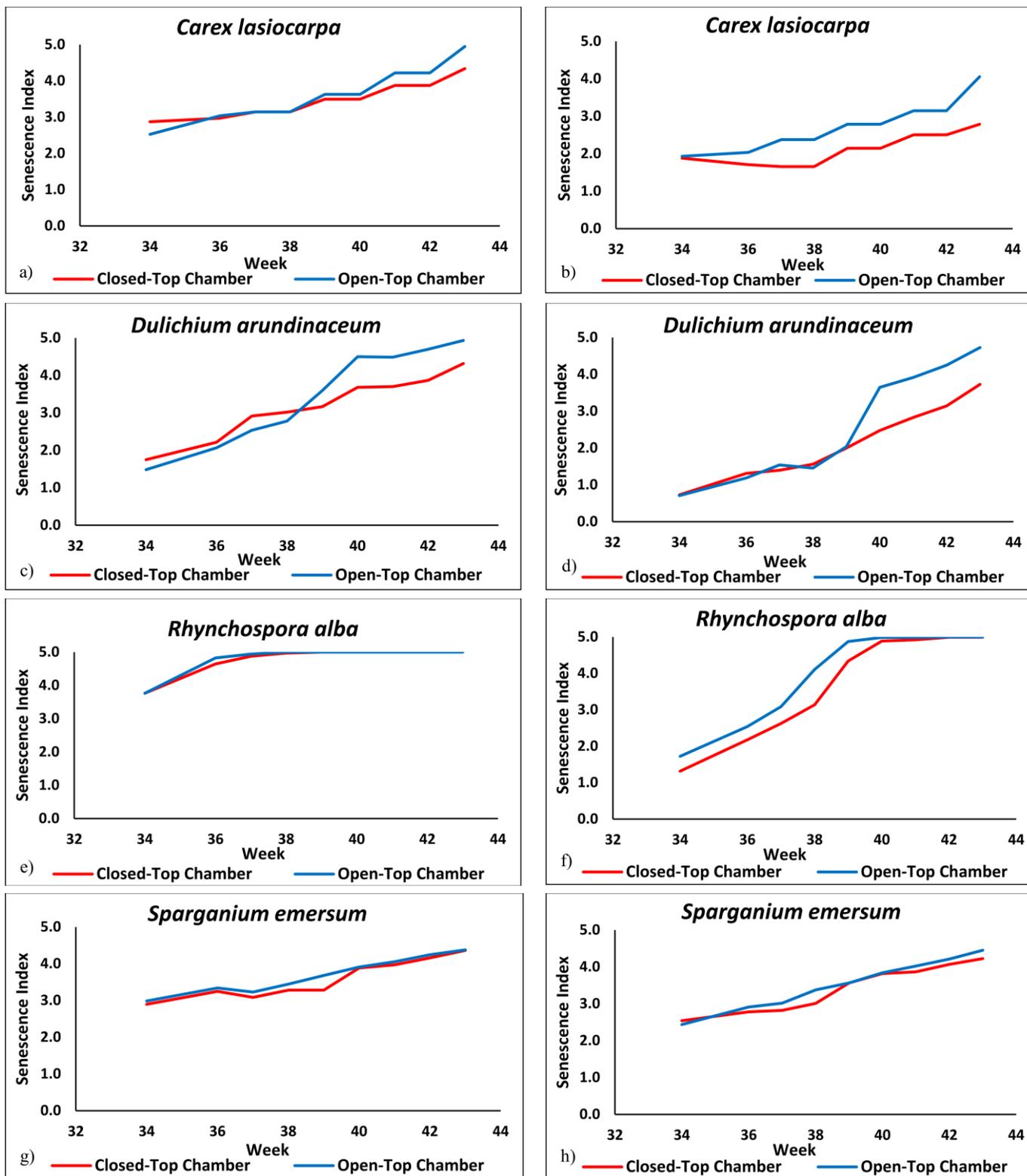


Figure 5. Senescence index in fall 2020 for the four study species, separately presented for the plants planted in 2019 (left) and those planted in 2020 (right), a) and b) are for *Carex lasiocarpa*, c) and d) are for *Dulichium arundinaceum*, and e) and f) are for *Rhynchospora alba*, and g) and h) are for *Sparganium emersum*.

Table 3. General linear model of senescence index in fall 2020 for the four studied species

Species	N	Treatment		Year		Week		Treatment x Year		Treatment x Week	
		F	P	F	P	F	P	F	P	F	P
<i>Carex lasiocarpa</i>	96	12.390	0.013	72.352	0.000	78.792	0.000	1.747	0.234	6.087	0.000
<i>Dulichium arundinaceum</i>	96	9.755	0.020	30.010	0.002	156.802	0.000	0.014	0.910	15.537	0.000
<i>Rhynchospora alba</i>	96	42.098	0.001	698.621	0.000	223.360	0.000	16.952	0.006	2.578	0.026
<i>Sparganium emersum</i>	96	4.756	0.072	3.034	0.132	118.591	0.000	0.053	0.826	0.411	0.890

*Note: Block effect was insignificant for all species therefore it wasn't added to the model.

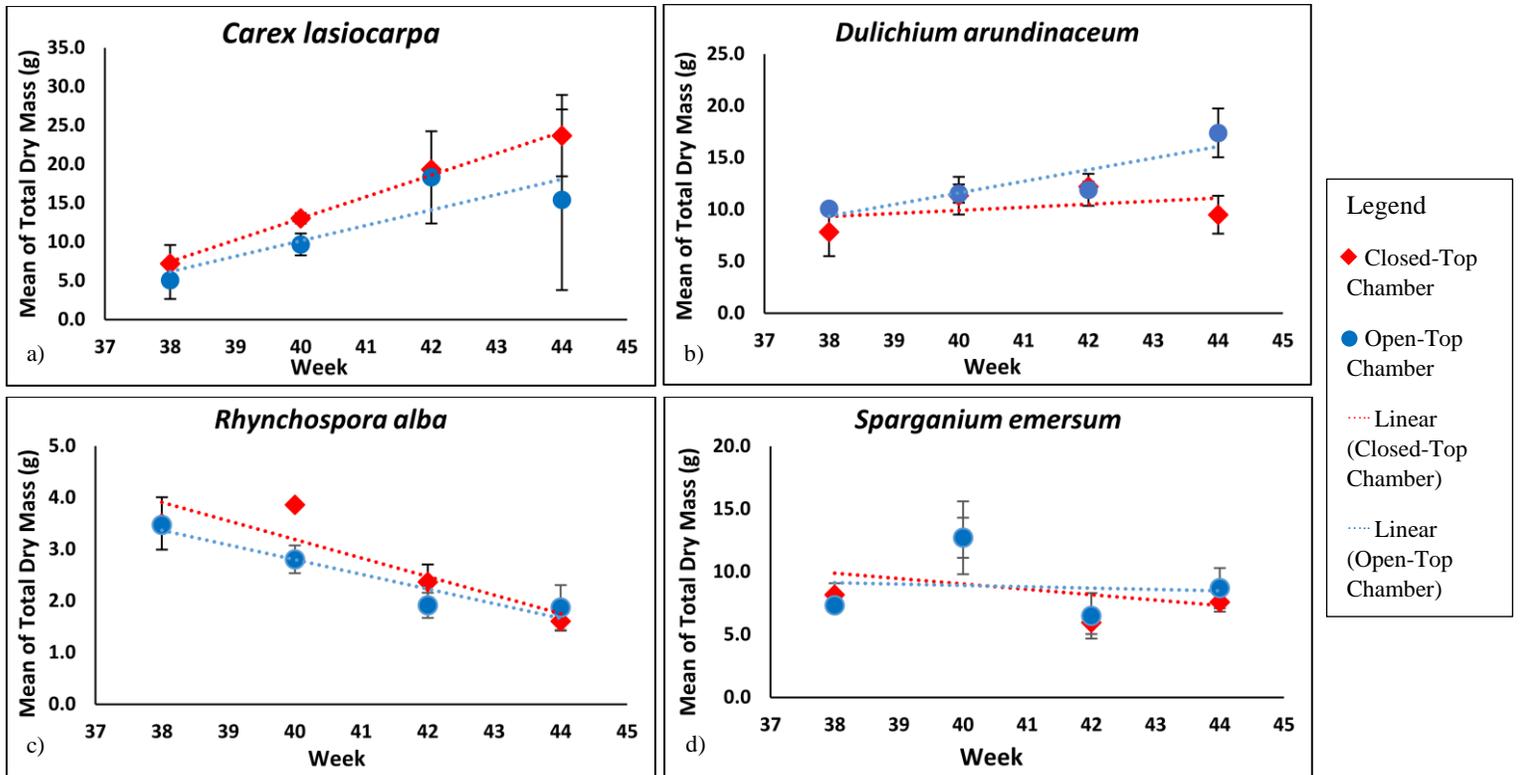


Figure 6. Total dry mass in the four harvests conducted during the fall of 2019 for a) *Carex lasiocarpa*, b) *Dulichium arundinaceum*, c) *Rhynchospora alba* and d) *Sparganium emersum*. Mean values ± 1 SE.

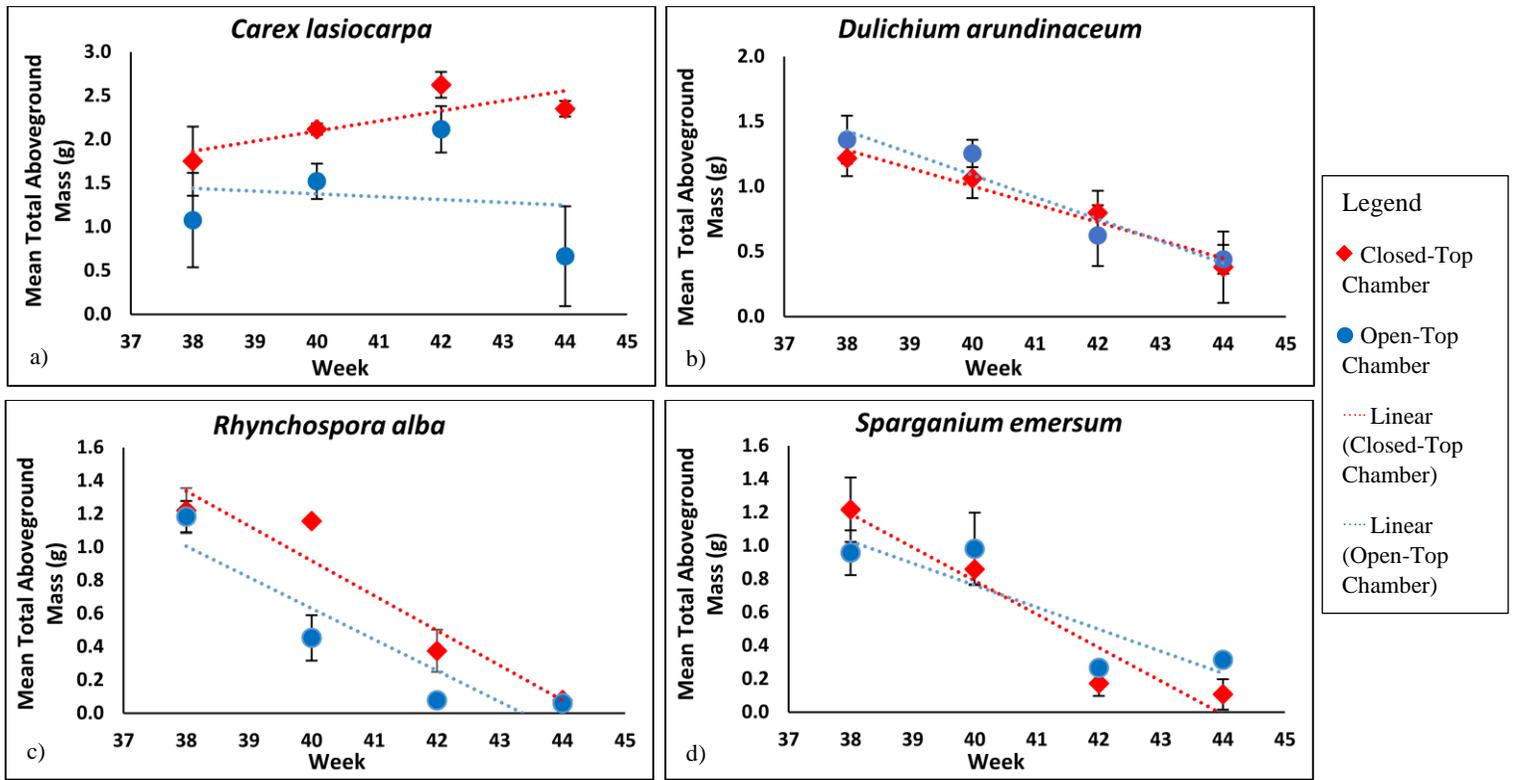


Figure 7. Total aboveground dry mass in the four harvests conducted during the fall of 2019 for a) *Carex lasiocarpa*, b) *Dulichium arundinaceum*, c) *Rhynchospora alba* and d) *Sparganium emersum*. Mean values ± 1 SE.

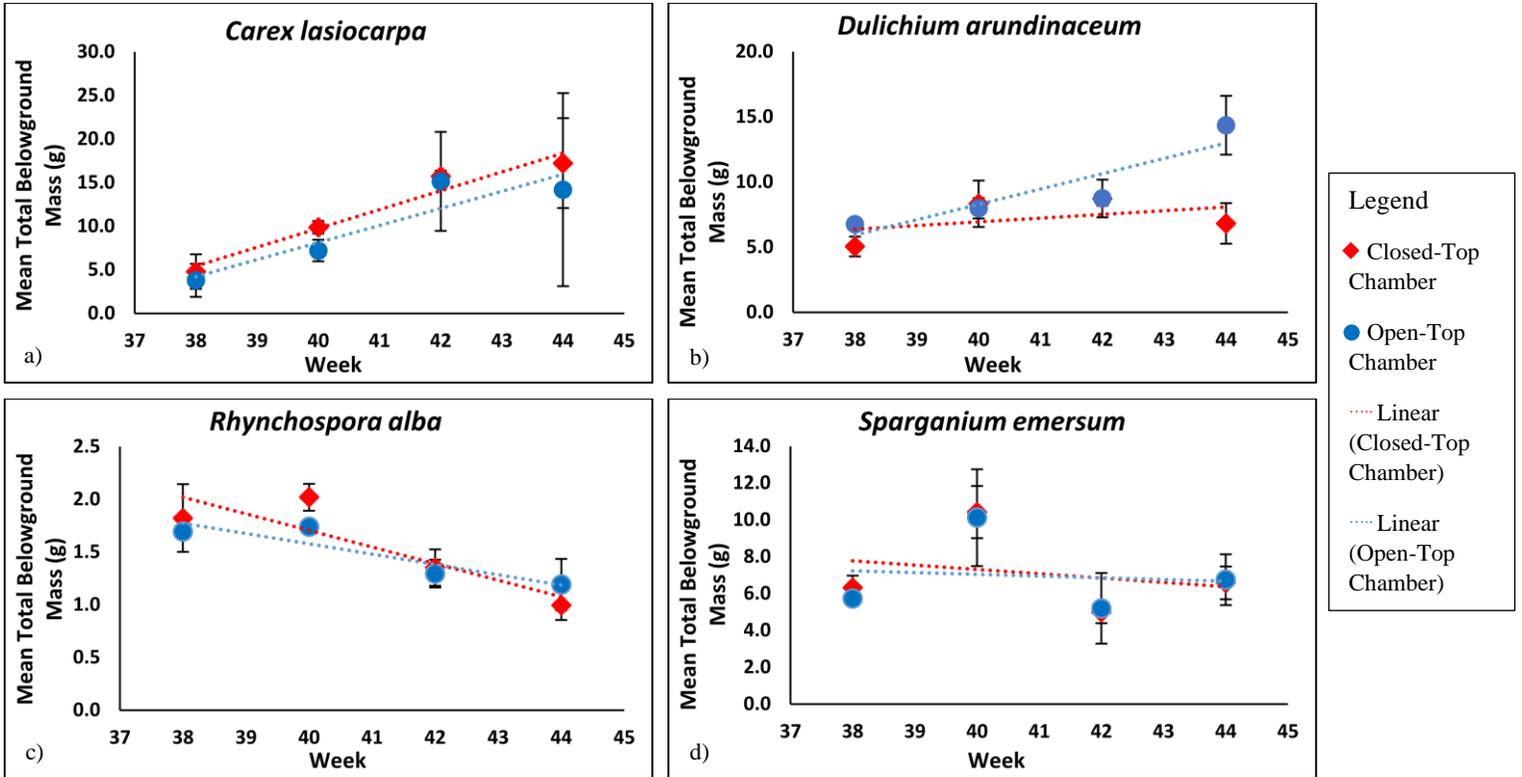


Figure 8. Total belowground dry mass in the four harvests conducted during the fall of 2019 for a) *Carex lasiocarpa*, b) *Dulichium arundinaceum*, c) *Rhynchospora alba* and d) *Sparganium emersum*. Mean values ± 1 SE.

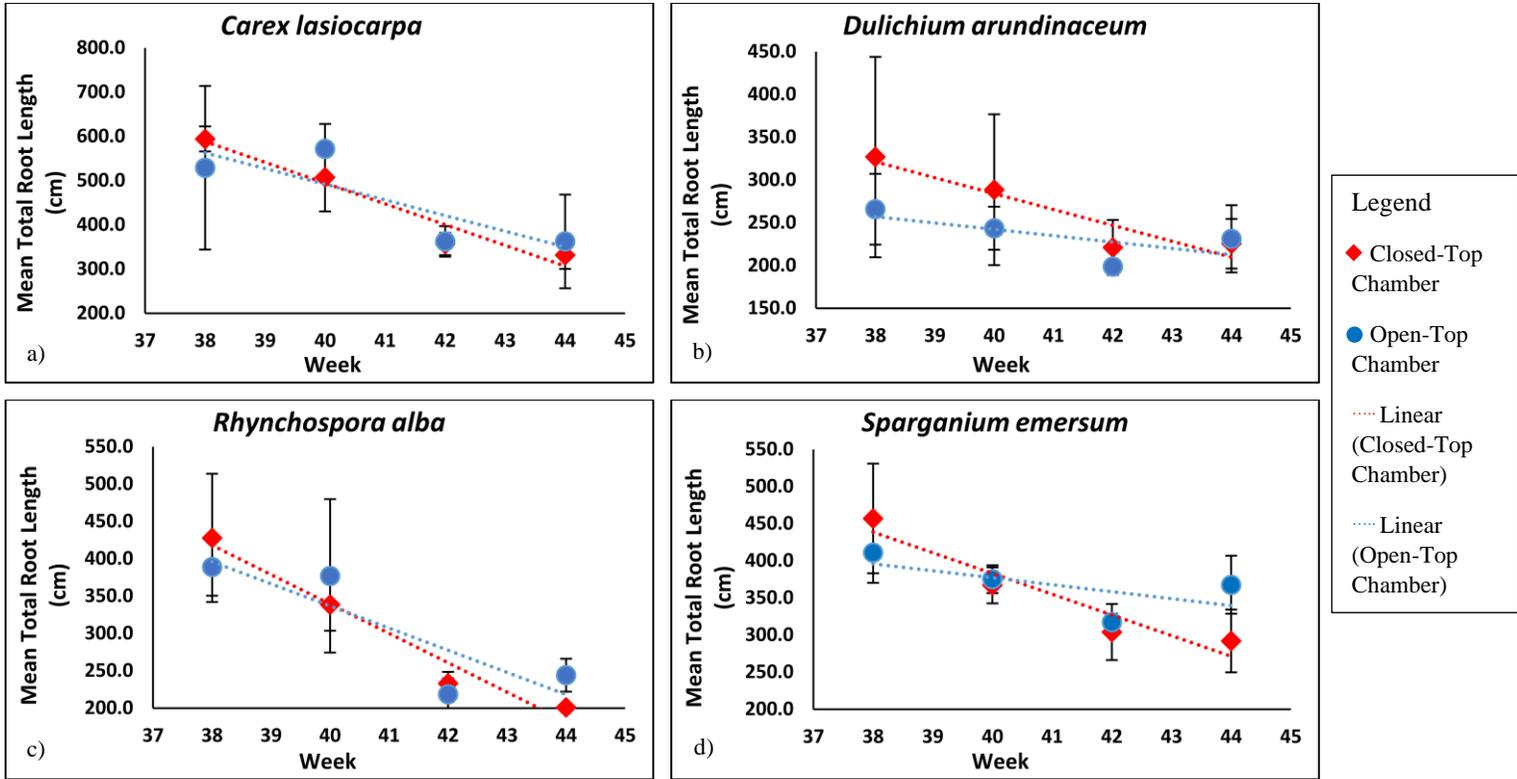


Figure 9. Total root length per plant in the four harvests conducted during the fall of 2019 for a) *Carex lasiocarpa*, b) *Dulichium arundinaceum*, c) *Rhynchospora alba* and d) *Sparganium emersum*. Mean values \pm 1 SE.

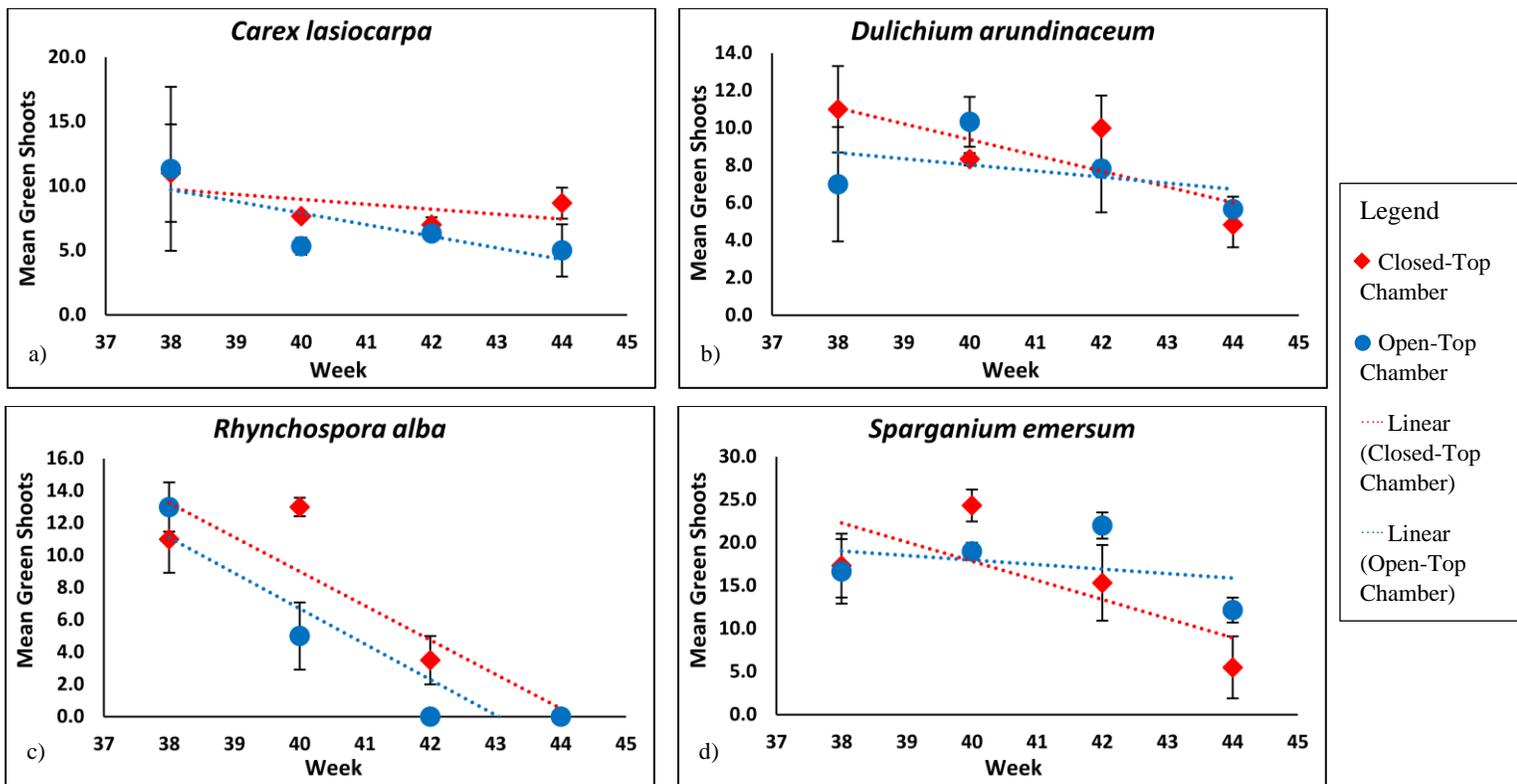


Figure 10. Number of green shoots in the four harvests conducted during the fall of 2019 for a) *Carex lasiocarpa*, b) *Dulichium arundinaceum*, c) *Rhynchospora alba* and d) *Sparganium emersum*. Mean values ± 1 SE.

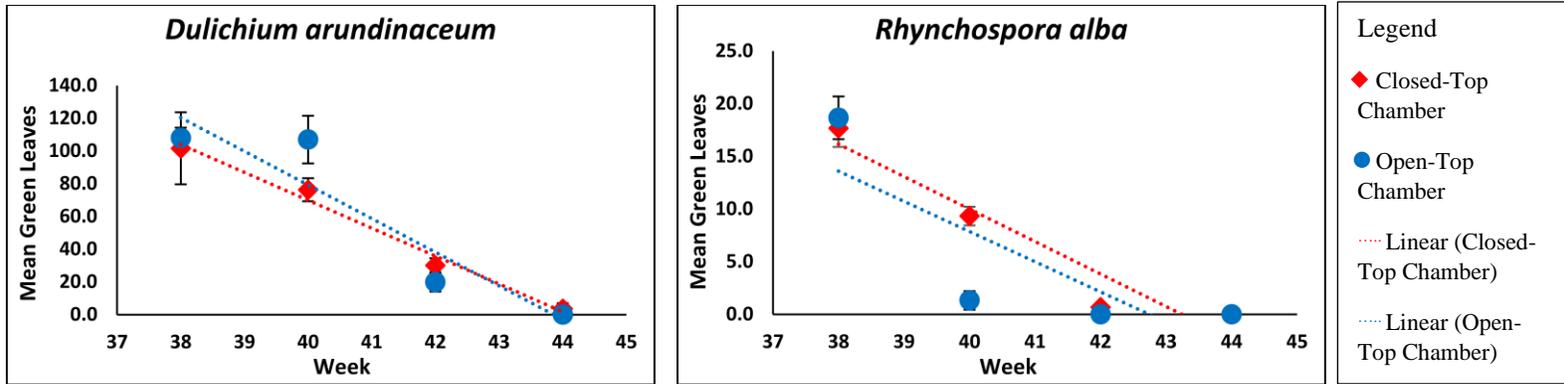


Figure 11. Number of green leaves in the four harvests conducted during the fall of 2019 for a) *Dulichium arundinaceum* and b) *Rhynchospora alba*. Mean values ± 1 SE.

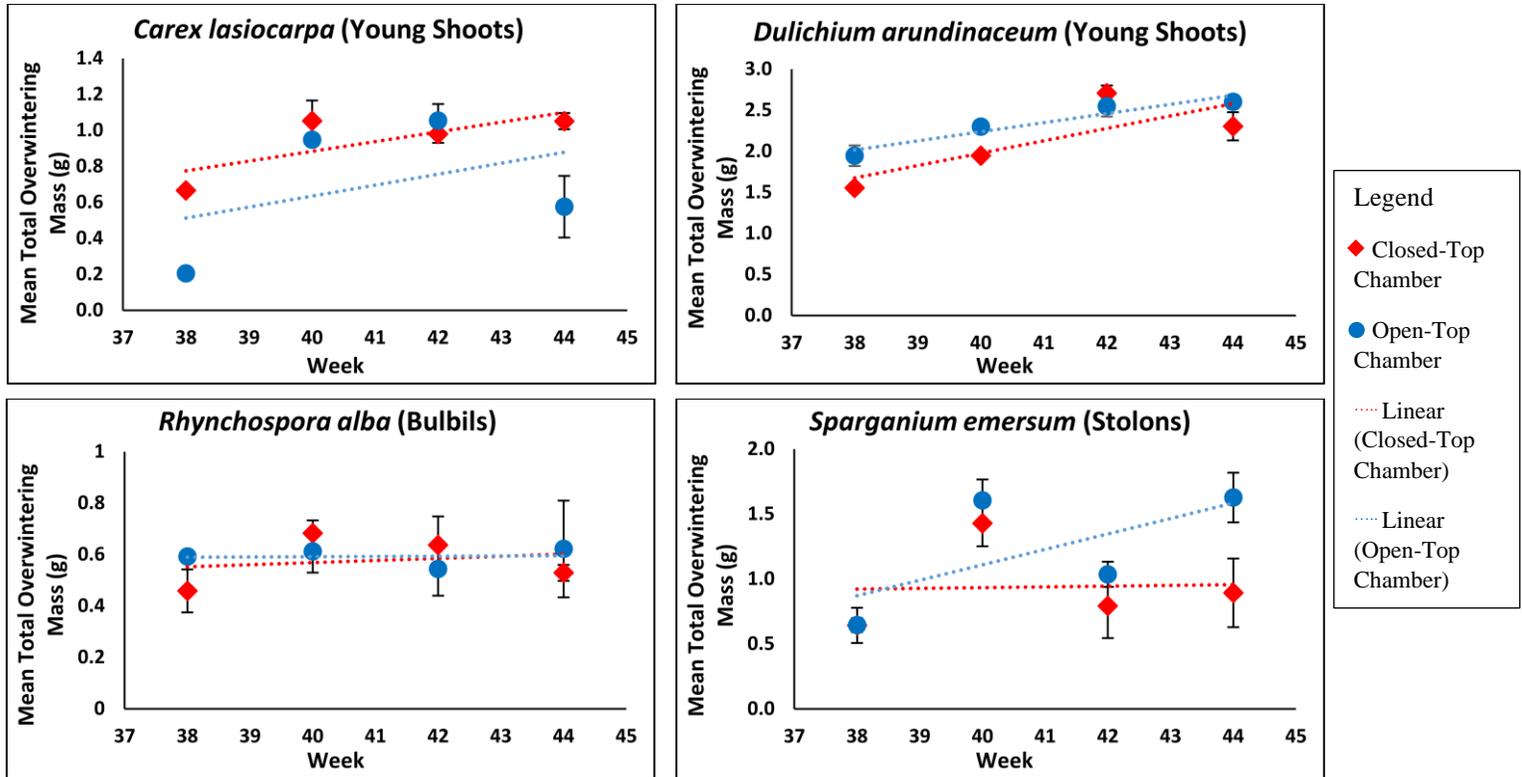


Figure 12. Dry mass of the overwintering structures (young shoots, bulbils and stolons) in the four harvests conducted during the fall of 2019 for a) *Carex lasiocarpa*, b) *Dulichium arundinaceum*, c) *Rhynchospora alba* and d) *Sparganium emersum*. Mean values ± 1 SE. Note: young shoots are shoots formed in the fall and with arrested growth during the winter.

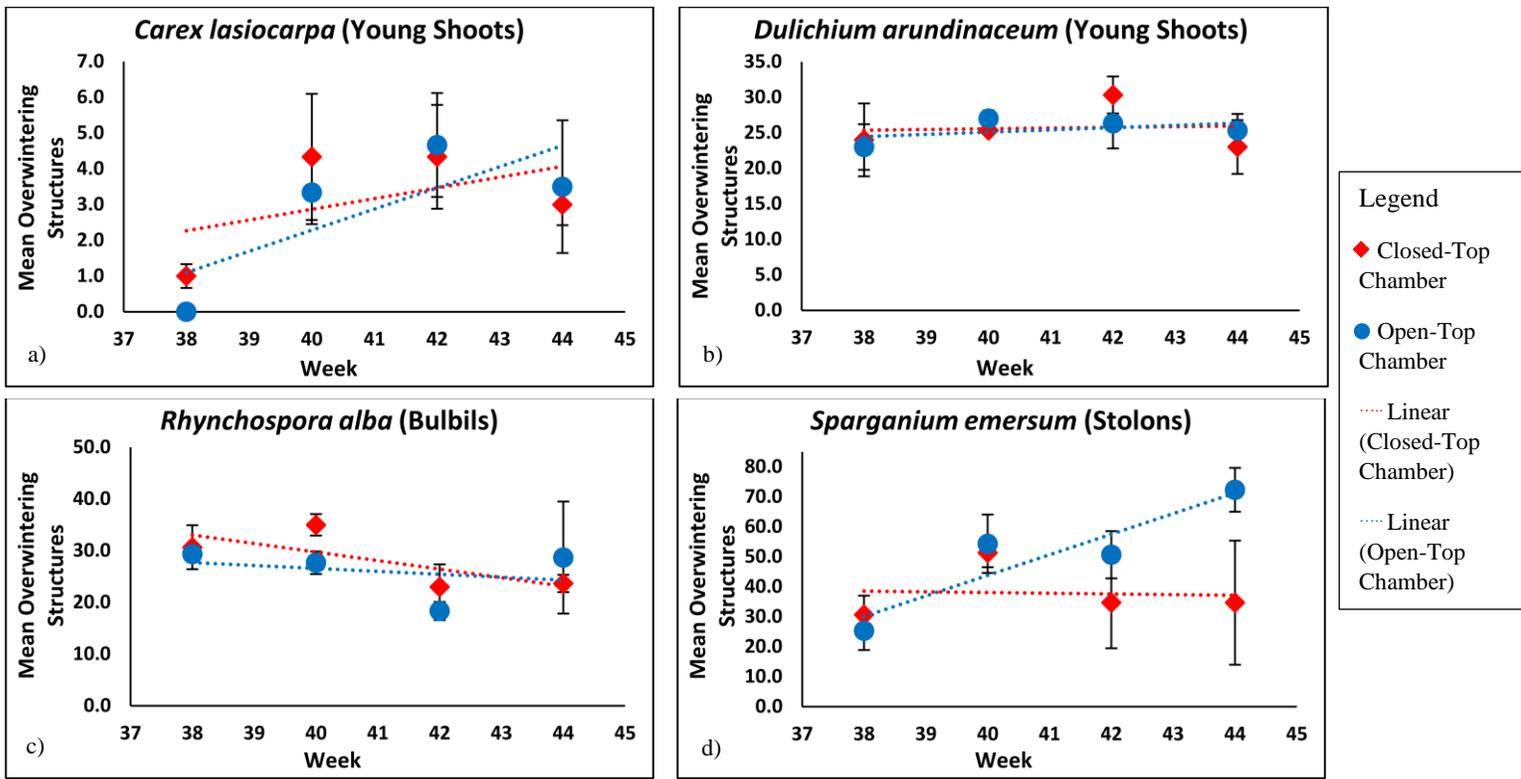


Figure 13. Number of overwintering structures (young shoots, bulbils, and stolons) in the four harvests conducted during the fall of 2019 for a) *Carex lasiocarpa*, b) *Dulichium arundinaceum*, c) *Rhynchospora alba* and d) *Sparganium emersum*. Mean values ± 1 SE.

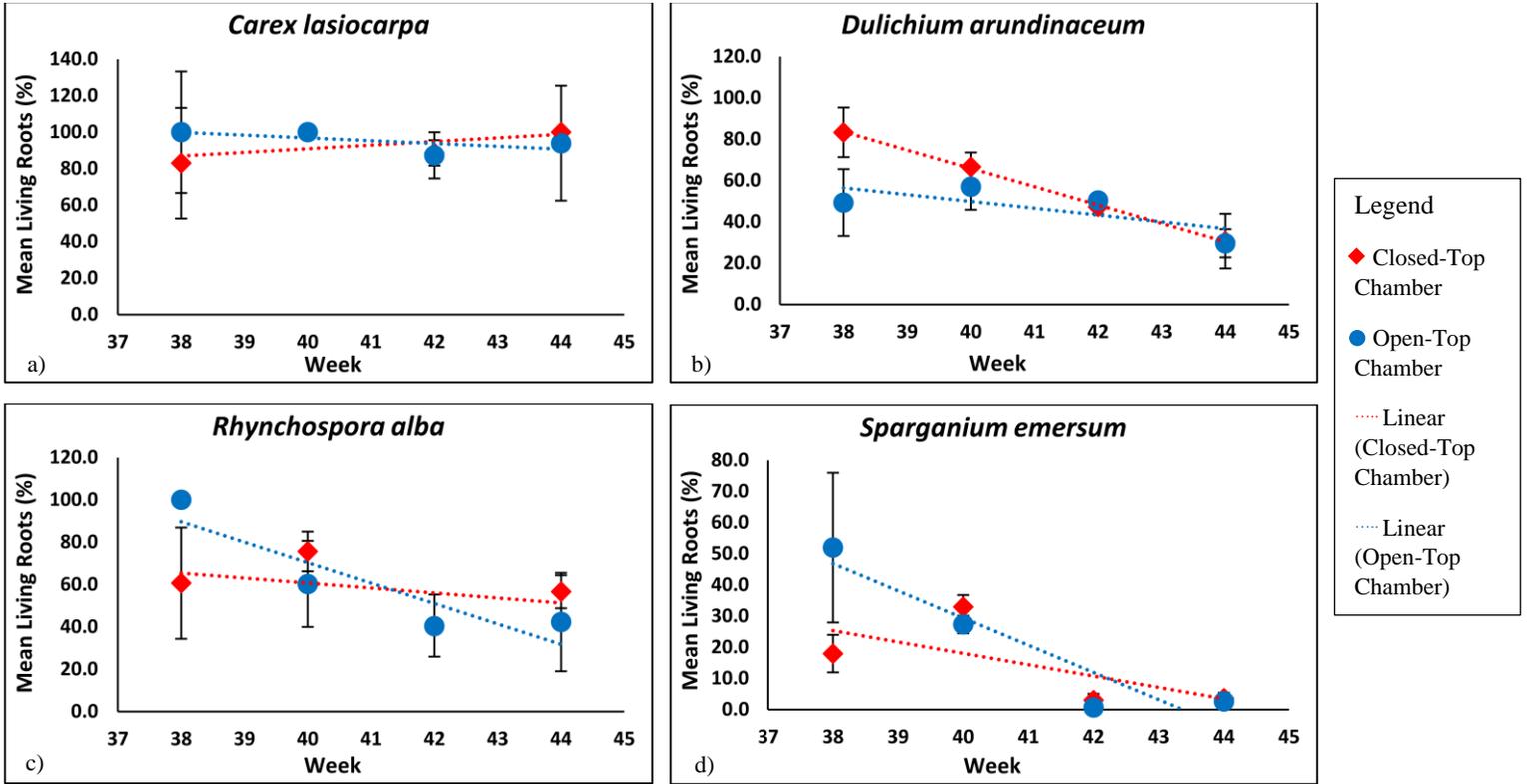


Figure 14. Percentage of living root length in the four harvests conducted during the fall of 2019 for a) *Carex lasiocarpa*, b) *Dulichium arundinaceum*, c) *Rhynchospora alba* and d) *Sparganium emersum*. Mean values ± 1 SE.

Table 4. Results of the general linear models from the data measured at the harvests in fall 2019.

Species	N	R ²	Treatment		Week		Treatment x Week	
			F	P	F	P	F	P
<i>Carex lasiocarpa</i>								
Aboveground Biomass	22	0.683	6.002	0.031	5.652	0.012	0.140	0.934
Belowground Biomass	22	0.629	0.264	0.617	5.757	0.011	0.181	0.907
Total Dry Mass	21	0.750	0.117	0.739	9.752	0.002	0.894	0.475
Total Root Length	21	0.667	7.681	0.018	3.952	0.039	1.424	0.288
Count of Green Shoots	22	0.690	1.360	0.266	5.340	0.014	2.953	0.075
Count of Total Overwintering Structures	18	0.569	0.479	0.500	5.777	0.009	0.148	0.929
Total Overwintering Structures Mass	24	0.384	0.854	0.371	1.614	0.231	0.749	0.541
Percentage of Living Roots	19	0.523	0.887	0.371	0.721	0.564	1.922	0.197
<i>Dulichium arundinaceum</i>								
Aboveground Biomass	23	0.485	0.757	0.400	2.595	0.097	1.142	0.369
Belowground Biomass	24	0.669	5.746	0.031	4.599	0.019	2.684	0.087
Total Dry Mass	24	0.634	5.821	0.030	3.187	0.057	2.704	0.085
Total Root Length	24	0.759	0.764	0.397	9.212	0.001	3.448	0.046
Count of Green Shoots	22	0.521	0.204	0.659	3.010	0.072	0.665	0.590
Count of Green Leaves	24	0.952	0.967	0.342	89.111	0.000	1.509	0.256
Count of Total Overwintering Structures	23	0.435	0.629	0.442	0.867	0.483	1.375	0.294
Total Overwintering Structures Mass	24	0.760	3.306	0.090	11.598	0.000	0.932	0.451
Percentage of Living Roots	24	0.672	1.218	0.288	6.237	0.007	1.155	0.362
<i>Rhynchospora alba</i>								
Aboveground Biomass	22	0.908	0.148	0.707	16.169	0.000	27.492	0.000
Belowground Biomass	23	0.708	0.220	0.647	8.688	0.002	0.805	0.513
Total Dry Mass	24	0.745	1.093	0.313	11.991	0.000	1.018	0.414
Total Root Length	24	0.814	0.385	0.545	18.643	0.000	1.025	0.412
Count of Green Shoots	23	0.915	12.435	0.004	35.353	0.000	5.434	0.012
Count of Green Leaves	24	0.978	19.339	0.001	178.473	0.000	20.884	0.000
Count of Total Overwintering Structures	23	0.617	3.734	0.075	5.640	0.011	0.351	0.789
Total Overwintering Structures Mass	23	0.375	0.736	0.406	0.936	0.451	1.595	0.239
Percentage of Living Roots	22	0.553	0.000	0.995	4.265	0.029	0.410	0.749
<i>Sparganium emersum</i>								
Aboveground Biomass	21	0.928	0.222	0.646	37.904	0.000	0.493	0.694
Belowground Biomass	24	0.540	0.084	0.776	5.416	0.011	0.025	0.994
Total Dry Mass	24	0.576	0.004	0.950	6.174	0.007	0.131	0.940
Total Root Length	23	0.478	1.886	0.193	2.390	0.116	0.142	0.933
Count of Green Shoots	21	0.649	0.590	0.458	3.734	0.045	0.327	0.806
Count of Total Overwintering Structures	24	0.448	2.495	0.137	1.424	0.278	1.503	0.257
Total Overwintering Structures Mass	22	0.658	0.739	0.407	5.587	0.012	0.817	0.509
Percentage of Living Roots	21	0.782	0.003	0.959	12.363	0.001	0.619	0.617

*Note: Block effect was examined, but was determined to be insignificant for all species & all measurements

Table 5. Plant growth in spring 2020 of three study species expressed as projected shoot area.

Species	Chamber Type	Mean Projected Plant Area (cm ²)					
		W1	SE	W2	SE	W3	SE
<i>Carex lasiocarpa</i>	Closed-Top	170.14	29.59	200.03	34.75	300.82	53.90
	Open-Top	122.46	22.41	158.52	21.55	197.32	32.63
<i>Dulichium arundinaceum</i>	Closed-Top	76.61	3.86	100.33	5.61	145.49	5.39
	Open-Top	75.20	3.12	108.79	3.37	153.13	4.30
<i>Rhynchospora alba</i>	Closed-Top		-	13.74	1.88	39.04	4.72
	Open-Top		-	11.03	1.88	29.60	4.33

*Note: W = Week

Table 6. Repeated general linear model results of plant growth in spring 2020 of three study species expressed as projected shoot area.

Species	N	Treatment		Week	
		F	P	F	P
<i>Carex lasiocarpa</i>	63	0.613	0.446	17.097	0.000
<i>Dulichium arundinaceum</i>	90	0.938	0.342	391.797	0.000
<i>Rhynchospora alba</i>	60	2.598	0.120	275.595	0.000

*Note: Block effect was examined, but was determined to be insignificant.

Table 7. Plant growth in spring 2021 of the four study species expressed as aboveground dry mass. In case of *R. alba*, dry mass of a single shoot is shown. Mean values ± 1 SE.

Species	Mean Aboveground Biomass (g)							
	Closed-Top Chambers				Open-Top Chambers			
	Harvest 1	SE	Harvest 2	SE	Harvest 1	SE	Harvest 2	SE
<i>Carex lasiocarpa</i>	2.581	0.190	2.752	1.001	1.530	0.301	2.116	0.236
<i>Dulichium arundinaceum</i>	3.678	0.384	4.423	0.740	2.709	0.162	4.009	0.221
<i>Rhynchospora alba</i>	0.068	0.009	0.075	0.106	0.040	0.013	0.105	0.034
<i>Sparganium emersum</i>	0.952	0.171	0.953	0.256	0.548	0.072	0.941	0.258

Table 8. General linear model results on plant growth in spring 2021 of the four study species expressed as aboveground dry mass.

Species	N	R ²	Treatment		Harvest		Block		Treatment x Harvest	
			F	P	F	P	F	P	F	P
<i>Carex lasiocarpa</i>	16	0.561	11.891	0.006	1.403	0.264	0.276	0.765	0.206	0.660
<i>Dulichium arundinaceum</i>	15	0.689	8.977	0.015	4.642	0.060	0.411	0.675	2.996	0.118
<i>Rhynchospora alba</i>	16	0.714	1.341	0.274	12.054	0.006	0.052	0.949	0.148	0.709
<i>Sparganium emersum</i>	13	0.806	4.529	0.071	0.180	0.684	5.004	0.045	5.039	0.060

Chapter 4: Discussion

4.1 Increased autumn temperature delays autumn senescence

Our study found that increased autumn temperatures had a positive effect on the plants, notably delay of senescence and an increased growth even in the following spring. There were differences among the species for all variables. It was expected that the species with short-lived roots, since they require a longer season to produce new roots every summer, may not gain any advantage of the warmer autumn. However, in contrast to the hypothesis, these differences among the species didn't match the root overwintering strategy. In the present study, the mean annual temperature increase by the treatment was for both years 1.2°C, i.e., fairly similar to the effect of climate change on the mean annual temperature in Ontario; the temperature has increased by 1.5°C (Ashiq & Anand, 2016). The effect of increased autumn temperatures has previously received less attention than the effect of spring temperatures. The results of the present study support the few previous observations of the senescence-delaying effect of warmer autumn temperatures, extending the growing season, but the differences among the studied species indicate that interspecific differences any at least partially explain the contrasting results of previous observations. Fu *et al.* (2018) discovered that summer and autumn warming significantly delayed leaf senescence dates suggesting that temperature may be the controlling factor of leaf senescence in European beech. Also, they discovered that autumn leaf senescence had a larger temperature response than spring leaf out suggesting a larger contribution of autumn senescence delays at extending the growing season under future warmer conditions (Fu *et al.*, 2018). In our study, autumn warming delayed leaf senescence specifically for *C. lasiocarpa* and *R. alba*. The results of 2019 showed a larger scatter, though likely due to the longer intervals between the observations compared to 2020. Fu *et al.* (2018) are the only one of the very few ones who specifically studied autumn temperatures. In this context, it is important to consider that timing of autumn senescence also depends on the temperatures during the whole growing season. Specifically, Menzel *et al.* (2006) found that the previous months' temperatures affected the plant phenology, observing that advancement of spring or summer delayed autumn and leaf colouring (Menzel

et al., 2006). Keenan and Richardson (2015) determined that either an earlier or later spring was related to earlier or later autumn senescence. In contrast to these studies, Starr *et al.* (2000) found that *Polygonum bistorta* didn't change the length of its growing period when exposed to an extended growing season. Under warmer temperatures, this species becomes active earlier but senesces earlier. This shows that the response of this species is limited by internal constraints which could put the species at a competitive disadvantage in a warming climate (Starr et al., 2000).

Plant response may also be primarily determined by the photoperiod. Li et al. (2003) found that for birch, shorter days are what triggers autumn phenology and not the temperature.

4.2 Increased autumn temperature increases or decreases above and belowground biomass depending on the species

At high latitudes, plants match their physiological processes to seasonal change through sensing environmental signals such as temperature which guarantees they grow in favourable seasons (Strømme *et al.*, 2015). But warmer spring temperatures may increase the phenological development rate, without any effect on plant biomass (Hatfield & Prueger, 2015). These authors studied maize, the experiments being conducted in climate-controlled chambers (Hatfield & Prueger, 2015). The lack of an effect on biomass maybe because maize is an annual crop plant. Zou *et al.* (2014) found that certain wetland plants, specifically *Calamagrostis angustifolia* had a higher tolerance to change in temperature and hydrology than others such as *Glyceria spiculosa* reflected in the amount of aboveground biomass grown and the maximum growth reached 4+°C. Such interspecific differences were obvious also in the present study, the closed-top chambers not having a clear effect on the amount of aboveground biomass of *D. arundinaceum* and *S. emersum* while the closed-top chambers affected the other two species. Such a difference in response may be a result of different environmental factors limiting the growth of the different species. Differences in hydrological requirements between the species possibly explained the results of Zou *et al.* (2014). However, in our experiment, hydrology unlikely played a role as the water levels did not vary with the treatments.

In a two-year study using eddy covariance data and remote sensing vegetation indices, it was determined that warmer temperatures during the growing season increased the GPP of the alpine wetlands which were studied (Kang et al., 2016). The same effect can be seen with *C. lasiocarpa* and *R. alba* in our study. This could be the case because the water in the closed-top chambers stayed warmer longer in the autumn. The positive effect of increased water temperatures is also indicated in the study by White and Visser (2016) in riverine ecosystems. They determined that the increase in temperature had a positive impact on the length of the growing season and it increased plant biomass (White & Visser, 2016). In the present study, the increased autumn temperatures had a positive impact on the growing season length and biomass of *C. lasiocarpa* and *R. alba*. White and Visser (2016) didn't establish an interspecific difference, they just measured the total wetland production while in our study we determined species-specific differences among four wetland plant species.

Day *et al.* (2008) found that the warming increased the aboveground biomass of all the forest vascular plants in the study. Similar results were also found for tundra shrub-dominated vegetation in Wang *et al.* (2016). Their investigation determined that this vegetation increased aboveground biomass when exposed to increased temperatures thus these plants could allocate biomass to aboveground during periods of warmer temperatures (Wang et al., 2016). Allocation patterns are possibly species-specific indicated by data in Zohner *et al.* (2021). In this study, the authors discovered that phenological shifts caused by an increase in temperatures may be changing the balance between aboveground and belowground growth. Specifically, the data show that earlier leaf-out is caused by increased spring temperatures which lead to an increase in total biomass whereas a delay in senescence caused a reduction in this biomass (Zohner et al., 2021). The advancement of leaf-out increased the growth of roots more than the growth of shoots, increasing the root-to-shoot ratio for the trees while for the shrub species a delay in senescence caused an increase in the roots only (Zohner et al., 2021). On the other hand, Ma *et al.* (2010) found that there is no interannual variation in grassland aboveground net primary productivity, but that there is the only variation within the growing season. They discovered that in May the monthly aboveground biomass increased, but not in June, July, or August, and there was no variation between the

22 years of their study (Ma et al., 2010). This is different in our study since it shows a possible interannual variation in spring growth during the 2020 and 2021 growing seasons. But this different effect in the two years may also reflect the large variation among the replicates.

4.3 Increased autumn temperatures increased spring growth

The present study is the first to study specifically how autumn temperatures affect the spring growth of wetland plant species. The results show that increased autumn temperature increased spring growth for herbaceous wetland plants. The effects of autumn temperatures have previously been studied in the context of the effect on short-day dormancy induction for three boreal trees, two *Betula* species and one *Alnus* species (Heide, 2003). This author determined that budburst in spring was delayed significantly by high temperature during this induction period specifically the temperature in September. This temperature increase also significantly increased the chilling requirement for dormancy to end (Heide, 2003).

4.4 Senescence, nutrient depletion and remobilization

Nutrient depletion may be an important factor contributing to the early senescence of the older plants in 2020 in our study. Plants growing for two summers in the same pots had most likely depleted the nutrient resources to a larger extent than plants in their first year. Plants need to take up various macro- and micronutrients from the soil for carbohydrates production which is needed in balanced proportions for optimal growth (Watanabe et al., 2010). Plants adapt their metabolism to imbalances of these nutrients and rely on the proper allocation of nutrients between organs. Proper allocation of nutrients is coupled with developmental senescence which occurs between the source and sink organs (Watanabe et al., 2010). Mechanisms to cope with nutrient depletion include remobilization of internal nutrient reserves which imply senescing mechanisms (Watanabe et al., 2010). Nutrient deficiencies lead to effects on chlorophyll content, reduction in photosynthetic carbon fixation, and growth retardation. The plants in our study

probably took their nutrients from the shoots and leaves and remobilized them into the overwintering structures such as young shoots with arrested growth, bulbils and stolons. Therefore, nutrient remobilization helps plants store nutrients that will be useful at the beginning of the next growing season (Achat et al., 2018). This can be done using leaf senescence which remobilizes nutrients to younger leaves increasing plant fitness (Jan et al., 2019). Nutrient remobilization rates are affected by precipitation, temperature, or climate (Achat et al., 2018) therefore, climate change could affect these rates. Temperature affects this rate noticeably in our study by the mass of the overwintering structures for *D. arundinaceum* and *S. emersum* changing over time in 2019.

4.5 Senescence and hydrology

With increased total precipitation at northern latitudes as a result of climate change, it is predicted that there will be changes in the seasonal distribution of discharges due to the increased temperature of winter and spring which can result in earlier snowmelt for Southern Ontario, Canada (Grillakis et al., 2011). This could mean a reduction in groundwater level which could affect the water table position (Guardiola-Albert & Jackson, 2011) that may affect wetland species differently. It is well known that the water table position is an important control for biogeochemical processes of a wetland specifically for the composition of plant species along with net ecosystem production rates (Whittington & Price, 2006). Northern wetlands and their plant life are particularly sensitive to climate change since they depend on specific climatic conditions such as low temperatures and high water availability which are needed for wetlands (Zou et al., 2014). But the IPCC projections predict a combination of increasing temperatures and stable or decreasing summer precipitation which might mean the end of those climatic conditions (Essl et al., 2012). Also, these new conditions could increase summer drought, and cause groundwater levels to decrease (Essl et al., 2012) which in turn would affect the plant life in the wetlands. These plants are important because they make up the physical structure in the water column, moderate water flow and stabilize sediments (Tanner, 2001). Overall biomass of these plants could decrease and changes in

resource allocation could occur along with a decrease in root shoot ratio (Yuan et al., 2017). This will depend on how warming temperatures affect plant phenology and growing season length.

Senescence is affected by plant age and environmental stresses (Jan et al., 2019). Environmental stresses such as drought cause leaf senescence to occur so plants can tolerate being exposed to an extreme lack of moisture (Jan et al., 2019). This stress leads to physiological interruptions that lead to senescence which has an important role in plant survival (Jan et al., 2019). In our study, increased autumn temperatures increased spring growth in both 2020 and 2021 growing seasons, but as Wang *et al.* (2020) point out this could, in a natural setting, just be temporary. They determined that increased warming promoted faster growth and earlier phenology, but then this decreased due to increased water stress by the middle of the growing season (Wang et al., 2020). This brings up an important point for wetlands, especially when considering the effects climate change could have on the water table. Our study only looked at the effect of warming autumn temperatures on wetlands plants in normal water conditions, but it would be good to study how wetland plants cope with lower water table levels and therefore water stress.

Chapter 5: Conclusion

Our study contributes to the understanding of how warmer autumn temperatures could affect autumn phenology including autumn growth and senescence along with possible effects on spring growth. *C. lasiocarpa*, *D. arundinaceum*, *R. alba* and *S. emersum* had their senescence delayed by the warming temperatures, therefore, extending their growing seasons, but this extended growing season didn't affect the autumnal growth in terms of biomass for *D. arundinaceum* and *S. emersum*. Therefore, the effect of the warmer autumn temperatures along with the extended growing season is species-specific. The effect of the warmer autumn temperatures on spring growth was also species-specific, only increasing spring growth in *C. lasiocarpa* and *R. alba*. In conclusion, the increased autumn temperatures delayed senescence along with increased autumn and spring biomass. Also, the data shows that species respond differently to warmer autumn, but this difference isn't obviously related to root overwintering strategies.

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Appendices

Appendix 1. Figures and tables

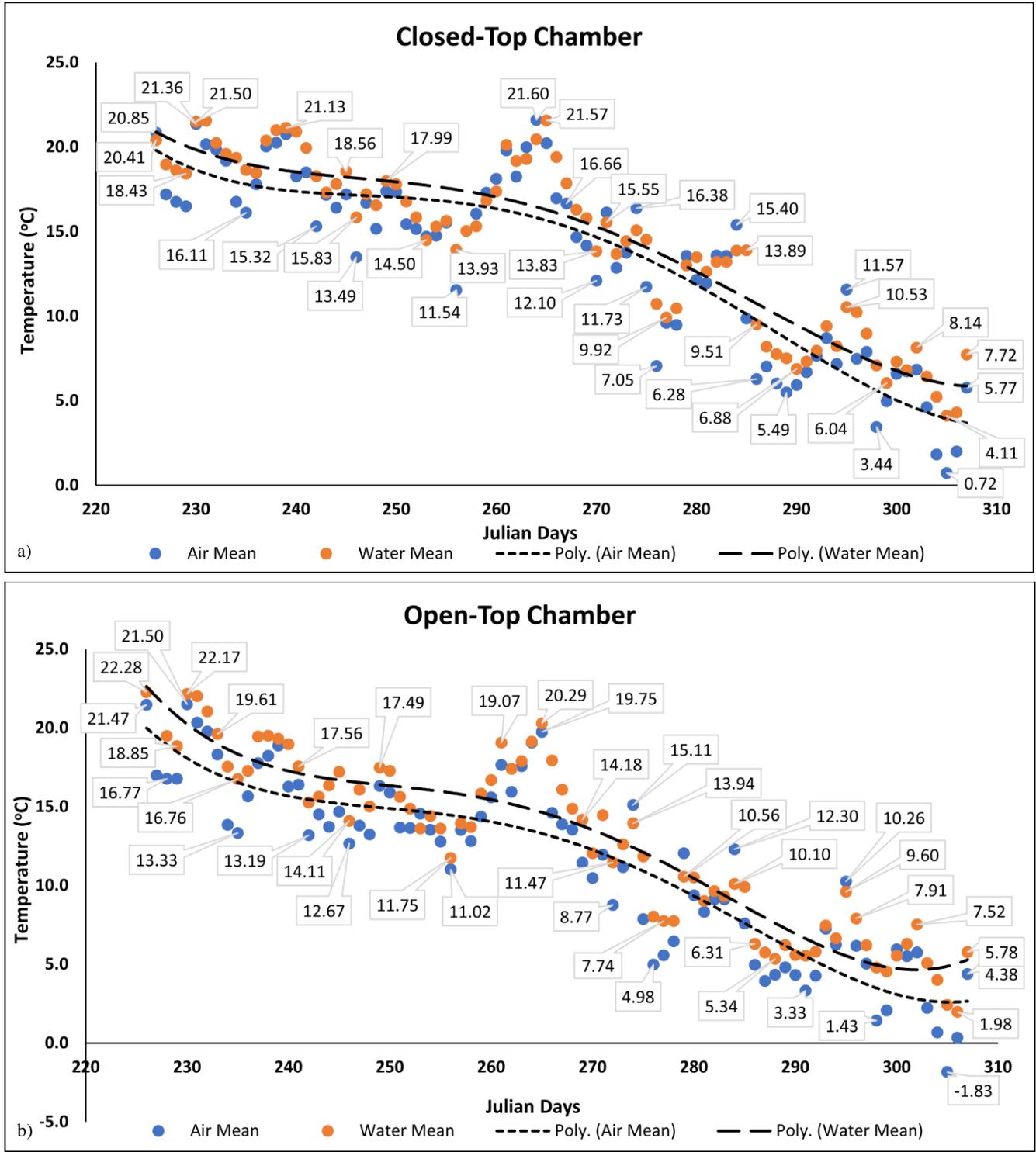


Figure S1. Air temperature and water temperature inside the a) closed-top chambers and the b) open-top chambers throughout first part of experiment, senescence count 2019

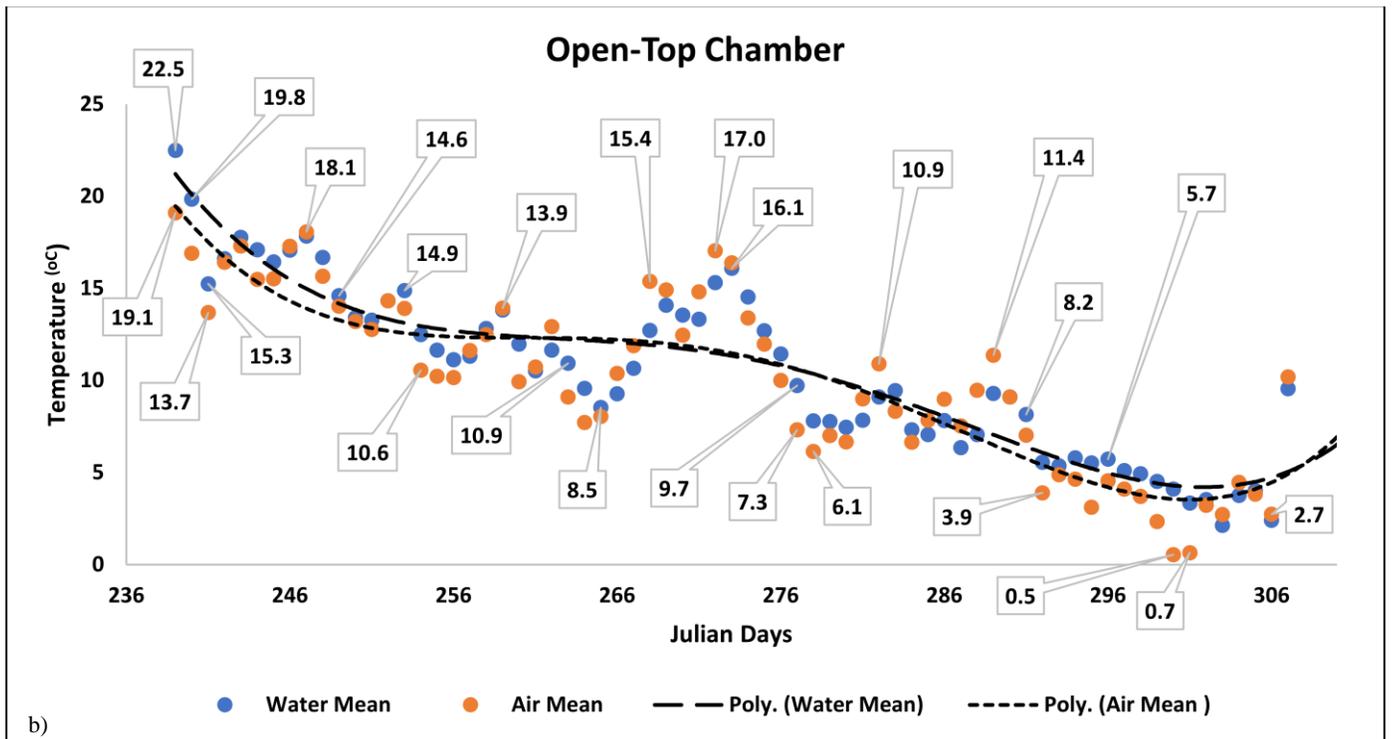
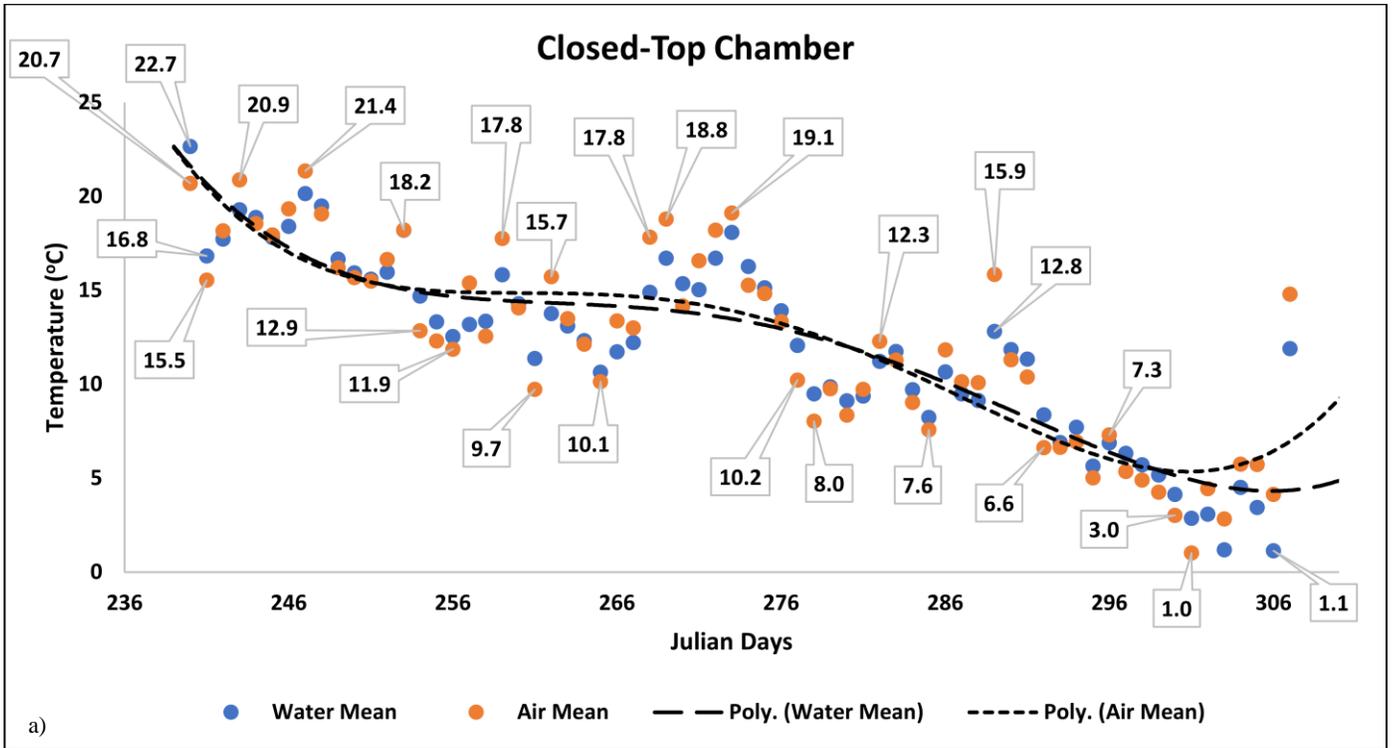


Figure S2. Air temperature and water temperature inside the a) closed-top chambers and the b) open-top chambers throughout second part of experiment, senescence count 2020.

Table S1. Air and water temperatures inside the closed-top and open-top chambers for 2019 and 2020

Time Period	Closed-Top Chambers		Open-Top Chambers	
	Air	Water	Air	Water
Year 2019				
226-239	18.83	19.88	17.81	20.09
240-253	16.30	17.52	14.45	16.08
254-267	17.27	17.66	15.20	16.27
268-281	12.54	13.53	9.81	11.36
282-302	8.04	9.15	5.91	6.96
Year 2020				
239-252	16.83	16.82	15.70	16.62
253-266	13.55	13.46	10.84	11.47
267-280	14.11	13.92	11.81	11.94
281-294	9.98	9.90	7.83	7.52
295-307	5.27	4.77	3.55	4.51

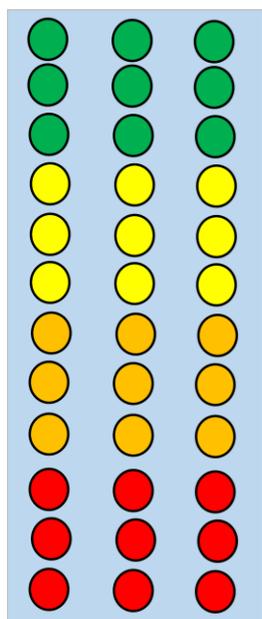


Figure S3. Schematic of Pool Setup. From top to bottom; the green circles represent *Rhynchospora alba* plants, the yellow circles represent *Sparganium emersum* plants, the orange circles represent *Carex lasiocarpa* plants, and the red circles represent *Dulichium arundinaceum* plants.

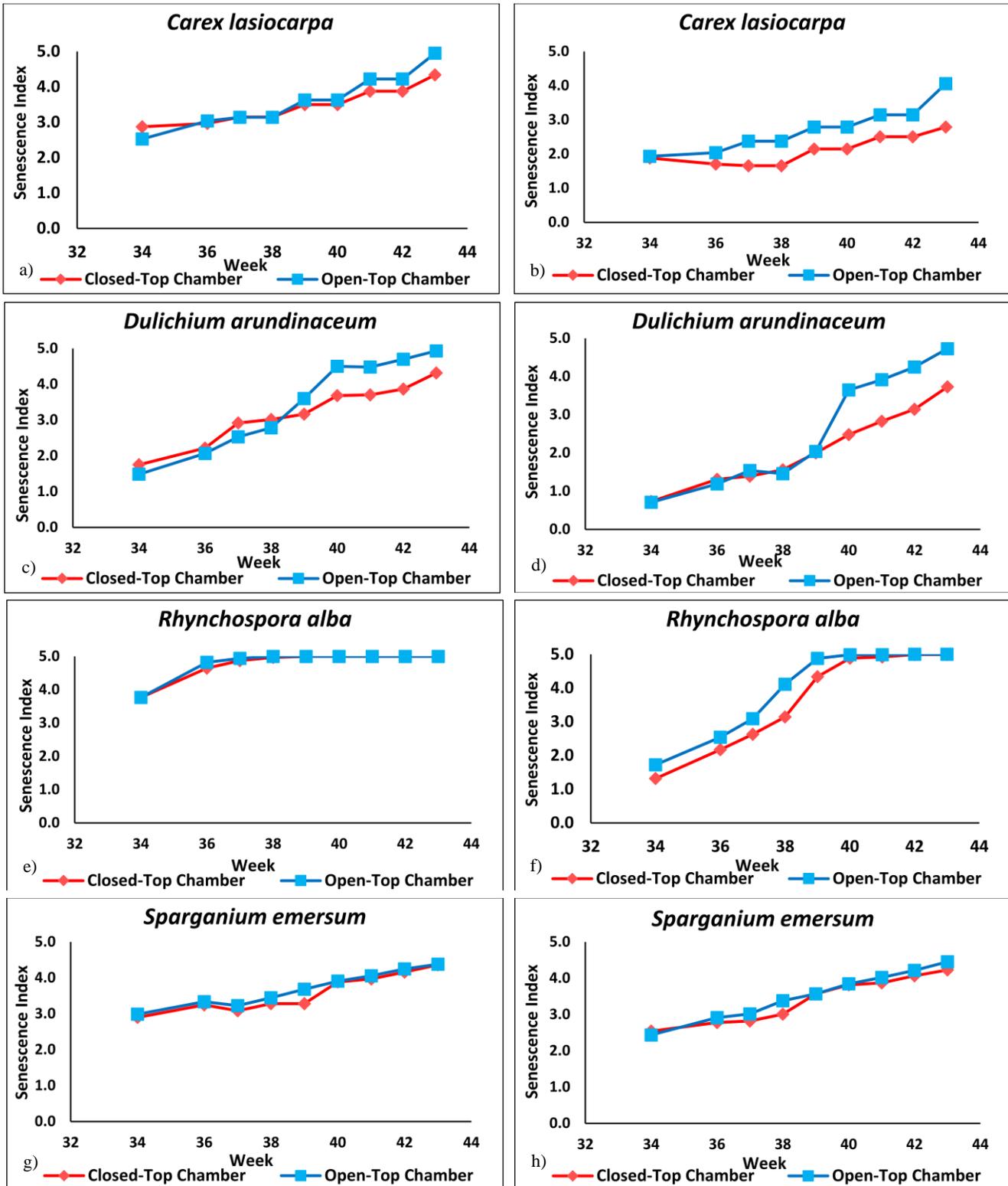


Figure S4. Senescence index for the four study species conducted in fall of 2020, separately presented for the plants planted in 2019 (left) and those plants planted 2020 (right), a) and b) are for *Carex lasiocarpa*, c) and d) are for *Dulichium arundinaceum*, and e) and f) are for *Rhynchospora alba*, and g) and h) are for *Sparganium emersum*.