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Autumn growth of three perennial weeds at high latitude benefits from climate change

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Abstract

In autumn, agricultural perennial weeds prepare for winter and can store reserves into creeping roots or rhizomes. Little is known about influence of climate change in this period. We tested the effect of simulated climate change in autumn on three widespread and noxious perennial weeds, Elymus repens (L.) Gould, Cirsium arvense (L.) Scop. and Sonchus arvensis L. We divided and combined simulated climate change components into elevated CO₂ concentration (525 ppm), elevated temperatures (+2-2.5°C), treatments in open-top chambers. In addition, a control in the open-top chamber without any increase in CO₂ and temperature, and a field control outside the chambers were included. Two geographically different origins and three pre-growth periods prior to the exposure to climate change factors were included for each species. All species increased leaf area under elevated temperature, close to doubling in E. repens and quadrupling in the dicot species. E. repens kept leaves green later in autumn. C. arvense did not benefit in below-ground growth from more leaf area or leaf dry mass. S. arvensis had low levels of leaf area throughout the experiment and withered earlier than the two other species. Below-ground plant parts of S. arvensis were significantly increased by elevated temperature. Except for root:shoot ratio of C. arvense, the effects of pure elevated CO₂ were not significant for any variables compared to the open-top chamber control. There was an additive, but no synergistic, effect of enhanced temperature and CO₂. The length of pre-growth period was highly important for autumn plant growth, while origin had minor effect. We conclude that the small transfer of enhanced above-ground growth into below-ground growth under climate change in autumn does not favour creeping perennial plants per se, but more leaf area may offer more plant biomass to be tackled by chemical or physical weed control.

KEYWORDS

Agropyron repens, Cirsium arvense, elevated CO₂, elevated temperature, Elymus repens, Elytrigia repens, global warming, Norway, Sonchus arvensis

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1 | INTRODUCTION

Globally, temperature and concentration of CO_2 are increasing. Climate change is considered to influence growth, competitiveness and geographical distribution of plants (McDonald, Riha, DiTommaso, & DeGaetano, 2009; Patterson, Westbrook, Joyce, Lingren, & Rogasik, 1999; Ziska, Blumenthal, Runion, Hunt, & Diaz-Soltero, 2011). Usually plant growth is favoured by higher CO_2 levels (Hatfield et al., 2011; Kirschbaum & Lambie, 2015; Poorter & Navas, 2003). At high latitudes, most plant species use the C_3 pathway. These plants profit more than C_4 plants from increasing CO_2 (Kimball, 2016; Patterson et al., 1999; Ramesh, Matloob, Aslam, Florentine, & Chauhan, 2017; Ziska, 2000). Up to a certain limit, plant growth is mainly enhanced by increasing temperature, while above this limit growth decreases (Kimball, 2016). When the temperature is sub-optimal, global warming generally increases plant growth in habitats such as temperate grasslands (Peñuelas et al., 2013).

We consider Norway as a country at high latitude, characterized by late spring, a relatively warm summer and a short autumn period. At high latitudes, plant growth is usually restricted by the length of the vegetation period. With global warming, the length of the vegetation period is predicted to increase in northern Europe (Bindi & Olesen, 2011; Trnka et al., 2011).

Human activities shape and steer agro-ecosystems. Altered land use due to climate changes will further alter these systems (Trnka et al., 2011; Wolz et al., 2017). Extreme weather events and changes in climate variability may have large impacts on weeds and other pests (Thornton, Ericksen, Herrero, & Challinor, 2014). While the majority of weed species occurring under arable conditions are annuals, a few species are creeping perennials. In northern Europe, hence at high latitude, *Elymus repens* (L.) Gould, *Cirsium arvense* (L.) Scop. and *Sonchus arvensis* L. are perennial weeds in all cropping systems. These species use the C_3 pathway in photosynthesis, and they have creeping subterranean organs for storage and spreading, these being either roots (*C. arvense*, *S. arvensis*) or rhizomes (*E. repens*; Håkansson, 2003). From these organs, new plants sprout early or late in crops, for example, in cereals. Combine harvest in summer cuts all sprouts at certain heights, but does not erase the plants (Figure 1, top part). After cutting, sprouts regrow from remaining subterranean plant parts. This re-growth of sprouts is more effective in plants that have had more time to grow and store reserves. Sprouts translocate resources from above-ground parts to the below-ground parts in autumn; this process stops when sprouts start withering.

The optimum temperature for the species of this study varies from 15 to 30°C (Majek, Erickson, & Duke, 1984; Tiley, 2010; Zollinger & Kells, 1991). *E. repens* is more important in northern areas with cool to moderately warm summers, and may continue to grow late in the autumn (Boström et al., 2013; Håkansson, 2003). In contrast to *E. repens*, previous studies under current climate conditions have revealed that *S. arvensis* is the earliest to wither in autumn, while *C. arvense* withers more gradually (Tørresen, Fykse, & Rafoss, 2010). While older sprouts produced more biomass, younger sprouts continued to grow later in the season. This extended growth of the above-ground plant parts in young sprouts resulted in increased biomass of the subterranean creeping roots of *C. arvense* and *S. arvensis*, while the rhizome biomass of *E. repens* was less affected (Tørresen et al., 2010).

Studies under controlled conditions and under field conditions at relatively high temperatures show that the three species increase growth under elevated CO_2 concentration: *E. repens* by 12%–90% (Tremmel & Patterson, 1993; Ziska & Teasdale, 2000), *S. arvensis* by 50% (Ziska, 2003) and *C. arvense* by around 70% (Ziska, 2002, 2003). These studies started with seeds (Tremmel & Patterson, 1993; Ziska, 2003), with plants grown in fully controlled environments (Ziska & Teasdale, 2000) or focused on full summer growth of the perennials (Ziska, Faulkner, & Lydon, 2004). To our knowledge, no other study has investigated climate change effects in the autumn period for plants established vegetatively.

This paper investigates the growth of *E. repens*, *C. arvense* and *S. arvensis* in response to simulated climate change in autumn. In

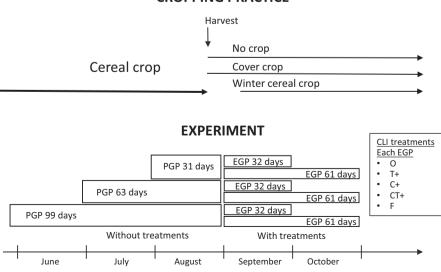


FIGURE 1 Timeline—cropping practice (top) and experiment (bottom). Top: Overview of cropping practice as simulated in the experiment. Bottom, left: Pre-growth period (PGP) without treatments. Three levels of different length, 31, 63 and 99 days. Bottom, right: Experimental growth period (EGP) with treatments. Two levels, length: 32 and 61 days. Each EGP includes five climatic treatments in factor CLI. For details, see Section 2: 'climatic treatment'. EGP 0 days is at start of climatic treatments right after harvest (top) simulated by cutting in the experiment. Factor origin not considered in the figure

CROPPING PRACTICE

open-top chambers, we separated climate change components into elevated CO_2 concentration and elevated temperatures. A combined treatment was also incorporated. A control treatment in the open-top chambers, without any increase in CO_2 and temperature, and a similar control in the field outside the chambers were included.

The autumn is a relatively short period in the life cycle of creeping perennials. However, changes in climate at this time of the year may allow perennial plants to effectively produce creeping organs in preparation for the forthcoming year. Plants defoliated or cut continue to live with their subterranean organs. The top part of Figure 1 illustrates the processes in arable cereal cropping. We simulated sprouted shoots in the main crops by different pre-growth periods (PGPs; Figure 1, bottom part). Cutting simulated combine harvesting. The experimental growth period (EGP) stands for the post-harvest period. The latter period can be used differently: a new autumn sown main crop can be established; a cover crop not intended to be harvested can be grown or open stubble is left to be treated chemically or physically.

The three species share the clonal lifestyle but establish their creeping roots or rhizomes at different depths and develop as dicots (*C. arvense*, *S. arvensis*) or a monocot (*E. repens*) with a different shoot and leaf architecture. Hence, we hypothesized (1) that each species responds specifically to elevated CO_2 and temperature.

While it is common knowledge that both elevation of temperature and CO_2 alone improve plant growth, we further hypothesized (2) that there is a synergistic effect when the two components are combined. A synergistic effect means that the effect is higher than can be expected when simply adding the effect of each of CO_2 and temperature.

Our third hypothesis focussed on a specific link between the subterranean biomass produced pre-harvest and the autumn growth. We expected (3) that plants with short pre-harvest growth benefitted relatively more from the climate change components compared to plants with a long pre-harvest growth period. We further expected that this applies to both above- and below-ground biomass production in autumn.

Two geographically different origins of each species, with plant material (rhizomes or roots) collected from different parts of Norway, were included. We expected (hypothesis 4) no differences between the origins in their reaction to the investigated climate change components, since they did not differ strongly under current climate conditions (Tørresen et al., 2010).

2 | MATERIALS AND METHODS

2.1 | Species and site

The experiments with climatic treatments took place at the Særheim research station of the Norwegian Institute of Bioeconomy Research (58°47′N, 5°41′E) in 2004 and 2005, and included the three perennial species *E. repens*, *C. arvense* and *S. arvensis*. Open-top chambers with plastic walls as described by Hanslin and Mortensen (2010) were used. The size of each chamber was 2.5 m × 3.4 m. The soil was a 60/40 (% by volume) mixture of fertilized fine peat and washed fine sand. For

details on the growth medium, see Hanslin and Mortensen (2010). In addition to natural precipitation, water was given when needed, from the day of planting until the end of the experiments. Nutrient supply comparable to that found in autumn stubble fields was given.

2.2 | Experimental design

The main experimental factor was simulated climate change (factor CLI). The experiment was arranged as a split plot design with replicates in four blocks in 2004 and three blocks in 2005. Climatic treatments were used as the main plot, and species, origins of species and pre-growth periods as the subplots (Figure 1).

Each **climatic treatment** within the factor CLI represented different conditions (Table 1):

O: Open-top chamber control without extra supply of CO_2 or heating.

C+: Open-top chamber with supply of CO₂ gas to approximately 525 ppm.

T+: Open-top chamber with heating, giving an approximate increase in temperature of $2-2.5^{\circ}$ C.

CT+: Open-top chamber with heating (like T+) and supply of CO_2 (like C+).

F: Field control outside open-top chambers (without plastic walls) to test for chamber effect.

Climatic situations without any experimental changes are referred to as 'ambient'. The main study period lasted from 2 September to 1 November in 2004 and from 1 September to 30 October in 2005. Figure 2 gives the field weather conditions during the experimental growth periods.

Two origins of each species consisting of plant material (rhizomes or roots) from a northern (63°N, all species from Stjørdal) and a southern area of Norway (59°N, E. repens, C. arvense and S. arvensis from Ås, Vestby and Sarpsborg respectively) were used in the experiments (for details, see Tørresen et al., 2010). The irradiance conditions varied considerably: the day lengths at summer solstice were 20:37 for the northern and between 18:44 and 18:36 for the southern area and at winter solstice 4:29 (northern) and 5:59 to 6:05 (southern) respectively (given as hours:minutes; www.timeanddate.no). The northern area had a more maritime climate with more even monthly precipitation during the year and slightly higher temperature during winter and lower temperature during summer than the southern area. The yearly average air temperature was 6.1 and 5.7°C and the yearly precipitation 994 and 860 mm at Stjørdal (northern) and Ås (southern) in the period 1995-2018 respectively. For comparison, the day lengths at the experimental site Særheim were 18:25/6:15 at summer/winter solstice, while the yearly mean air temperature was 7.9°C and yearly precipitation 1,448 mm in the period 1995-2018.

Each experimental period started with a **pre-growth period** (factor PGP), raising the plants before the main period started (Figure 1). Three pre-growth periods were installed: 31, 63 and 99 days—the short and medium pre-growth period in 2005 and the long pre-growth period in 2004.

TABLE 1 Air temperature at plant level, soil temperature at 10 cm soil depth, relative humidity (RH) and CO_2 concentration in the opentop chambers (O, C+, T+, CT+, see text for explanation) and the field control (F) during the experimental growth period in 2004 (2/9-1/11) and 2005 (1/9-30/10; average, minimum and maximum of daily mean climate)

	Climatic treatments in the factor climate change									
Measured climate	0		C+		T+		CT+		F	
	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Air temp. (°C)										
Mean	10.8	11.5	10.4	11.4	12.3	13.8	12.4	13.5	10.0	11.0
Min.	5.2	3.3	4.9	3.3	7.5	5.6	7.7	6.0	4.6	2.8
Max.	17.1	18.4	16.9	18.3	18.8	20.3	18.6	18.0	16.3	18.0
Soil temp. (°C)										
Mean	10.1	11.4	10.1	11.4	11.5	12.9	11.7	12.9	8.2	11.2
Min.	6.9	3.3	7.3	3.5	8.4	5.8	8.5	5.1	5.7	3.1
Max.	14.4	19.7	14.9	19.1	16.1	19.1	15.9	20.1	10.5	19.2
RH (%)										
Mean	84.0	80.8	85.1	69.5	73.4	72.6	73.7	72.9	83.2	86.1
Min.	59.2	61.2	61.2	43.2	49.9	48.3	50.5	48.4	56.5	62.9
Max.	99.0	95.6	100.6	90.9	89.5	87.5	90.6	87.6	97.3	99.0
CO ₂ conc. (ppm)										
Mean	375	338	529	561	376	365	523	547	374	381
Min.	353	230	421	421	356	319	423	418	352	353
Max.	426	531	679	692	433	401	641	666	409	411

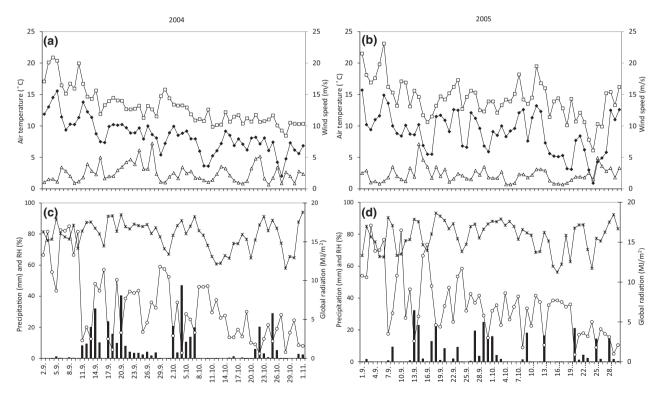
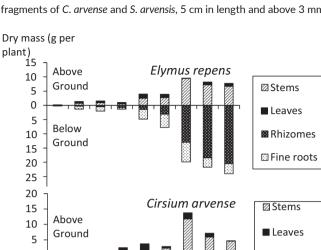


FIGURE 2 Field weather conditions at the meteorological station Særheim: (a, b) air temperature (minimum = closed diamonds, maximum = open squares), wind speed (open triangles), (c, d) precipitation (black bars), relative humidity (stars) and global radiation (open circles) during the experimental growth period in 2004 (a, c) and 2005 (b, d)



The plant material was prepared at the beginning of each pre-growth period. In 2004, rhizome fragments of three nodes of *E. repens* and root fragments of *C. arvense* and *S. arvensis*, 5 cm in length and above 3 mm

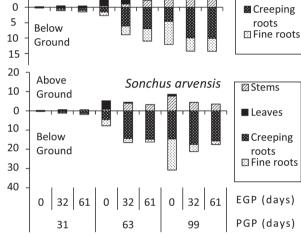


FIGURE 3 Dry mass (DM) partitioning into above- and belowground parts (stems + leaves = DM Above Ground, Leaves = DM Leaves, Rhizomes or Creeping roots + Fine roots = DM Below Ground, Rhizomes or Creeping roots = DM Creeping R) for *Elymus repens, Cirsium arvense* and *Sonchus arvensis* affected by pre-growth period (PGP) and experimental growth period in autumn (EGP, days with climatic treatments). Except for DM Leaves and Stems of *E. repens*, all variables are back-transformed data from In(x + 1). EGP 0 indicate values at start of the experimental period

Global Change Biology

in diameter, were used. Two fragments were planted directly at 5 cm soil depth in 10 L black plastic sacks (in this paper referred to as pots), one origin of one species in each pot. One month later, the plants were thinned to one fragment per pot. In 2005, fragments of roots of *C. arvense* and *S. arvensis*, 4 cm long and 3–4 mm thick, and rhizomes of *E. repens*, two nodes in length, were planted in 5 cm pots at 1.5 cm depth. Each pot contained one fragment. Three to 4 weeks later, the plants were transplanted into 10 L pots filled with the same soil mixture as in 2004.

In 2004, the pre-growth period started on 26 May for all plants and the plants were grown outdoors. In 2005, the pre-growth period was subdivided into two starting dates: 30 June and 1 August, and all pots were placed under greenhouse conditions at approximately 20°C for 2–4 weeks to speed up the development of the plants. After that period, the pots were placed outdoors as in 2004.

To simulate cereal harvesting at the end of the pre-growth period, the plants were cut to 20 cm height on 27 August 2004 and 22 August 2005, Figure 1. In 2005, only *E. repens* planted on 30 June (PGP 63 days) were cut. All the other plants in 2005 were lower than 20 cm.

Six and 10 days after cutting, the experimental growth period (EGP) started. EGP 0 represents this starting point. Pots were subjected to different climatic treatments (Figure 1). The experimental pots were randomly placed centrally in each plot and surrounded by one row of border pots. A 20 cm high wooden frame insulated with 5 and 15 cm thick styrofoam plate surrounded the border pots at the ends and the sides of the chambers, respectively, minimizing the systematic effects of climatic treatment conditions and variation of soil temperature.

Destructive assessments for analyses of the plant material were done 32 and 61 days (median day) after start of the **experimental growth period** (factor EGP), that is, starting 30 September and 1 November in 2014 (lasting for 2 days), and 3 and 31 October in 2005 (lasting for 3 days).

2.3 | Observed variables

The above-ground plant parts were cut at the soil surface and separated into green leaves (laminae) and other above-ground plant parts (excluding withered leaves in 2004, not in 2005). The area of the green

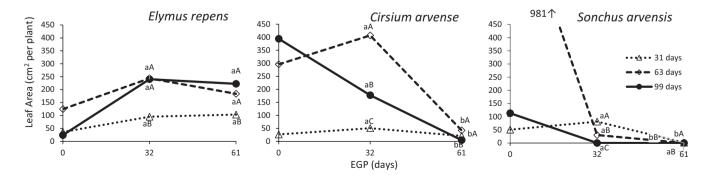


FIGURE 4 Leaf Area (cm² per plant) for *Elymus repens*, *Cirsium arvense* and *Sonchus arvensis* as affected by the pre-growth period (PGP 31, 63 and 99 days) and experimental growth period in autumn (EGP, 0, 32 and 61 days with climatic treatments). The Leaf Area values of *C. arvense* and *S. arvensis* are back-transformed data from ln(x + 1). Significant effects in each PGP (line) between EGPs are indicated by different lowercase letters (a, b) and between the PGPs at each EGP by different capital letters (A, B, C)

ILEY— Global Change Biology

laminae was determined using a Li-3100 Leaf Area Meter (Li-Cor) on the whole material or a representative fraction (>70 cm² for *E. repens*, >120 cm² for *C. arvense* and >160 cm² for *S. arvensis*). The variables Leaf Area (capital letters for variable names), dry mass of leaves (DM **Leaves**) and dry mass of the total above-ground plant (**DM Above Ground**) resulted from these measurements. The below-ground plant parts were separated from the growth medium by washing with tap water on a metal mesh of 1.5 cm mesh size. The creeping roots or

Weed species	Leaf Area	DM Leaves	DM Above Ground	DM Creeping R	DM Below Ground	RS Ratio	DM Plant
Elymus repens							
Transformation	None	None	None	Ln(x + 1)	Ln(x + 1)	None	Ln(x + 1)
Climate change (CLI)	<0.001	0.001	0.033	n.s.	n.s.	0.006	0.024
CLI sig. contrasts of effects	Т	т	Т	_	_	Т	Т
Experimental growth period (EGP)	n.s.	n.s.	n.s.	<0.001	<0.001	<0.001	<0.001
Pre-growth period (PGP)	<0.001	<0.001	<0.001	<0.001	<0.001	< 0.001	<0.001
CLI × PGP	n.s.	n.s.	n.s.	n.s.	n.s.	0.012	n.s.
EGP × PGP	n.s.	0.033	n.s.	0.001	0.022	0.031	n.s.
Origin (O)	0.009	0.026	0.003	n.s.	n.s.	0.031	n.s.
CLI × O	n.s.	0.043	n.s.	n.s.	n.s.	n.s.	n.s.
PGP × O	0.001	0.009	<0.001	<0.001	<0.001	n.s.	<0.001
EGP × PGP × O	n.s.	n.s.	n.s.	0.003	0.020	n.s.	n.s.
All other interactions	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Cirsium arvense							
Transformation	Ln(x + 1)	Ln(x + 1)	Ln(x + 1)	Ln(x + 1)	Ln(x + 1)	None	Ln(x + 1)
CLI	0.001	<0.001	n.s.	n.s.	n.s.	0.045	n.s.
CLI sig. contrasts of effects	Т	T, C	_	_	-	Т	-
EGP	<0.001	<0.001	<0.001	n.s.	0.025	<0.001	n.s.
CLI × EGP	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
PGP	<0.001	<0.001	<0.001	<0.001	<0.001	< 0.001	<0.001
EGP × PGP	<0.001	<0.001	0.005	n.s.	n.s.	n.s.	n.s.
0	n.s.	n.s.	n.s.	0.002	0.005	0.008	0.010
PGP × O	n.s.	n.s.	0.001	n.s.	n.s.	n.s.	n.s.
All other interactions	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Sonchus arvensis							
Transformation	Ln(x + 1)	Ln(x + 1)	Ln(x + 1)	Ln(x + 1)	Ln(x + 1)	Ln(x + 1)	Ln(x + 1)
CLI	<0.001	<0.001	0.005	0.004	0.004	n.s.	0.001
CLI sig. contrasts of effects	Т, С	Т, С	<i>T</i> , <i>C</i> , Ch	T, Ch	Т	-	<i>T</i> , <i>C</i> , Ch
EGP	<0.001	<0.001	<0.001	n.s.	n.s.	<0.001	n.s.
CLI × EGP	n.s.	0.004	n.s.	n.s.	n.s.	n.s.	n.s.
PGP	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
CLI × PGP	n.s.	n.s.	n.s.	0.015	0.019	n.s.	0.006
EGP × PGP	<0.001	<0.001	0.043	0.004	0.001	<0.001	0.002
0	<0.001	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.
EGP × O	<0.001	<0.001	0.005	n.s.	n.s.	0.004	n.s.
PGP × O	0.002	<0.001	0.022	0.030	0.004	n.s.	0.003
$EGP \times PGP \times O$	<0.001	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.
All other interactions	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Note: For further explanation, see Section 2. n = 200.

Abbreviations: C, main effect of elevated CO2; Ch, chamber effect; DM, dry mass; n.s., not significant; T, main effect of elevated temperature; x, original variable.

rhizomes (DM Creeping R), diameter >1.5 mm, were separated from the other below-ground plant parts (fine roots and the below-ground parts of the main shoot and secondary shoots). In 2004, the secondary shoots were included in the fraction creeping roots or rhizomes. Total below-ground dry mass (DM Below Ground) was determined in both years. Dry mass of plant parts was determined after drying at 60°C for at least 48 hr. The variables total plant dry mass (DM Plant = DM Above Ground + DM Below Ground) and root-shoot-ratio (RS Ratio = DM Below Ground/DM Above Ground) were calculated. After each destructive assessment, the rest of the pots were again placed tightly within the central and border pots arrangement.

2.4 | Statistical analyses

The species were analysed separately. In both years, the initial assessment was excluded from the analyses because these plants had no climatic treatments. Data for the initial assessment time of the treatment 'Field control' were separately analysed in Tørresen et al. (2010). Averages of the initial assessment (EGP 0 days) without climatic treatments for illustrating sequential developments of observed variables are included in Figures 3 and 4.

Dependent variables (x) in the analyses were Leaf Area, RS Ratio, dry mass of various plant fractions (DM Leaves, DM Above Ground, DM Creeping R, DM Below Ground) and DM Plant (Table 2). Visual inspection of residual plots (two plots: [a] normality plot of residuals and [b] plot of predicted values vs. residuals) from each model was used to consider if the dependent variable had to be transformed to achieve a dependent variable being approximately normally distributed with homogeneous variance. We used the natural logarithm function for transformation and because there are some values of the dependent variable being equal to zero, we added the constant 1 to each value. Mixed models were applied on all assessed variables with the procedure 'proc mixed' (SAS Institute Inc., 2002–2012). The factors climate change, origin, pregrowth period and experimental growth period were fixed effects. Twoand three-factor interactions were included in the analyses. Replicate and the interaction replicate × climate change were random effects.

If significant influence of the factor climate change (CLI) was indicated in the mixed model, contrasts were tested with an approximated t test (SAS Institute Inc., 2002-2012). Contrasts were defined, estimated and tested whether they can be claimed to be different from zero. In these contrasts, (O), (C+), (T+), (CT+) and (F) represent the least squares means for the climate treatments O, C+, T+, CT+ and F respectively (for explanation of these letters in text and tables, see Section 2, Experimental design). To test for main effect of elevated CO₂, the contrast C = [(O) + (T+)] - [(C+) + (CT+)] was used; for main effect of elevated temperature, the contrast T = [(O) + (C+)] - [(T+) + (CT+)] was used; for the interaction $CO_2 \times temperature$, the contrast CT = [(O) + (CT+)] -[(C+) + (T+)]) (interpreted as synergistic effect if positive) was used; and for chamber effect (control in open-top chambers vs. field), the contrast Ch = [(O) - (F)]) was used (Table 2). In addition, contrasts were used to detect if treatments in open-top chambers were significantly different from the control in open-top chambers (C+: [(O) - (C+)], T+: [(O) - (T+)],

Global Change Biology –WILE

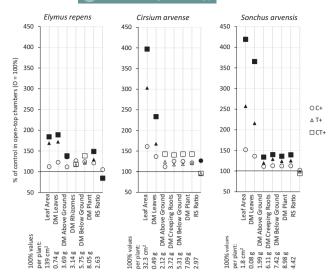


FIGURE 5 Average effect of elevated CO₂ and temperature in open-top chambers. Average of original values or back-transformed means if In-transformed values were used in variance analysis, expressed as percentage of the control in open-top chambers (100% = values given). Filled symbols indicate significant contrasts compared to control in open-top chambers

CT+: [(O) – (CT+)]; Figure 5). If other effects or interactions were significant in the mixed model, Tukey–Kramer tests were performed to detect significant differences. Main effects, interactions and differences between climatic treatments were considered significant if $p \le .05$.

3 | RESULTS

The variance analyses revealed that the plant growth (DM Plant, DM Leaves, DM Above Ground, DM Below Ground, Leaf Area) was highly influenced by the pre-growth period (PGP) and the experimental growth period (EGP) and much less by the factor climate change in the experiment (Table 2). DM Plant increased with pre-growth period for all three species (Figure 3). DM Plant of E. repens increased with experimental growth period for all pre-growth periods, while for DM Plant of C. arvense and S. arvensis, the experimental growth period interacted with the pre-growth period. The below-ground parts dominated the plant dry matter the more the later in the autumn. The DM Above Ground and DM Below Ground of S. arvensis were the highest in the pre-growth period 99 days at the experimental growth period 0 days (at start of experimental period) due to more time to develop before experiment started and variables for biomass values were lower at 32 and 61 days experimental growth period due to earlier withering than at shorter pre-growth periods. The Leaf Area of S. arvensis decreased earlier and more during autumn, C. arvense less so and E. repens the least (Figure 4). Longer pre-growth period resulted in a quicker decay of Leaf Area in autumn especially for S. arvensis. A 'chamber effect' (field control vs. open-top chamber with ambient temperature and CO2 concentration) was only detected for DM Above Ground, DM Creeping R and DM Plant of S. arvensis (Table 2) with slightly higher values at the field control than in the open-top chamber control (Table 4).

3.1 | Species-specific effects of elevated temperature and CO₂ concentration

The variables DM Leaves and Leaf Area always reacted to the main factor climate change (Table 2). Elevated temperature significantly affected Leaf Area and DM Leaves of all three species averaged over pre-growth periods, experimental growth periods and origin. Compared to control in the open-top chambers, the Leaf Area of E. repens was close to doubling, while it almost guadrupled for C. arvense and S. arvensis (Figure 5). The increase in DM Leaves with temperature was close to that of Leaf Area for E. repens and S. arvensis. In C. arvense, however, the increase was only half compared to Leaf Area. Elevated temperature also resulted in a lower, but significant, increase in DM Above Ground and DM Plant of E. repens and a decrease in RS Ratio of E. repens and C. arvense (Figure 5; Table 2). S. arvensis increased significantly in the variables DM Creeping R, DM Below Ground and DM Plant. Only in S. arvensis, the below-ground plant parts (DM Creeping R, DM Below Ground) significantly benefitted from elevated temperature, but to a much lesser extent than the leaves (T+; Figure 5). All variables for below-ground parts of C. arvense and E. repens were statistically not different under elevated temperature (T+).

TABLE 3 Leaf Area (cm² per plant) for *Cirsium arvense*, and dry mass (DM) leaves (g per plant) for *Sonchus arvensis* at various experimental growth periods (EGP) affected by different climatic treatments (O, C+, T+, CT+, for explanation, see text). n = 20

	Climatic treatments							
EGP	0	C+	T+	CT+				
Leaf Area of C. arvense								
32 days	144.5 a A	142.1 a A	228.9 a A	196.4 a A				
61 days	6.6 ab B	18.6 bc B	41.3 cd B	83.4 d A				
DM Leaves of S. arvensis								
32 days	0.166 a A	0.212 a A	0.357 ab A	0.587 b A				
61 days	0.000 a A	0.013 a B	0.011 a B	0.050 a B				

Note: Values are back-transformed data from ln(x + 1). Significant effects in each row are indicated by different lowercase letters (a, b, c, etc.) and in each column for each species by capital letters (A, B).

	Climatic trea	Climatic treatments							
PGP	F	0	C+	T+	CT+				
DM Plant									
31 days	2.4 ab A	1.3 a A	1.5 a A	2.4 ab A	3.2 b A				
63 days	19.2 a B	16.8 a B	19.3 a B	23.9 a B	22.5 a B				
99 days	23.2 a B	23.0 a B	25.6 a B	20.9 a B	24.1 a B				
DM Creeping Roots									
31 days	1.2 ab A	0.7 a A	0.7 ab A	1.4 ab A	1.7 b A				
63 days	14.2 a B	11.5 a B	13.7 a B	17.7 a B	16.9 a B				
99 days	16.7 a B	16.3 a B	18.8 a B	14.6 a B	16.7 a B				

Note: Mean values are back-transformed data from ln(x + 1). Significant effects in each row are indicated by different lowercase letters (a, b) and in each column by capital letters (A, B).

Elevated CO_2 concentration averaged over ambient and elevated temperature, affected above-ground variables (Leaf Area, DM Leaves, DM Above Ground) and DM Plant of *S. arvensis*, while for *C. arvense* only DM Leaves was significantly affected and no variables of *E. repens* (Table 2). The relative effects compared to the control in the open-top chambers revealed that only RS Ratio of *C. arvense* was significantly increased by elevated CO_2 without any increase in temperature (Figure 5). Compared to control in the open-top chambers, the treatment CT+ increased most measured variables in *E. repens* and *S. arvensis*, while *C. arvense* reacted significantly only in Leaf Area and DM Leaves.

Leaf Area of *C. arvense* and DM Leaves of *S. arvensis* were significantly influenced by the interaction climate change by experimental growth period (Tables 2 and 3). For *C. arvense*, the increase by elevated temperature (T+, CT+) was only significant after experimental growth period 61 days. In *S. arvensis*, DM Leaves increased at the CT+ treatment compared to other treatments with ambient temperature at the experimental growth period 32 days.

These results show that the three species reacted differently to the single effects elevated temperature and CO_2 concentration. Hence, our first hypothesis was confirmed.

3.2 | Interaction elevated temperature and CO₂ concentration

No interaction between temperature and CO_2 was significant for any variable of the three species and this interaction is therefore not shown in Table 2. No synergistic effect of elevated CO_2 (C+) and temperature (T+) occurred, but the combined treatment (CT+) gave just additive effects (Figure 5). Thus, the second hypothesis was rejected.

3.3 | Effect of pre-growth period

The below-ground parts (DM Creeping R, DM Below Ground) and DM Plant of *S. arvensis* were influenced by an interaction of climate change and pre-growth period (Table 2). In the CT+ treatment biomass was increased compared to the open-top

TABLE 4 Effect of various pre-growth periods (PGP 31, 63 and 99 days, *n* = 12, 12 and 16, respectively) and climatic treatments (F, O, C+, T+, CT+) on dry mass (DM) Plant and DM Creeping Roots of *Sonchus arvensis* (g per plant)

Global Change Biology

chamber control for the 31 days pre-growth period (Table 4). For plants with 63 and 99 days pre-growth period, less effect of climatic treatments occurred. In *E. repens* and *C. arvense*, no significant interaction of climate change and pre-growth period was detected with the only exception being RS Ratio of *E. repens* (Table 2). The RS Ratio of *E. repens* decreased with the combination elevated temperature and CO_2 for the pre-growth period 31 days compared to the open-top chamber control and the C+ treatment (not shown). The interaction climate change × pre-growth period × experimental growth period was not significant for any variables of the three species, and is, consequently, not included in Table 2. Thus, for *S. arvensis*, our results support the third hypothesis: More benefit of elevated temperature at shorter pre-growth periods. The hypothesis was, however, rejected for the other two species.

3.4 | Effect of origin

The origins of *E. repens* and *S. arvensis* from 63°N had higher Leaf Area and DM Leaves than the origins from 59°N (Table 2; Figure 6). For *E. repens*, DM Above Ground was higher and RS Ratio was lower for the 63°N origin compared to the 59°N origin. The DM Leaves of *C. arvense* reacted in the opposite way (59°N > 63°N), while there was no difference between origins for Leaf Area (Table 2). For *C. arvense*, DM Creeping R, DM Below Ground, RS Ratio and DM Plant were also higher for the 59°N origin compared to the 63°N origin.

The interaction of pre-growth period and origin was highly significant for many variables of the species, indicating different reactions by origin to each pre-growth period (Table 2). The leaf areas of *E. repens* and *S. arvensis* responded oppositely to pre-growth period and origin (Figure 6). However, the dry mass of several plant parts' responses to pre-growth period showed a similar pattern for the two origins of each species even if the interaction was significant. The response of the DM Creeping R of the two origins is given as an example (Figure 6).

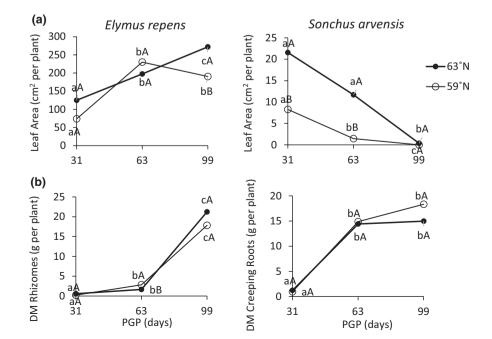
Except for DM Leaves of *E. repens*, no interaction of climate change and origin and no three-factor interaction containing climate change and origin was detected (Table 2). Our fourth hypothesis was thereby confirmed.

4 | DISCUSSION

Our results indicate that all three investigated species, the monocot *E. repens* and the dicots *C. arvense* and *S. arvensis*, profit from changed climate conditions in autumn, but the detailed reaction of each species was different.

With respect to the lower temperature at high latitudes, the effect of elevated temperature is not surprising. While the effects of temperature on leaves were very strong, this surprisingly did not result in the same strong effects on the rest of the plant. In general, perennials use their photosynthetic activity above ground to extend their below-ground storage system. One could suspect that the experimental growth period (EGP) in autumn was simply too short to effectively do the latter. For S. arvensis and C. arvense, the decrease in almost all variables from short (32 days) to long experimental growth period (61 days) clearly speaks for the opposite. These species lose leaf area and dry mass above and to a lesser extent below ground in the longer autumn period-climatic treatments did not stop or turn around this process. The reaction of E. repens was different: In the same period, Leaf Area indicating above-ground growth did not decrease significantly (Figure 4). Elevated temperature (T+, CT+) increased Leaf Area significantly and kept it growing and green irrespective of experimental growth period. Hence, E. repens used higher temperature in autumn to keep green leaves above ground and we cannot rule out that the

FIGURE 6 Leaf Area (a) and dry mass (DM) Creeping R (b) of *Elymus repens* and *Sonchus arvensis* affected by pre-growth periods (PGP) and origins (63° N or 59° N). Except for Leaf Area of *E. repens*, values are back-transformed data from ln(x + 1). Significant effects between PGPs are in each origin (line) indicated by different lowercase letters (a, b, c) and between the origins at each PGP by capital letters (A, B)



ILEY- Global Change Biology

long experimental growth period with 61 days might have been too short for successful transfer from above- to below-ground biomass.

The effects of pure elevated CO_2 were not significant for any variables, except for an increase in RS Ratio of *C. arvense*, when contrasted to the open-top chamber control (Figure 5). Hence, an increase in CO_2 alone would not allow any of the three species investigated to profit in their autumn growth. This is in contrast to other studies with larger increase in biomass of these species (12%–90%, largest range in *E. repens*, Ziska & Teasdale, 2000) and a higher increase in root:shoot ratio of both *C. arvense* and *S. arvensis* due to projected future elevated CO_2 concentrations (reviewed by Ziska et al., 2011).

Although the leaf variables increased in a range of doubling to quadrupling in the treatment with both enhanced temperature and CO_2 (CT+), the effect was just additive. No synergistic effect of temperature and CO_2 in comparison to the open-top chamber control occurred for any of the species.

Our findings that in all three investigated species, the origins (more southern or more northern origin) did not differ in their reaction to climate change factors mean that we can generalize our results about the influence of climate change on these species. However, the various reactions of the measured variables to the interaction between origin and the length of the period before harvest (PGP) and the length of the autumn growth period (EGP) indicate complex reactions of creeping perennials to this interplay. A small or no 'chamber effect' is promising and shows that the control in opentop chambers is close to field conditions, and that the future effect of elevated temperature and CO_2 can be indicated based on these data.

To sum up, similar reactions of the species show that under climate change in autumn mainly leaf growth profited. Elevated temperature was much more important than elevated CO_2 .

The overall massive effect of the pre-growth period shall be accounted for, before characterizing each species. Plants were grown in this period without any modification of climate; thus, it is just the length of the period that differed. The period in early to high summer is important for arable perennial weeds, because they need to perform both shoot competition in dense crop stands as well as translocating nutrients into the vegetative survival organs. The longer the pre-growth period, the more below-ground dry mass was produced. It is an experimental weakness that different pre-growth periods in different years do not allow separating the two effects 'year' and 'pre-growth period'. However, the influence of the three pre-growth periods regarding dry mass partitioning is consistent (Figure 3).

To what extent the pre-growth period (PGP) triggers the plant growth in the experimental growth period (EGP) under the factor climate change is strongly species specific. The shorter the pregrowth period, the more above-ground growth was increased by the CT+ treatment relative to below-ground growth (decreased RS Ratio) in autumn for *E. repens* (Table 2), while for *S. arvensis* especially more DM Creeping R (and DM Below Ground and DM Plant) occurred at the CT+ treatment (Tables 2 and 4). In the settings of the experiments, it appeared that the length of pre-growth period was more important for autumn plant growth than the length and the conditions of experimental growth period. We speculate that these effects may have been more pronounced if the pre-growth period had happened under climate change, too.

Elymus repens is the only monocot of the three species. Compared to dicots, monocot plants have many shoots. The absolute leaf area and leaf biomass at ambient conditions were high throughout autumn. In our trial without competition, the growth of green leaves continued until the end of the experiment. At locations with warmer winters, as in the United Kingdom, E. repens shoots (green leaves) may even survive the winter (Palmer & Sagar, 1963). In colder climates, most of the above-ground biomass dies during winter (Håkansson, 1967). All above-ground parts of *E. repens* benefitted more equally from enhanced climate change conditions than the other two species. This species can grow and produce rhizomes as long as the temperature is above 5-6°C (Håkansson, 1969). However, in our study, rhizome dry mass and the whole below-ground part did not increase under climate change. Our interpretation of the observed growth pattern is that E. repens utilizes the altered autumn growth conditions to produce only a moderate amount of above-ground biomass which, however, was kept green without withering longer than the two other species.

Cirsium arvense responded to climate change in the leaf variables (Leaf Area, DM Leaves) and RS Ratio only. The response in the leaf variables was huge. In other studies, with future estimated CO₂ levels, plants established from seeds increased their biomass by 69% (Ziska, 2002), while in studies under field conditions, plants established from root fragments responded even more strongly: 2.5-3.3 times more below-ground parts and 1.2-1.4 times more shoots with elevated CO₂ (Ziska et al., 2004). In our study, we did not find such an effect in neither DM Below Ground nor in DM Above Ground. For optimal root growth, Tiley (2010) described this species as requiring 15°C. Our experiments met these temperatures; thus, the temperatures would have allowed for more reaction in the below-ground parts. Thomsen, Brandsæter, and Fykse (2013) found that C. arvense plants profited from an undisturbed root system but could stand disturbance as soon as the roots had reached a minimum depth. The root systems in the pots were not disturbed and could reach the full pot depth. Hence, we suspect that even under the ambient climate, the C. arvense plants in the experiments were enough prepared for the coming winter. Better conditions dramatically increased green leaves but were either not necessary or not usable for more below-ground growth.

Sonchus arvensis had the lowest levels of leaf area throughout the experiment; the species withered earlier than the other two (Tørresen et al., 2010). Benefits in above-ground leaves from climatic treatments (T+, CT+) were even greater than in *C. arvense*. Moreover, there was translocation into below-ground dry mass. Hence, *S. arvensis* seems to start preparations for winter earlier than the other two species. This is regulated by photoperiod and temperature, indicating that short photoperiod in combination with warmer autumns may suppress sprouting from root buds (Liew et al., 2012; Taab, Andersson, & Boström, 2018). According to Munné-Bosch (2008), the onset of withering of leaves is influenced by photoperiod. We speculate that higher temperature may slightly delay withering of leaves in *S. arvensis*. The summer growth

period (PGP) already influenced these processes with more leaves in autumn if the summer growth period has been short. More leaves mean that the plant can respond more to the climate change factors resulting in more translocation of assimilates into the below-ground parts as a result of climate change in autumn (CT+) and a short pre-growth period. The below-ground parts for the medium and long pre-growth periods were already much larger at the start of the experimental period in autumn and could already be prepared enough for winter. We assume more active preparations in *S. arvensis* for the next year, which make the reaction to the experimental factors more complex in this species than in the other two. Although *S. arvensis* responded most to the simulated climate change, the strong periodicity of the withering processes did not allow for direct and simple reaction in autumn growth.

Our results indicate short-term implications for arable farming: the small transfer of enhanced above-ground growth into below-ground growth under climate change in autumn does not favour creeping perennial plants per se. Reduced control of E. repens and C. arvense by glyphosate under elevated CO₂ is observed in other studies (Ziska et al., 2004, 2011; Ziska & Teasdale, 2000). For C. arvense, the reason for this could be that more roots were developed with elevated CO₂ causing a dilution of glyphosate. In our study, the root biomass was almost unaffected by elevated CO2-this can result in less effect on herbicide efficacy than observed by Ziska and co-workers. However, herbicide efficacy depends on various conditions, and different herbicides may cause different reactions (Patterson et al., 1999; Waryszak, Lenz, Leishman, & Downey, 2018; Ziska, 2016). Physical and chemical treatments will not necessarily become more difficult as climate change can give a longer time period in autumn suitable for both types of weed control (top part of Figure 1) and elevated temperatures during autumn may in general increase efficacy of herbicides. In autumn, more above-ground leaf biomass of perennials under climate change means bigger and hence more competitive perennial weeds. A following cover crop or main crop such as winter wheat in autumn can change above-ground growth via competition. However, it is very likely that the cover crop or main crop benefit in the same way as the perennial weed species under climate change (cf. winter wheat; Hanslin & Mortensen, 2010). So far it is unknown how the plants will react to various winter kill factors, and this may influence the overwintering of the species and hence the spread/competitive ability in the next year. Warmer winters may increase winter survival and distribution of perennial weeds (McDonald et al., 2009; Østrem, Folkestad, Solhaug, & Brandsæter, 2017).

Long-term implications for arable land use under climate change will be even more complex. All three species reacted positively to temperature for leaf area and leaf dry mass—measured on plant level. Longterm implications must consider the population level. In general, weeds can react to climate change through different processes and at different scales (Peters, Breitsameter, & Gerowitt, 2014). Range and niche shifts cannot occur in a pot experiment, as used in our study. Applying the concept of trait shifts to the perennials in our experiment is also crucial, because perennials stay the same plants before and after the simulated harvest. Perennials can become several years old without successful sexual reproduction and no obvious possibility to genetically adapt to - Global Change Biology -WILE

changing conditions. Hence, our experiments observed the scope of immediate reactions of plants, which indicate their future opportunities or necessities to perform trait shifts. Even without considering genetic adaptations, all three species will not suffer but profit under climate change, giving them a good position in the long-term race for resources on arable fields. At high latitude, we expect *E. repens* to profit most via longer growth in autumn. *C. arvense* is successful in most arable systems—under ambient current and elevated conditions. *S. arvensis* is a candidate to profit from climate change, but for fully understanding the complicated internal regulation of dormancy, sprouting and withering in this species further research are required.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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