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Caloric restriction-mediated reproductive lifespan extension across multiple strains of the clonal aquatic plant *Lemna turionifera*

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Lifespan extension due to caloric restriction (CR) is a well-established aspect of animal senescence that has been observed in many taxa. Contrastingly, there is much less evidence in plants, even though it is straightforward to manipulate CR by restricting photosynthesis through reduction in light intensity. One of the few studies to report CR-mediated plant lifespan extension investigated reproductive lifespan in a single strain of the duckweed *Lemna minor*, a tiny, floating, aquatic plant. Here, with an aim of beginning to test the generality of this phenomenon in plants, we considered a congeneric species, *L. turionifera*, and examined CR-mediated lifespan extension in eight strains collected from Alberta, Canada. We grew plants in the lab under axenic conditions, and manipulated light intensity (and hence, putatively, CR) with neutral density filters. Plants that grew under dimmer conditions had longer reproductive lifespans, on average, than those that grew under brighter conditions, consistent with CR-mediated lifespan extension. However, this came at the expense of a reduction in the capacity to contribute to population growth: plants in dimmer conditions produced about the same total offspring spread across their longer lifespans, leading to a reduced intrinsic rate of increase, measured at the level of the individual. Expanding the taxonomic scope of studies on CR-mediated lifespan extension – especially in plants – remains an important goal in senescence research.

Keywords: aging, caloric restriction, intra-specific variation, Lemnaceae, Lemnoideae, longevity

Introduction

In animals, calorie-restricted but non-starvation-level diets have been found to extend average lifespan in many taxa (McCay et al. 1935, Weindruch et al. 1986, Partridge et al. 2005; for recent reviews see Fontana et al. 2010, Hwangbo et al. 2020, Chmilar et al. 2024). Does an analogous phenomenon occur in plants? We assert that plants both have the opportunity to experience caloric restriction (CR), and that it is likely to promote their longevity. First, whereas animals predominantly acquire

calories heterotrophically (e.g., by ingestion), plants rely primarily on autotrophic processes – namely, photosynthesis. Thus, CR in plants could result from multiple environmental conditions that slow the photosynthetic process (Ferroni and Živčak 2023). Second, the main evolutionary and mechanistic theories that have been applied to CR-mediated lifespan extension – such as adaptive shifts in resource–allocation tradeoffs favouring somatic maintenance over reproduction (Kirkwood and Shanley 2005), and lower rates of collateral damage by reactive oxygen species (Walsh et al. 2014) – involve fundamental principles of life-history evolution and metabolism, and thus should apply to plants as well as animals. Investigating CR-mediated plant lifespan extension is our focus here.

Two recent studies have reported that CR extends plant lifespan in a pair of model species; both studies manipulated plants' capacity for photosynthesis by varying light intensity: 1) Minina et al. (2013) demonstrated CR-mediated lifespan extension in the terrestrial plant *Arabidopsis thaliana* (Brassicaceae). 2) Chmilar et al. (2024), focusing on reproductive lifespan, likewise demonstrated the phenomenon in the aquatic plant *Lemna minor* ('common duckweed'; Araceae or Lemnaceae; Landolt 1986, Sree et al. 2016). The comparative rarity of research dedicated to CR-mediated lifespan extension in plants versus animals reflects the situation in the wider program of senescence research (Salguero-Gómez et al. 2013; but see recent developments in Roach and Smith 2020). As a next step, studies focused on establishing the generality of CR-mediated plant lifespan extension are warranted.

Chmilar et al. (2024) used a single strain of *L. minor* (CPCC 492; Canadian Phycological Culture Centre, Waterloo, Canada), grew plants (i.e. ramets) individually in sterile conditions in petri dishes containing growth media, and manipulated light intensity using neutral-density filters. Here, we take a similar approach to investigate a congeneric species, *L. turionifera* ('turion duckweed'), using eight strains collected from locations across Alberta, Canada (Barks et al. 2018). Duckweeds' small stature, ease of culturing, and short lifespan (at the ramet level) make them an excellent model system in ecology and evolution in general (Laird and Barks 2018), and senescence research in particular (Ashby and Wangermann 1949, Claus 1972, Barks and Laird 2015), among other disciplines (Hillman 1976, Wang 1990, Cheng and Stomp 2009, Ziegler et al. 2016). They are therefore a sensible group in which to expand taxonomic coverage of the study of CR-mediated plant lifespan extension. In this study, we demonstrate that CR consistently increased reproductive lifespan across the *L. turionifera* strains examined.

Material and methods

Study species and strains

Lemna turionifera is a tiny, floating macrophyte found predominantly in North America and Eurasia (Landolt 1986). It reproduces mainly clonally (exclusively clonally in this experiment). Here we investigate CR-mediated reproductive lifespan extension in *L. turionifera* ramets. The eight *L. turionifera* strains' collection locations are given in Fig. 1 (original collection in 2013 from ponds and sloughs in Alberta, as reported by Barks et al. 2018; see the Supporting information for details about strain collection, stock cultures, species identification, and strain discrimination).

Initial steps and growing conditions

Fourteen plants from each strain (initial n = 112) were removed from their respective stock cultures and placed, individually, in axenic conditions in sterile petri dishes (nominal diameter × height = 60 × 15 mm; cat. no. 25384-090, Avantor Sciences, Allentown, PA, USA) containing 10 ml of quarter-strength (0.8 g l^{-1}) Schenk and Hildebrandt growth medium (cat. no. S6765, Sigma-Aldrich, St. Louis, MO, USA), the pH of which was adjusted to 4.6. The plants were randomly arrayed across four wire racks, 23.5 cm under a grow light (cat. no. FLT46, Agrobrite Hydrofarm, Petaluma, CA, USA; six 122 cm, 54 W, T5 HO fluorescent bulbs). The photoperiod was 15:9 (light:dark), matching that of Alberta in midsummer. The air temperature during the light and dark phases was 24°C and 22.5°C, respectively. The wire racks' positions were randomized daily throughout the experiment (except Sundays).

Acquisition of focal plants and final sample size

Plants taken from the stock cultures (P) were marked with a dot of dilute, autoclaved India ink and were observed daily (except Sundays) for reproduction (defined as having an offspring plant spontaneously detach). When they reproduced, the offspring plant (F1) was marked and retained, and the parent plant was discarded. In cases where there was more than one offspring plant, one was chosen randomly for retention. This process was repeated for a total of five times, with the last clonal descendant in each lineage (F5) used as a focal plant in the subsequent common garden experiment.

Some clonal lineages died out before producing a focal plant. The final sample size was n = 95. This was spread roughly evenly across seven of the strains, but was lower in the eighth (Prk C), which only had two samples per light treatment (see the Supporting information for details).

Experimental procedures

On the day they were discovered to have spontaneously detached from their parent, focal plants were transferred individually into smaller sterile petri dishes (nominal diameter × height = 35 × 10 mm; cat. no. 229683, Celltreat Scientific Products, Pepperell, USA) containing 4 ml of quarter-strength Schenk and Hildebrandt growth medium. To manipulate light intensity, these dishes were placed, individually, inside an outer container, the lid of which was the lid of a 60 mm petri dish (to which neutral density filters were affixed; LEE Filters) and the base of which was an opaque aluminum weigh boat (nominal diameter × height = 43 × 13 mm; cat. no. 087-32-105, Fisher Scientific) (see the Supporting information for details). The neutral density filters allowed two light

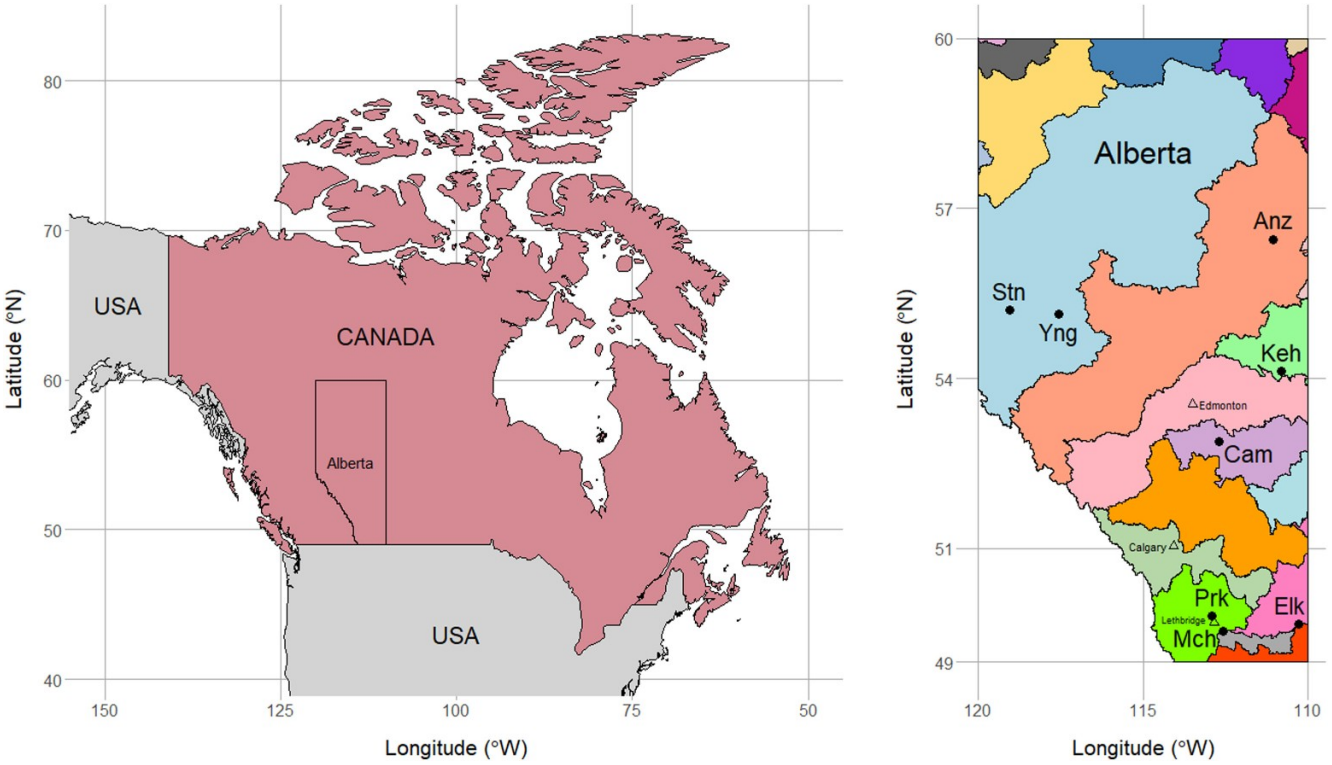

Figure 1. Collection sites (Anz, Cam, Elk, Keh, Mch, Prk, Stn, Yng) of the eight *L. turionifera* strains (Anz C, Cam C, Elk C, Keh C, Mch C, Prk C, Stn C, Yng C; additional details in the Supporting information). All sites (circles) are in Alberta, Canada. Watersheds of Alberta, as defined by Alberta Environment and Protected Areas (2018), are shown as the different regions in the right-hand map (contains information licensed under the Open Government Licence - Alberta). The cities of Calgary, Edmonton, and Lethbridge (triangles) are included for visual reference. The longest distance between a pair of sites (Anz and Mch) is 774 km; the shortest distance between a pair of sites (Mch and Prk) is 40 km.

intensities to be examined, full light (L_1) and quarter light ($L_{1/4}$); within each strain, half the focal plants were randomly assigned to each light intensity treatment. When measured through the set-up with a HOBO Microstation data-logger and PAR sensor (PAR = Photosynthetically Active Radiation; Hoskin Scientific), the PAR was 281 µmol m^{-2} s^{-1} for L_1 and 69 µmol m^{-2} s^{-1} for $L_{1/4}$. This reduction in PAR values represents a substantial decrease in light available for photosynthesis, which, according to previous studies, leads to a marked decline in relative growth rate in *L. turionifera* (Docauer 1983; see the Supporting information for details). Moreover, studies on other *Lemna* species indicate that photosynthetic carbon assimilation decreases linearly with decreasing PAR within this range of values (Miyashita et al. 2005). Thus, our L_1 and $L_{1/4}$ treatments are suitable for investigating the effects of CR. Each focal plant in its assembled outer and inner container assumed the spatial position that its clonal ancestors occupied during its acquisition.

Focal plants were observed daily for reproduction (except Sundays; see the Supporting information for our handling of the lack of Sunday data collection). Offspring were recorded and discarded. Focal plants were deemed to have died on the date that their last offspring detached, following a buffer period of two weeks with no new offspring. Thus, 'lifespan' in our study is equivalent to 'reproductive lifespan' (hereafter simply called 'lifespan').

Data analysis

Data analyses were performed in R ver. 4.4.0 (www.r-project.org). Data and code are available on Dryad (https://doi.org/10.5061/dryad.rv15dv4n7).

Lifespan was calculated for each focal plant as the number of days between the date the focal plant detached from its parent and the date the focal plant's last offspring detached, inclusive. Lifespan was then compared across light intensity treatments and strains – and their interaction – using a two-way ANOVA (*aov()* and *anova()* functions). Normality and homoscedasticity were assessed visually using a histogram and a normal quantile-quantile plot (*hist()* and *qqnorm()* functions). Following this assessment, lifespan was log-transformed to better meet the ANOVA assumptions (*log10()* function), and the test was repeated. In the case of a significant effect of strain, pairwise differences among strains were assessed using a Tukey–Kramer post hoc test (*TukeyHSD()* function).

Although lifespan extension was the primary focus of this study, the daily reproduction data that were used to pinpoint date of death also allowed us to calculate metrics related to plant performance, specifically total offspring production and the intrinsic rate of natural increase measured at the level of the individual (*r*; McGraw and Caswell 1996). The latter is calculated as the natural log of the leading eigenvalue of a Leslie matrix whose survival and reproduction elements

refer to a single focal plant (*log()* and *eigen()* functions). As with lifespan, total offspring production and r (again log-transformed) were compared across light intensity treatments and strains using two-way ANOVAs, with significant effects of strain followed-up with Tukey–Kramer post hoc tests.

Results

Effects of light intensity treatment and strain on log(lifespan)

Plants in the dim $L_{1/4}$ light intensity treatment experienced significantly longer lifespans (log-transformed) than plants in the bright L_1 treatment (Table 1a, Fig. 2A). The mean percent lifespan extension in the $L_{1/4}$ treatment ranged from 12.8% (Ync C) to 56.9% (Cam C) above the L_1 treatment (Fig. 2A), comparable to the degree of lifespan extension found in *L. minor* (46.6% and 27.1% in experiment 1 and 2, respectively, in Chmilar et al. 2024). There was no significant effect of strain on lifespan, nor a significant interaction between strain and light treatment (Table 1a, Fig. 2A).

Effects of light intensity treatment and strain on log(total offspring)

Strain had a significant effect on total number of offspring produced (log-transformed; Table 1b, Fig. 2B). However, there was no significant effect of light intensity treatment, nor a significant interactive effect of strain and light treatment (Table 1b, Fig. 2B). The strain differences were driven primarily by the Cam C strain, which produced a significantly lower total number of offspring than Anz C, Keh C, Mch C and Stn C (Fig. 2B). There were no other significant differences among strains.

Effects of light intensity treatment and strain on log(*r*)

Plants in the L_1 treatment had a significantly higher intrinsic rate of increase (log-transformed) than plants in the $L_{1/4}$ treatment (Table 1c, Fig. 2C). There was also a significant effect of strain (Table 1c, Fig. 2C), but no significant interactive effect of strain and light treatment (Table 1c, Fig. 2C). Once again, strain differences were driven primarily by the Cam C strain, which had a significantly lower intrinsic rate of increase than Anz C and Mch C (Fig. 2C). No other significant differences were found among strains.

Discussion

Effects of CR via variation in light intensity

This study provides evidence suggesting that CR via light restriction resulted in lifespan extension across multiple *L. turionifera* strains (Fig. 2A). Given the paucity of experiments on CR-mediated plant lifespan extension (Minina et al. 2013, Chmilar et al. 2024), studies like this one that investigate additional species and strains are needed. An important goal is to increase taxonomic coverage to the extent that phylogenetically informed comparative work is possible.

In addition to its effects on lifespan, we also found that CR reduced the intrinsic rate of increase of *L. turionifera* plants, measured at the level of the individual (Fig. 2C). As suggested elsewhere, this is due to a faster pace of life in plants grown in bright conditions, with similar offspring output (Fig. 2B) over shorter lifespans (Fig. 2A) (Chmilar et al. 2024). Faster growth in bright conditions is hardly surprising (Docauer 1983); more interesting is that light-induced variation in population growth appears to be driven more by reproductive timing rather than total output.

Strain differences

In none of our three response variables (log-transformed lifespan, total offspring, and intrinsic rate of increase) did we detect a significant interaction between light intensity treatment and strain (Table 1, Fig. 2). Thus, our results on the effects of light intensity appear to be consistent across strains – with the caveat that increased sample sizes, as well as

Table 1. Two-way ANOVA results for the interactive effects of *L. turionifera* strain (STRAIN) and light intensity treatment (LIGHT) on (a) log(lifespan (days)), (b) log(total offspring), and (c) log(*r*). *p ≤ 0.05.

Response variable	Source of variation	df	Sum of squares	Mean square	F	p
(a) log(lifespan (days))	STRAIN	7	0.164	0.023	0.923	0.493
	LIGHT	1	0.402	0.402	15.857	0.000151*
	STRAIN × LIGHT	7	0.123	0.018	0.695	0.676
	ERROR	79	2.001	0.025		
	TOTAL	94	2.689			
(b) log(total offspring)	STRAIN	7	0.579	0.083	3.977	0.000902*
	LIGHT	1	0.004	0.004	0.174	0.678
	STRAIN × LIGHT	7	0.254	0.036	1.748	0.110
	ERROR	79	1.643	0.021		
	TOTAL	94	2.480			
(c) log(*r*)	STRAIN	7	0.454	0.065	3.825	0.00126*
	LIGHT	1	0.262	0.262	15.481	0.000178*
	STRAIN × LIGHT	7	0.187	0.027	1.574	0.155
	ERROR	79	1.339	0.017		
	TOTAL	94	2.241			

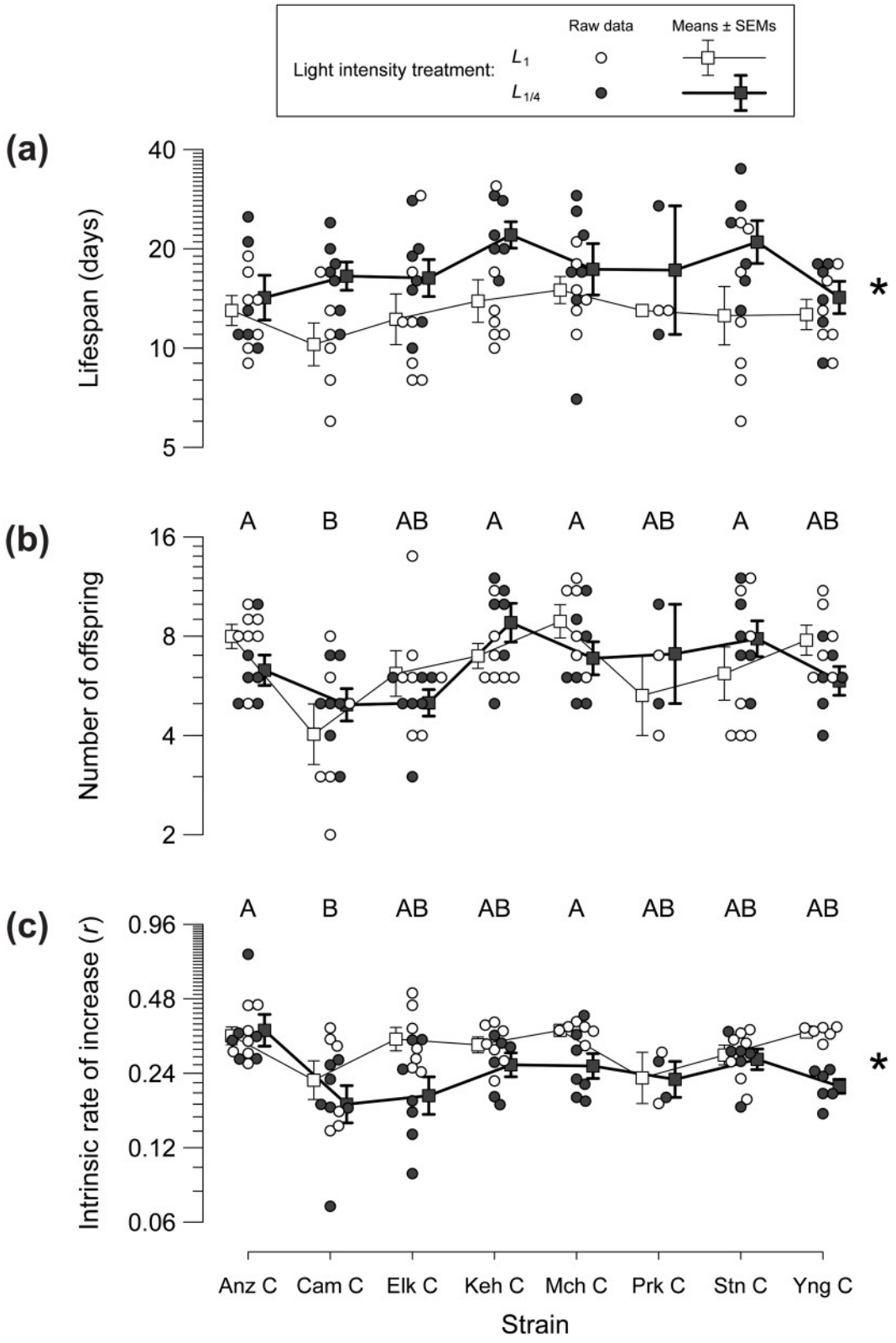

Figure 2. Interactive effects of strain and light treatment on (A) lifespan, (B) total number of offspring, and (C) intrinsic rate of natural increase, measured at the level of the individual (r). Note the logarithmic vertical axes – in (A) and (B), the minor ticks have an interval of 1; in (C), the minor ticks have an interval of 0.02. White symbols represent the full light treatment (L_1); dark grey symbols represent the quarter-light treatment ($L_{1/4}$). Circles represent the raw data, deflected horizontally – when necessary – to prevent symbol overlap; squares with error bars represent the means ± SEM (determined from log-transformed response variables and then back-transformed), also deflected

Figure 2. Continued.

horizontally to prevent symbol overlap. In cases with very small SEM, the error bars are hidden behind the symbols. For visual reference, the squares are connected with thin lines for the L_1 treatment and thick lines for the $L_{1/4}$ treatment. The total sample size was n = 95 (see the Supporting information for treatment-specific sample sizes). Letters at the top of (B) and (C) indicate significant differences among strains; strains that share a common letter are not significantly different, and those that do not share a common letter are significantly different. Asterisks to the right-hand side of (A) and (C) indicate significant differences between light intensity treatments.

including additional strains/species and environmental conditions, may reveal more nuanced findings. In any case, the strains themselves did differ, at least in terms of number of offspring (Table 1b, Fig. 2B) and intrinsic rate of increase (Table 1c, Fig. 2C). This is consistent with Barks et al. (2018) where several trait differences were reported among strains grown under common garden conditions.

Speculations: the potential impact of strain availability

Of the 27 strains of *L. turionifera* originally collected in 2013 and used in the common garden experiment of Barks et al. (2018), only 14 remained alive by September 2024 when the current study commenced (we used eight). This substantial reduction was likely non-random – the surviving strains were probably those best-suited to lab conditions. Along similar lines, we have made anecdotal observations that 1) there is considerable variation in the ease with which different strains can be kept alive in the lab; and 2) strains acquired from repositories (e.g. Canadian Phycological Culture Centre; Rutgers Duckweed Stock Cooperative), some of which have been cultured for decades, typically outperform recently collected strains. Some authors have hypothesized that CR-mediated lifespan extension is an effect of domestication, and primarily occurs in lab organisms (Le Bourg 2010, Nakagawa et al. 2012, Adler and Bonduriansky 2014). Although this domestication hypothesis is currently aimed at animals, in duckweed it could take the following form:

- If fast reproduction and population growth favour ease-of-culture and persistence of lab strains, then those strains that are naturally fast growing may become overrepresented in lab collections.
- Given a trade-off between reproduction and ramet lifespan (e.g. due to resource allocation constraints limiting resources for both rapid reproduction and somatic maintenance), these fast-reproducing domesticated strains – composed of short-lived individuals – may have greater scope for lifespan extension under conditions that slow reproduction (e.g. CR).

Could our 11-year-old lab strains be among those most amenable to domestication, and therefore overestimate the magnitude – though not necessarily the existence or prevalence – of CR-mediated lifespan extension? Future studies investigating lifespan extension and growth rate in wild versus domesticated strains of duckweed could help resolve this speculative question.

Conclusions and future directions

Our study is among the few suggesting CR-mediated lifespan extension in plants, and it therefore helps expand our knowledge of what appears to be a fundamental aspect of senescence. This is particularly relevant given the extensive use of duckweeds as a model system for population-level senescence. More broadly, our work contributes to wider goals of 1) remedying the general bias of senescence research towards animals over plants (Salguero-Gómez et al. 2013), and 2) integrating intrinsic (e.g. genetic) and extrinsic (e.g. environmental) sources of variation in aging research (Monaghan et al. 2008).

In addition to the aforementioned needs to expand taxonomic coverage of CR-mediated lifespan extension, and to compare wild versus domesticated strains, we consider the following as priorities for future studies:

- *Solidifying the link between light intensity reduction and CR*. Although our light intensity treatments should be expected to reduce photosynthetic carbon assimilation and thus lead to CR (Miyashita et al. 2005), studies directly investigating this link within the context of lifespan extension would be highly valuable.
- *Tracking CR-induced changes in plants on a molecular level*. Here, we have focused on coarse-scale endpoints of CR – namely its effect on plant lifespan, total reproduction, and intrinsic rate of increase at the level of the individual. Connecting these outcomes with specific molecular mechanisms (e.g. the roles of reactive oxygen species (Arora et al. 2002) and the TOR (target of rapamycin) signaling pathway (Loewith and Hall 2011)) would help move this line of research from identifying patterns to understanding processes.
- *Extending CR studies from the lab to the natural environment*. Lab-based research provides essential control, but testing whether and how CR-mediated lifespan extension occurs in field conditions is crucial for understanding its ecological relevance and evolutionary significance.

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Author contributions

Julian A. Ketler: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (lead); Methodology (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (supporting). **Nicola M. Herman**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Investigation (lead); Methodology (equal); Software (supporting); Validation (equal); Visualization (supporting); Writing – review and editing (supporting). **Suzanne L. Chmilar**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Investigation (supporting); Methodology (lead); Project administration (supporting); Software (equal); Supervision (lead); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (supporting). **Robert A. Laird**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Methodology (lead); Project administration (lead); Resources (lead); Software (equal); Supervision (lead); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rv15dv4n7 (Ketler et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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