

RESEARCH ARTICLE

Functional Ecology



Spenders versus savers: Climate-induced carbon allocation trade-offs in a recently introduced woody plant

Randall W. Long¹ | Tom L. Dudley² | Carla M. D'Antonio¹ | Kevin C. Grady³ | Susan E. Bush⁴ | Kevin R. Hultine⁴

¹Department of Ecology, Evolution and Marine Biology, University of California-Santa Barbara, Santa Barbara, CA, USA

²Marine Science Institute, University of California-Santa Barbara, Santa Barbara, CA, USA

³School of Forestry, Northern Arizona University, Flagstaff, AZ, USA

⁴Department of Research, Conservation and Collections, Desert Botanical Garden, Phoenix, AZ, USA

Correspondence

Randall W. Long
Email: rlong@holdenfg.org

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Abstract

1. Non-structural carbohydrate (NSC) storage may be under strong selection in woody plant species that occur across broad environmental gradients. We therefore investigated carbon (C) allocation strategies in a widespread non-native woody plant, *Tamarix*. We predicted that genotypes with exposure to episodic freeze events would show elevated NSC concentrations compared to warm-adapted genotypes with the trade-off of reduced growth and reproduction relative to warm-adapted populations.
2. We established an experimental common garden using genotypes of *Tamarix*, sourced across a strong thermal gradient within the introduced range. We measured seasonal NSC storage in coarse roots and stems, above-ground growth and flower production.
3. Autumn NSC concentrations were 50% higher in genotypes from sites with episodic spring freeze events compared to genotypes from warmer sites. These cold-adapted genotypes also had a 2.3-fold higher starch to soluble sugar ratio than warm-adapted genotypes. Across all genotypes and seasons, NSC storage was inversely correlated with growth and reproduction.
4. Results suggest that *Tamarix* from colder locations cope with freeze events by maintaining large storage pools to support tissue regrowth, but with the trade-off of overall reduced growth and reproduction. Our results are consistent with rapid selection in C allocation strategies in response to climate in introduced woody species.

KEYWORDS

experimental common garden, local adaptation, non-structural carbohydrates, plant starch concentrations, *Tamarix chinensis* × *ramosissima* (saltcedar), temperature gradients

1 | INTRODUCTION

Plant economic theory predicts that plants are under selection to maximize individual fitness by allocating limited resources to competing energetic demands of growth, reproduction and storage (Bloom et al., 1985; Hinman & Fridley, 2018). If so, long-lived plant species that are exposed to frequent and predictable events that

remove biomass but do not result in mortality should exhibit a more conservative growth strategy by actively allocating a higher percentage of their overall carbon (C) gain to non-structural carbohydrate (NSC) stores, which serve as reserves in perennial woody plant species (Clarke et al., 2013; Hudgeons et al., 2007; Kozłowski, 1992). This 'bank account' (of NSCs) can facilitate recovery after tissue loss, and should be larger in populations that are exposed to more

frequent sublethal disturbances that do not result in mortality (Iwasa & Kubo, 1997; Long et al., 2017). Thus, cyclical disturbances that remove live biomass are likely a selective force that results in intraspecific variation in relative C allocation to storage rather than competing pools (e.g. growth, reproduction) across a single species.

Populations exposed to late-winter or spring cold temperatures are at risk from two different, potentially damaging or lethal, phenomena. The first risk is cell death in newly grown tissues due to freezing temperatures shortly after leaf flush (Sakai & Larcher, 1987). The second is the risk of freeze-thaw cavitation in xylem tissue (Pockman & Sperry, 1997; Rodrigo, 2000; Sperry & Sullivan, 1992). Low temperature events should select for genotypes that allocate a high percentage of photosynthate to C storage relative to other C pools for multiple reasons including (a) plants can mobilize NSC from storage pools in the roots or woody stems for regrowth following dieback of sensitive above-ground tissues (Clarke et al., 2013), (b) soluble sugars in xylem sap reduce the risk of cavitation by lowering the freezing point (Regier et al., 2009) and (c) NSCs could be used in reversing cavitation from freeze-thaw events through phloem unloading of sugars or for growth of new xylem after cavitation (Lintunen et al., 2016; Nardini et al., 2011; Secchi & Zwieniecki, 2012). Alternatively, populations from arid sites where freeze events are rare or absent could accumulate NSC, specifically as soluble sugars to maintain high osmotic pressure to prevent turgor loss during high temperature/low moisture conditions (Bartlett et al., 2014; O'Brien et al., 2014).

There is debate as to whether plants actively allocate C to storage for later use or if accumulation of NSC is a passive process (Bloom et al., 1985; Chapin et al., 1990; Hartmann & Trumbore, 2016; Hoch et al., 2002; Korner, 2003), and reviews and syntheses have indicated that the regulation of C storage processes is not well-understood (Furze et al., 2019; Hartmann et al., 2018; Sala et al., 2012). Regardless of regulation mechanisms and/or potential constraints on C uptake, increased C allocation to labile storage should result in fitness trade-offs because C that is stored is not readily available for other immediate uses such as growth, reproduction or defence (Baker, 1974; Bloom et al., 1985; Chapin et al., 1990; Long et al., 2017). Some studies have categorized species as either C 'savers' or 'spenders', depending on relative C storage (Hinman & Fridley, 2018). 'Spender' species are those exhibiting higher than average growth and/or reproduction and lower total NSC concentrations, while 'savers' preferentially allocate C to storage (NSC) at the expense of the other uses.

We established a common garden using different populations of a widely distributed, introduced woody plant, *Tamarix*, to evaluate if a trade-off was detectable between spending and storage. Although invasive plants often have higher growth and/or photosynthetic rates than native species and would be broadly categorized as 'spenders', some invaders have been found to have higher storage of NSCs in the spring compared to natives (Hinman & Fridley, 2018). Further, some invasive species occur across wide environmental conditions so selection could be divergent for saving versus spending depending on the environment. Here we tested if the trade-off

between saving and spending was influenced by local environmental conditions in populations sourced across a broad environmental gradient to evaluate the patterns of local adaptation in C allocation strategy (Blumstein & Hopkins, 2020; Chaney et al., 2017; Lazarus et al., 2019; Richardson et al., 2014). Studies on intraspecific variation in C allocation strategies among perennial populations are rare (but see Blumstein et al., 2020; Oleksyn et al., 2000), especially for invasive species, potentially due to the logistical difficulties and high expense of establishing trials for long-lived woody plant taxa (Wiley & Helliker, 2012).

The *Tamarix* species complex in North America, comprised of at least five species and their hybrids, spread rapidly after its introduction in the 1800s and now occupies a wide range of environments throughout riverine systems and wetlands in the American West (Baum, 1978). This invasion is predominately composed of *T. chinensis*, *T. ramosissima*, their F1 hybrids and subsequent backcrosses (Gaskin & Schaal, 2002). Hybrid individuals in their introduced range dominate riparian environments from low-elevation deserts that experience extreme mid-summer heat and aridity, to high-elevation locations with harsh winters and late-spring freeze events (Friedman et al., 2008). This broad climate distribution provides a compelling model system for studying within-species variation in C allocation across environmental gradients, since many recently introduced plant species with large geographic extents often exhibit high local genetic variation and/or phenotypic plasticity (Liao et al., 2016; Oduor et al., 2016). Some of the expressed phenotypic diversity may be due to the hybridization of *Tamarix* species, as introgression rates have been found to be influenced by large latitudinal gradients and river network in the western United States (Lee et al., 2018; Williams et al., 2014). However, these studies did not find evidence for introgression gradients to exist over elevation gradients or small latitudinal ranges, and Lee et al., 2018 found that variation within a watershed was less than it was within populations. Using populations of *Tamarix* collected from the Colorado River basin, we established a common garden experiment to test for inter-population variation related to C allocation strategies in the *T. chinensis* × *T. ramosissima* hybrid complex (hereafter referred to as *Tamarix*) in its introduced range. Variation in plant traits that vary predictably across this environmental gradient would provide strong evidence of selection in this dominant, widely distributed taxon.

In this study, we addressed the following questions: (1) Is there evidence for inter-population variation in NSC storage?; (2) is this variation among populations consistent with an allocation trade-off towards growth or reproduction?; and (3) is this variation correlated with more frequent exposure to extreme temperatures? We tested the hypothesis that labile C storage, as simple sugars or starch as opposed to hemicellulose, would increase with sublethal disturbance potential (due to freezing or cold stress) of source populations, but with the trade-off of reduced allocation to growth and reproduction. This overarching hypothesis gives rise to two inter-related predictions: (a) strong trade-offs will be detected in C allocation strategies such that plants with high above-ground growth rates and reproductive yields (e.g. flower production) will

consequently have seasonally lower tissue concentrations of NSC, and (b) genotypes sourced from cold climates that are regularly exposed to early growing season freeze events will display higher NSC storage in their stems particularly during the winter when storage becomes important for producing new tissues especially after unexpected freeze events.

2 | MATERIALS AND METHODS

2.1 | Common garden site and provenances

A *Tamarix* common garden was established in April 2015 in Yuma, AZ (lat. 32.6151°N, long. -114.6365°W, elev. 60 m) at the University of Arizona Mesa Facility, within the southern extent of its distribution in North America (Figure S1). The site is a former agricultural field that was fallow for several years prior to the study and was tilled and levelled to facilitate evenly applied flood irrigation. Soils were classified by the National Resource Conservation Service as 'superstition sand' comprised of approximately 95% sand and 5% clay, the area around Yuma is classified as cambisol soils by the Food and Agricultural Organizations (World Reference Base 2015). The climate is typically hot, with dry summers interrupted by rare monsoonal precipitation, and cool wetter winters. Climate means for the garden, as well as population source locations (hereafter *provenance sites*), are provided in Table 1. *Tamarix* cuttings were collected from provenance sites throughout Arizona and SE Utah (Figure 1). Sites were selected to represent an elevational gradient (45–1,791 m), which was a proxy for both minimum (range: -7.6–6.3°C) and maximum temperatures (range: 32.4–42.4°C; Table 1). Precipitation at the collection sites varied from 90 to 449 mm (Table 1). However, because *Tamarix* is associated with riverine areas and wetlands, collected genotypes were located within riparian terraces and presumably had continuous access to groundwater.

We collected cuttings, each approximately 15–20 cm long and 2–4 cm in diameter, from 16 individuals from each of the nine populations in fall 2014. The nine populations were selected to represent an elevation gradient, generally representing low (45–82 m), mid (135–1,017 m) and high (1,077–1,791 m) elevation zones. This represented a testable range for measuring foliage and flowering phenology, labile C storage and biomass accumulation. Cuttings were treated with root hormone and grown in a vermiculite/perlite potting mix in 328-cm³ pots at the Northern Arizona University greenhouse facility in Flagstaff, Arizona. Populations were planted in a randomized block design, with each population being represented once in eight blocks (*n* = 8). For each population replicate, each of the 16 individuals was assigned a random location in a 4 × 4 planting arrangement with 2 m spacing between plants (Figure S1). Although eight blocks were available at the common garden, we used only a subset of the blocks to sample due to time and cost constraints. We also selected a subset of three populations for more intense seasonal monitoring of NSC storage, including one population each from a high-, mid- and low-elevation site. Hereafter we will refer to this subset as focal populations (*P_f*) when only these three were used in sampling and use the term garden populations (*P_g*) when referring to sampling that included all nine provenance sites (Figure 1; Tables 1; Table S1).

2.2 | Carbon saving: Non-structural carbohydrates

We sampled the stem and root tissues in the *P_g* individuals in the spring and fall to assess relationships between provenance site and NSC concentrations across populations. Six individuals were randomly selected from three different blocks for NSC analysis and were sampled on 26 May and 21 October 2016 (*n* = 18 for each population, Table S1). For the seasonal sampling of *P_f*, collections occurred in one of the three blocks used in the *P_g* sampling

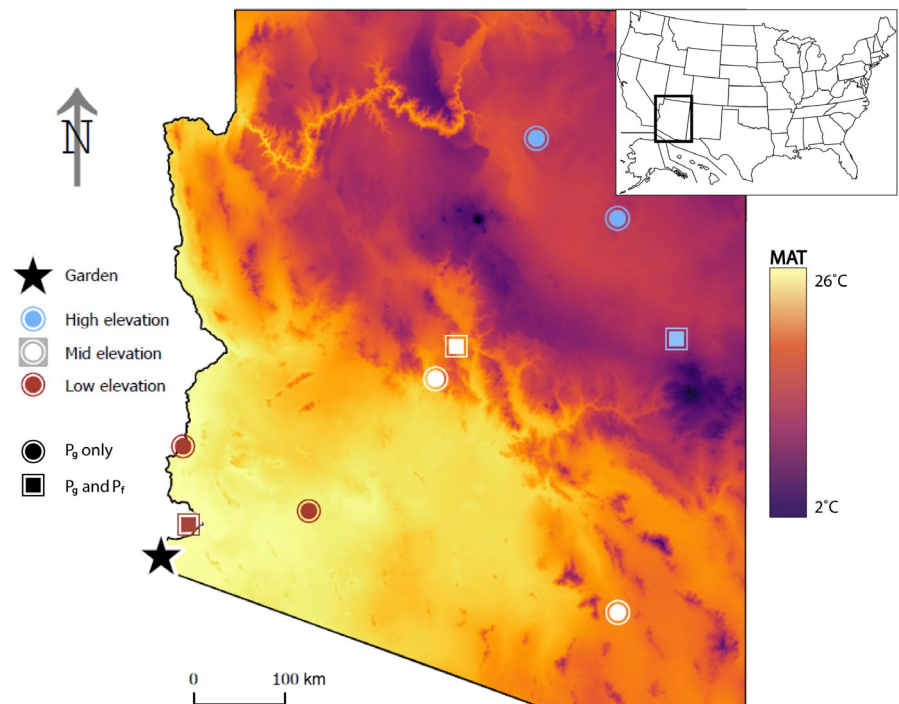
TABLE 1 Origin of *Tamarix* source populations for the common garden in Yuma, AZ. Source population sites are ordered from low-to-high elevation. Weather data were collected from the PRISM Climate Group, Oregon State University (<http://prism.oregonstate.edu>, created 10 January 2018)

Name	Elevation (m)	Minimum temperature (°C)	Maximum temperature (°C)	Annual precipitation (mm)	Longitude	Latitude	Elevation group
CYM ^b	45	6.3	41.7	90	-114.485	32.823	Low
Garden ^a	58	6.1	41.5	86	-114.636	32.615	N/A
CBL	82	5.6	42.4	101	-114.536	33.595	Low
GAC	135	4.1	41.7	124	-113.305	32.962	Low
VRD ^b	943	-1.9	38.0	332	-111.856	34.573	Mid
CAF	1,017	1.3	36.6	449	-112.063	34.257	Mid
BEN	1,077	0.1	36.3	348	-110.279	31.968	Mid
HNT ^b	1,654	-6.4	33.3	247	-109.706	34.648	High
KKA	1,747	-6.4	34.2	213	-111.076	36.612	High
KKH	1,791	-7.6	32.4	216	-110.282	35.828	High

^aCommon garden site.

^bFocal populations.

FIGURE 1 Distribution of the nine 'garden' population (P_g) sources used in the *Tamarix* common garden study. Focal populations (P_f) are indicated by squares. The common garden was in Yuma, AZ, indicated by the star. Inset indicates the location of Arizona within the United States. Map colours represent mean annual temperature variation across Arizona. Source: Esri. 'USA Mean Temperature' [basemap]. 'USA Mean Temperature'. 20 September 2018: https://landscape3.arcgis.com/arcgis/rest/services/USA_Mean_Temperature/ImageServer. (downloaded 18 November 2019)



and used the same eight individuals throughout the sampling period ($n = 8$ for each population, Table S1). The stem and root tissues from P_f (Figure 1) were collected on 26 May (Spring), 22 July (summer) and 21 October 2016 (fall) and 26 February 2017 (winter). Temperature ranges for the collection dates were as follows: spring 16–31°C, summer 31–45°C, fall 21–36°C and winter 12–21°C (Figure S2). Total precipitation between 1 March 2016 and 1 March 2017 was 86.9 mm, and all plots were flood irrigated to supplement precipitation and maintain soil moisture. At the start of first sampling for NSCs, the trees were over 2 m tall (SF1). The mature second-year stem samples (7–12 mm diameter, 3–5 cm length) were collected at breast height (1.37 m above soil surface), and coarse root tissue samples (5–10 mm diameter, 3–5 cm length) were collected by excavating roots from the soil at a depth range of 10–15 cm within 25 cm from the tree base. Three roots and stem samples were collected from each individual and pooled together for analysis, using the entire collected sample including bark and cambial layers.

For the NSC analysis, we used the methods adapted from Quentin et al. (2015). Samples were placed on dry ice immediately after excising from the tree and microwaved within 24 hr to prevent enzymatic degradation. Samples were then oven-dried at 60°C for 48 hr and kept in a freezer (–20°C) until they were prepared for extractions. Samples were first coarse ground with a #20 mesh Wiley Mini-Mill (Thomas Scientific), and then fine ground with a dental amalgamator (Wig-L-Bug, Dentsply Rinn). A subsample of 50 mg (± 1.5 mg) was used for extractions with the final weight recorded. For every 10th sample, a second subsample was taken for quality control in addition to using glucose (Sigma-Aldrich G7528) and starch (Sigma-Aldrich S5926Fluka) laboratory standards. The laboratory standards for starch and glucose were used to verify that our

methods were robust (quantified concentration = $-1.70 + 1.08 \times \text{actual concentration}$, $r^2 = 0.94$, $F_{1,25} = 336.4$, $p < 0.001$) by mixing the two to achieve a total of 50 mg (± 1.5 mg) at various ratios ranging from absent to 100% of either standard. Across our subsample duplicates, we found little variation in final concentrations for sugar (mean errors 0.74%, SE = 1.67) or starch (0.067%, SE = 1.79), indicating that adequate homogenization of samples had been achieved. Low molecular weight sugars were extracted using 80% ethanol in an 85°C water bath. After being centrifuged, the supernatant was removed and saved for later analysis; this process of extraction was repeated three times. Total soluble sugars were quantified using a phenol-sulfuric acid reaction to determine the relative sugar concentration by quantifying at 490 nm (Chow & Landhäusser, 2004). Any remaining ethanol after the third extraction was evaporated and an enzymatic digestion using alpha-amylase and amyglucosidase was used to degrade starches into glucose. The glucose concentration was quantified using the peroxidase-glucose oxidase/o-diansidine enzyme method at 525 nm (Chow & Landhäusser, 2004). The glucose concentration per unit dry mass was equivalent to the starch concentration in the sample.

Many factors can cause non-systemic errors in NSC measurements, including matrix effects of woody plant material and secondary metabolites, as well as other pools of C storage not accounted for in our extraction methods (e.g. hemicellulose or lipids), and some soluble sugars measured may not be readily available (Germino, 2015; Quentin et al., 2015). We minimized these potential errors by using starch, glucose and internal standards to test for reproducibility of data. Differences in secondary metabolites should also have been minimized by using only one species and growing all of the populations in the common garden with similar environmental conditions. Further, secondary metabolites in *Tamarix* were not found to vary

across a broad latitudinal gradient of source populations in a similar common garden study (Hussey et al., 2011).

2.3 | Relative risk of freeze events

We used the risk of freeze events as a predictor of C allocation. We defined freeze events as any day between 1 January and 1 June when the minimum temperature was below 0°C and the maximum temperature from the proceeding day was above 0°C. We chose 1 January as the start date to emphasize the importance of freeze events as plants become metabolically active as dormancy breaks and would be exposed to potentially damaging temperatures via freeze–thaw or cell death of new growth. To determine the number of events where temperatures would rise above, and then drop below the freezing point, we interpolated daily maximum and minimum temperatures from 1992 to 2012 for all P_g sites using data from the PRISM Climate Group, Oregon State University (<http://prism.oregonstate.edu>, created 10 January 2018). The freeze–thaw risk of each site was calculated as the mean number of total freeze events at a given site divided by the mean number of events at the site with the highest number of freeze events (42.2 events). This metric allowed us to compare relative risks across sites as a proportion of the highest risk sites.

2.4 | Carbon spending: Reproduction and growth

2.4.1 | Phenology and reproductive output

The *Tamarix* hybrid complex in the North America is a deciduous group that has shown differences in timing of spring flowering and leaf flush and across its introduced range, as well as in common gardens (Friedman et al., 2011; Long et al., 2017). Bimonthly spring phenological observations were made from February 2016 until June 2016 on 12 individual plants from three randomly selected blocks of each of the P_g genotypes, and included those individuals sampled for the NSC monitoring. *Tamarix* has small (<2 mm), perfect (bisexual) flowers that are on secondary racemes, each supporting an average of 50–60 flowers although some can support as many as 750,000 flowers on a single individual (Andersen & Nelson, 2013; Gaskin & Schaal, 2002; Warren & Turner, 1975). Due to this high number of flowers per plant, reproductive output was evaluated by estimating the number of flowering racemes on each individual during each measurement period. Measurements were calibrated during each sampling event for each population by estimating the area that would represent 100 racemes and then counting each raceme within that area for six different individuals. If there was a discrepancy of greater than $\pm 10\%$ between the estimation and actual number of racemes, then the area was recalibrated.

We also recorded the progression of canopy development during the spring of 2016 by assigning the canopy a greenness score ranging from 0 to 4 (0 = dormant, 1 = any green expanding tissue present, 2 = most of buds expanding, 3 = fully expanded leaves

and 4 = full canopy). In the fall, we documented the progression from green to yellow or senesced foliage every 3 weeks, using a percentage of canopy as yellow or senesced from October 2016 until January 2017 on the same individuals used for spring phenology measurements.

2.4.2 | Basal area and canopy volume

The basal area on the same six individuals used for NSC analysis from each P_g was measured in three different blocks ($n = 18$ for each population) to determine basal area mean growth increments of each population during the growing season. Initial measurements were taken in late spring (25 May 2016) and again in the fall (25 October 2016). All stem diameters were measured with a caliper at 10 cm above the soil surface to determine the basal area (A_b). Due to irregular stem shapes, two measurements were taken at orthogonal directions from each other and area was calculated as an ellipse. Three representative stems on each individual were selected for repeat measurements and marked with paint pens at 10 cm above the ground surface so that they could be remeasured at the same points. Mean basal area increment was calculated for each population from the measurements at each of the three stems. Basal area increments (BAI; mm^2/day) were calculated according to Lambers et al. (2008), where A_{bf} is the final measured basal area, A_{bi} is the initial basal area and d is the number of days between A_{bf} and A_{bi} :

$$\text{BAI} = \frac{A_{bf} - A_{bi}}{d}. \quad (1)$$

Canopy volume was measured on 25 May 2016 for the same individuals used for basal area and NSC sampling ($n = 18$ for each P_g) by measuring the width of the trees at their widest point and the corresponding orthogonal width. The canopy volume (Vol_{can} ; m^3) was calculated using the radii of two widths (W_1 and W_2) and the max height (H) of the tree and the formula for the volume of ellipse.

$$\text{Vol}_{\text{can}} = \frac{(4\pi)(H)(W_1)(W_2)}{3}. \quad (2)$$

2.5 | Statistical analyses

Relationships were analysed using linear regressions and factorial ANOVAs. All comparisons done with factorial ANOVAs were followed by Tukey's Honestly Significant Difference post hoc analysis using the STAT package in R (R Core Team, 2017). The spring phenology was analysed using a repeated-measures MANOVA using the nlme package in R (Pinheiro et al., 2017) to account for measurements completed on the same individuals during the sampling period by assigning observation date as an error term. Version 1.1.423 of RStudio was used for all analyses. Log transformations were used for visualization in figures when differences between sample means were an order of magnitude or greater.

We used the scale function in the *stats* package (R Core Team, 2017) to determine z-scores of individual plants compared to the garden mean for reproduction (total racemes), growth (canopy volume and total basal area) and storage (total NSC in stems collected in the fall). This allowed us to compare spending and storage by adding together growth and reproduction, the two different components of spending, into an aggregated spending score. The scale function generated z-scores by determining how many standard deviations an individual genotype was from the garden mean of each trait. The stems that had been collected in the fall were selected to represent storage since we predicted higher storage of NSCs in the stems to provide adequate carbohydrates to fuel regrowth after spring freeze events.

3 | RESULTS

3.1 | Carbon saving

Among the three P_t , NSC levels were dynamic throughout the year, but the total concentrations of NSC (soluble sugars plus starch)

of the high and mid-elevation population were higher in the root tissue than in the stems across all seasons (Figure 2). In the roots, there were significant differences among populations ($F_{6,104} = 5.21$, $p < 0.001$, Figure 2B), and a post hoc analysis revealed that NSC levels in the high and the mid-elevation population were greater than those from the low-elevation population in the fall ($p < 0.001$ for both). In fact, high-elevation root concentrations in the fall ($M = 176 \text{ mg/g}$, $SE = 6.35$) were nearly twice as high as those found in low-elevation roots ($M = 90.14 \text{ mg/g}$, $SE = 11.49$). The high-elevation population also had greater concentrations of NSC than the low-elevation populations in winter ($p = 0.003$). Similarly, we found significant differences across the seasons and populations in the stems ($F_{6,104} = 2.65$, $p = 0.021$, Figure 2A), but a post hoc analysis revealed these patterns were driven by differences between the mid and low-elevation populations in the fall ($p < 0.001$). We also found the time of year affected the composition of the NSC pool. In the stems, there was a significant change in the composition ($F_{3,182} = 169.65$, $p < 0.001$, Figure 3A), which was driven by a shift from soluble sugars to starch from summer to fall. The roots also showed a significant interaction between season and pool

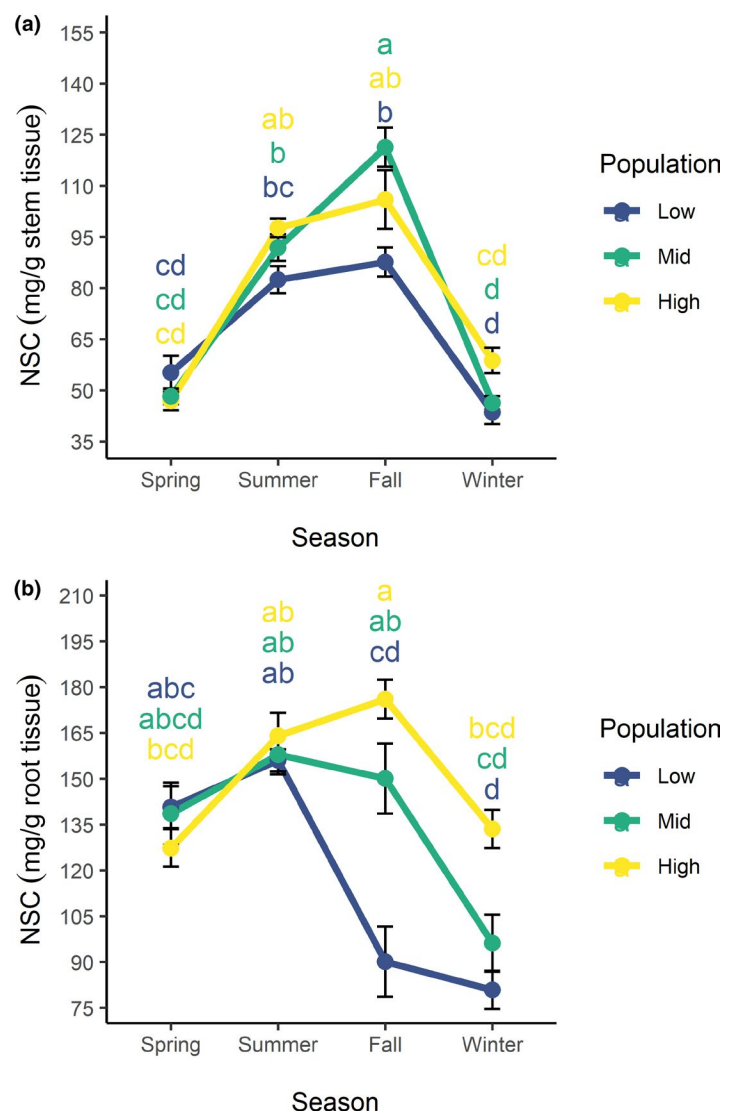


FIGURE 2 Seasonal dynamics of non-structural carbohydrate (NSC) concentrations in *Tamarix* occurring in an experimental common garden. Total concentrations of NSC were measured as total extracted sugars and starch in the stems (A) and roots (B) from focal populations (P_t) representing low, mid and high-elevations ($n = 8$ for each tissue \times date \times elevation source). Error bars represent the $\pm SE$ of the means. Letters denote significant groups identified by a post hoc Tukey's HSD analysis across all elevation groups and seasons, and are colour-coded to match the elevation groups

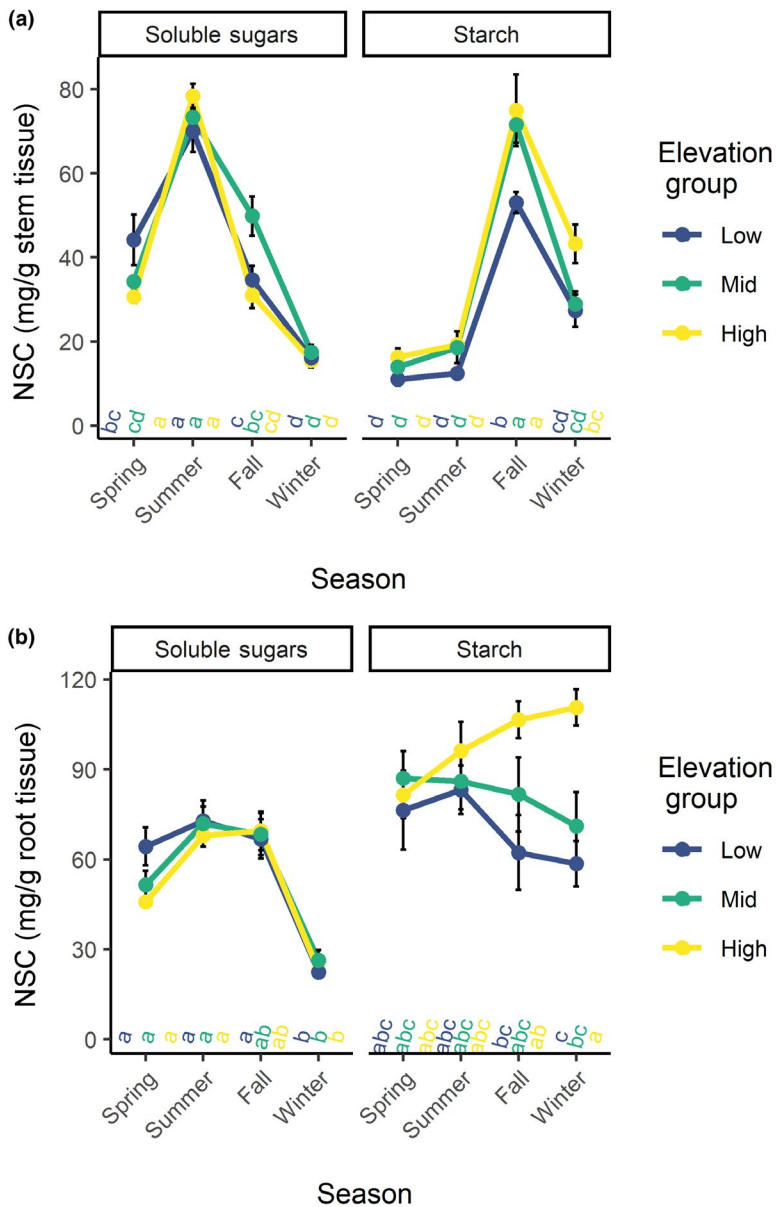


FIGURE 3 Concentrations of individual pools of starch and soluble sugars measured separately for both the stems (A) and roots (B) in *Tamarix* occurring in an experimental common garden. Three focal populations (P_f) representing low, mid and high-elevations were analysed over one growing season ($n = 8$ for each tissue \times date \times elevation source). Error bars represent the $\pm SE$ of the means. Letters denote significant groups identified by a post hoc Tukey's HSD analysis, where the letters are significant groups across all elevation groups and seasons, but within the separate pools

($F_{3,182} = 12.37$, $p < 0.001$, Figure 3B), but lacked the marked shift in allocation from sugars to starch.

The highest risk site based on the PRISM climate data had an average of 42.2 freeze-thaw days between January and June when the minimum temperature dropped below 0°C at night after being above 0°C during the day. Across the nine provenance sites for the P_g , none of the low-elevation sites were at risk of exposure to freeze events, while mid-elevations had a low risk relative to the coldest site (0.07–0.19) and high-elevation sites had the highest risk (0.64–1.00). For all populations, we observed that the risk of freeze events at the provenance site was positively related to NSC storage in the fall stems (Figure 4A), both as total NSC (total NSC = $103.64 + 24.78 \times \text{relative risk}$, $r^2 = 0.48$, $F_{1,7} = 6.50$, $p = 0.038$) and starch (total starch = $64.75 + 21.47 \times \text{relative risk}$, $r^2 = 0.61$, $F_{1,7} = 10.75$, $p = 0.014$). We observed a similar, but slightly weaker, trend in the fall root tissue for total NSC (Figure 4B, Total NSC = $130.58 + 41.34 \times \text{relative risk}$, $r^2 = 0.34$, $F_{1,7} = 3.6$, $p = 0.099$).

The ratios of starch to extracted sugars in the three P_f were found to vary across tissues, sampling date and population source ($F_{6,219} = 4.02$, $p < 0.001$, Figure 5). The highest starch to sugar ratio was found in the roots of the high-elevation population (10.39:1) and lowest in the stems of the low-elevation populations during the summer (0.092:1). No differences were detected between tissues and source populations during the spring and summer, but differences were found in the fall and winter. In the fall, the high-elevation population had a significantly higher ratio of starch to soluble sugars in both the roots and stems compared to the low-elevation population (Tukey's HSD $p < 0.0001$ and $p = 0.022$ respectively). During the winter, there were no differences found in the stem tissue, but in the roots the high-elevation genotypes had a marginally higher ratio than the mid-elevation population, and a significantly higher ratio than the low-elevation population (Tukey's HSD $p = 0.10$ and $p = 0.003$ respectively).

FIGURE 4 Relationship between non-structural carbohydrates in the fall stems (A) and roots (B) and the risk of freeze events in *Tamarix* genotypes sourced across a broad climatic gradient. Non-structural carbohydrates were measured as total starch and water-soluble sugars in the fall in the stems of nine populations (P_t) and compared to the relative risk of freeze-thaw events. Relative risk of freeze-thaw was defined as the frequency of freeze-thaw events divided by the greatest number of events experienced at the coldest site. Different populations within elevation groups are denoted by shapes, and are the same in all graphs. Points are the means of samples, which were pooled samples of six individual genotypes from three different blocks ($n = 18$) within the common garden, plotted with the linear regression and 95% confidence interval

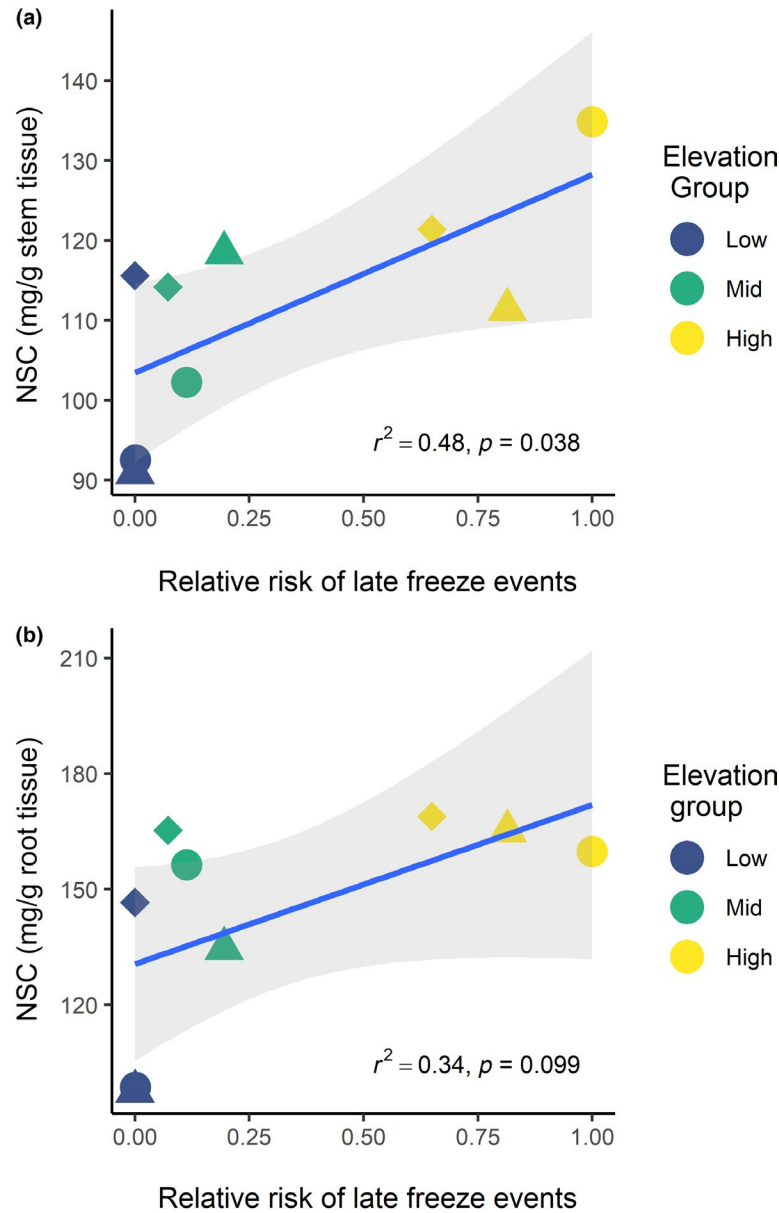
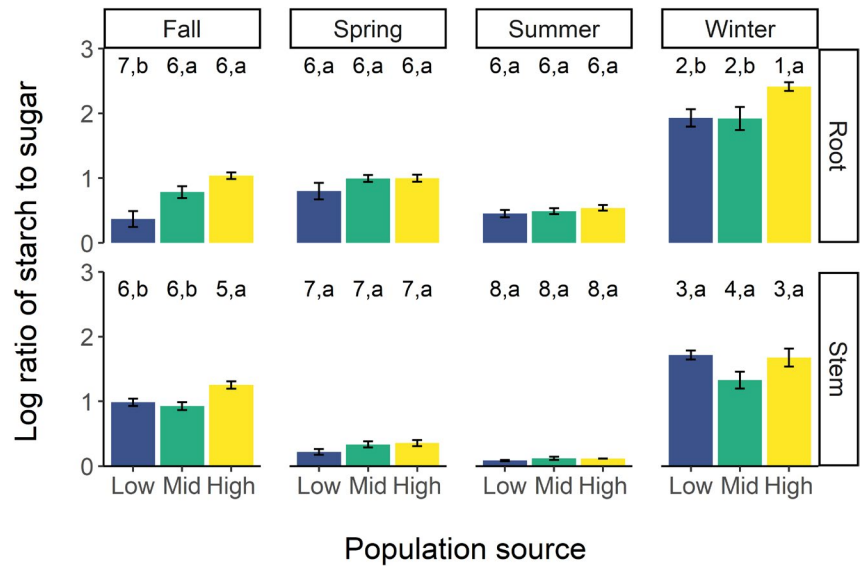


FIGURE 5 Log ratio of starch to sugar of root and stem tissue ($n = 8$ for each tissue \times elevation source) in *Tamarix* genotypes sourced across a broad climate gradient. Higher starch to sugar ratios indicates increased allocation to long-term storage. Error bars are \pm SE of the means, and letters and numbers indicate significant groups identified by a post hoc Tukey's HSD analysis. Numbers are the groupings across all tissue sampling and dates, and letters are the results from within a date and tissue. Log ratios have been used for visualization purposes only



3.2 | Carbon spending

3.2.1 | Phenology and reproductive output

Flowering differed considerably over the spring among P_g source elevations ($F_{18,135} = 3.8$, $p < 0.0001$, Figure 6A). Most notably, the average peak number of racemes of the low-elevation populations was substantially higher than the other elevation groups ($p < 0.0001$) but not between mid and high elevations. During our initial measurements, we noted that the number and size of flowers did not vary much across populations and fell within previously reported values for *Tamarix* by Andersen and Nelson (2013). Peak flowering dates were 5 March, 2 April and 19 March for low, mid and high elevations respectively. At their respective peak flowering, low-elevation populations ($M = 922$, $SE = 175$) had more than four times the number of racemes than the high-elevation populations ($M = 200$, $SE = 30.7$). There was also a significant

difference between elevation groups in total racemes produced per individual over the full study period from 4 February to 11 June 2016 (ANOVA $F_{2,356} = 22.04$, $p < 0.001$). Unlike NSC accumulation, there was no relationship between the number of racemes produced and the risk of freeze events at the provenance site (Figure 6B).

When phenology measurements began in the first week of February (4 February), we noted that some genotypes in the low-elevation and mid-elevation groups had already started to flush out. The low-elevation populations had mean greenness score of 0.96 ± 0.15 , indicating that on average all individuals had some green expanding tissue, while the mid-elevation populations had a score of 0.55 ± 0.12 . The mid and high elevation populations were not on average above a score of 1 until measurements on 20 February and 5 March respectively. In the fall, all populations progressed from green to yellow or senesced foliage until late December, at which point the high and mid-populations became fully senesced, while

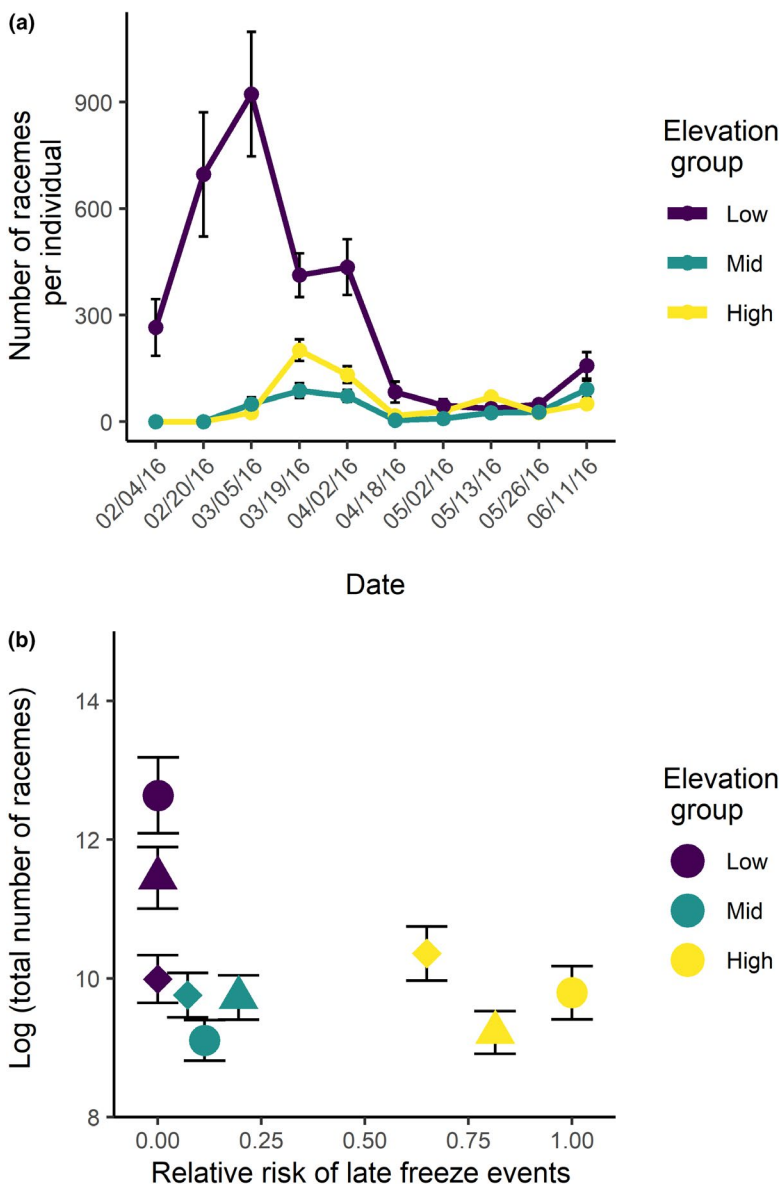


FIGURE 6 Reproductive output of *Tamarix* populations from different elevation groups. (A) Seasonal dynamics of reproductive output for low, mid and high-elevation groups. Each point represents the mean of all individual genotypes observed for the three different populations per elevation groups ($n = 144$ per elevation). Error bars represent the $\pm SE$ of the means. The same individuals were measured at each of the time points. (B) The log-transformed (for visualization purposes) total reproductive output from 4 February to 11 June 2016 for all nine populations. Colours are the elevation groups and shapes are different populations within groups. Points are the means of samples, which were pooled samples of 12 individual genotypes from three different blocks ($n = 36$) within the common garden, error bars represent the $\pm SE$ of the means

the low-elevation populations maintained a low level of green foliage. We did not track these individuals into spring 2017, but it was observed in 2016 that the low-elevation populations were deciduous and shed the previous year's foliage when current year's growth flushed.

3.2.2 | Basal area and canopy volume

Although there was a negative trend with some growth measurements and risk of exposure to freeze events, relative risk was not a significant predictor. Specifically, there was no relationship between the risk of freeze events and both spring basal area (Figure S3) and canopy volume (Figure S4a). BAI also showed no relationship with relative risk (Figure S4b).

3.3 | Trade-offs in carbon allocation

To visualize the trade-offs between saving and spending of C, we developed a comparison of normalized scores encompassing growth, reproduction and labile C storage (see Section 2). Generating z-scores allowed us to sum the normalized values of the different 'spender' metrics (i.e. canopy volume, basal area and raceme production) into one variable to compare to storage. Although our method of using normalized scores does not consider the relative C costs of the different pools, it allowed us to evaluate how allocation was prioritized by comparing individual scores to the average values of all the populations. Since we only studied *Tamarix*, the C costs of specific tissues (e.g. flowers) should be similar across all genotypes. We

found the saver z-score was a predictor of the average of the spender z-scores (spender z-score = $-0.057 - \text{storage z-score} \times 1.14$, $F_{1,7} = 16.07$, $r^2 = 0.70$, $p = 0.0051$, Figure 7). The strategy exhibited by the different populations can be described by which quadrant they occupy in a Cartesian plane (Figure 7). Populations occupying quadrant II were defined as spenders since they have positive spending scores and negative saver scores; while those in quadrant IV were classified as savers since they exhibit the opposite scores. Populations in quadrant III could still be considered spenders since they had less than average saver scores, assuming there is some spender category that we did not account for in our analysis (e.g. herbivore defence, Herms & Mattson Jr., 1992). Quadrant I could only be occupied by populations that had higher than average spending and saving rates, none of our population means existed in this space, but a few individual genotypes did. In our study system, high-elevation populations all occupied the saver space of the coordinate plane, while mid and low populations were found in spender quadrants.

4 | DISCUSSION

Using a common garden design, we detected considerable differences among populations in allocation to NSC pools that was predicted by the source population's exposure to freeze risk. Specifically, populations from colder environments allocated more C to storage, and had reduced C allocation to growth and/or reproduction. The variation in the degree of allocating C to storage instead of growth/reproduction may help to explain the widespread success of *Tamarix*, and other woody deciduous species, across broad climatic

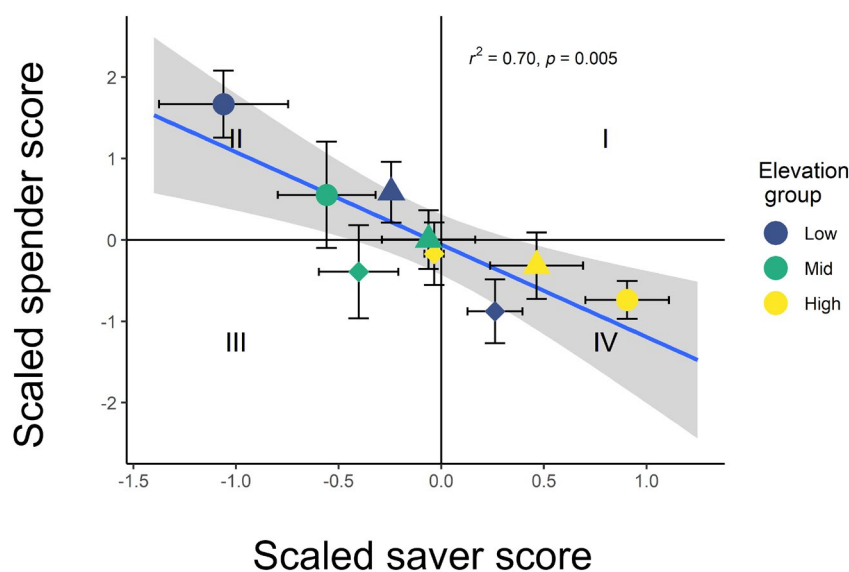


FIGURE 7 Individual measurements for saving and spending were scaled by assigning z-scores compared to the global mean of *Tamarix* genotypes sourced across a broad climate gradient. Colours are the elevations of provenance sites and shapes are elevation groups. Spender score was derived from the total NSC in the fall stems, an indication of winter storage pool, while spender score is the sum of z-scores derived from the total numbers of racemes produced from February to June 2016 and the canopy volume and basal areas measured on 25 May 2016. Populations in quadrant II represent spender populations (negative storage z-score and positive spender z-score) and populations in quadrant IV are considered saver populations. Error bars represent the \pm SE of the means ($n = 18$ per population)

gradients as populations adapt to local stressors (Alexander, 2013; Gleason & Ares, 2004). More broadly, these results highlight the possible importance of active NSC accumulation at the cost of reduced growth and/or reproduction in long-lived woody taxa.

4.1 | Carbon saving: Non-structural carbohydrates

All *Tamarix* genotypes showed an accumulation of NSC in the fall that is consistent with patterns found in many winter deciduous species that accumulate or translocate carbohydrates in storage organs prior to foliage senescence (Furze et al., 2019; Hoch et al., 2003; Hultine et al., 2015; Martinez-Vilalta et al., 2016). In addition, we observed that the risk of freeze events at the provenance site was positively related to NSC storage in both the roots and stems in the fall, with greater accumulation in freeze-adapted populations (Figure 4). This was consistent with our prediction that genotypes from cold environments would maintain higher NSC concentrations, primarily as starch. These patterns are also consistent with the hypothesis that cold-adapted plants have been selected to store labile C as insurance in response to freezes or other related canopy dieback events (Charrier & Ameglio, 2011; Clarke et al., 2013; Hudgeons et al., 2007; Pratt et al., 2014). Likewise, populations of *Tamarix* from colder northern latitudes have been shown to maintain higher root to shoot ratios than those from warmer southern locations (Sexton et al., 2002; Williams et al., 2014). Similarly, genotypes from the coldest location in the present study had root area to leaf ratios that were at least 100% higher than non-freeze-adapted genotypes (Bush et al., 2021), potentially amplifying the already higher per-dry mass NSC concentrations in freeze-adapted genotypes.

Maintaining a high NSC storage may decrease mortality from sublethal disturbance events and/or facilitate rapid recovery following tissue damage (Dietze et al., 2014; Hultine et al., 2021; Long et al., 2017). A greater storage of NSC in the stems as well as roots could also be adaptive in high-elevation genotypes to minimize freeze-thaw cavitation events, despite the risk of lost NSCs in stems due to breakage during the winter. The localized storage of NSC could provide osmotic gradients that are necessary to refill embolized xylem vessels, specifically when starch stored in xylem-associated tissue (parenchyma) is degraded to simple sugars and loaded into the embolized xylem (Brodersen et al., 2010; Hartmann & Trumbore, 2016; Nardini et al., 2011). Although it is unclear which responses or mechanisms (e.g. regrowth, tissue repair, osmotic regulation or starch accumulation in cells) may be driving selection in our study system, the differences in the ratio of starch to simple sugars across the provenance sites may highlight the different adaptive uses of NSC for regrowth versus osmotic regulation in relation to seasonal temperature variations.

During the growing season (spring, summer, fall) we detected lower ratios of starch to sugars, where osmotically active NSC (i.e. soluble sugars) can play an important role in osmotic regulation and drought tolerance at the cellular and tissue level (Regier et al., 2009). Compared to a recent synthesis on the dynamics of

NSCs in terrestrial plants (Martinez-Vilalta et al., 2016), *Tamarix* showed an atypical pattern of having larger relative pools of soluble sugars during the summer (Figure 3A,B) rather than in the winter as found in most temperate and boreal plants. In all of our study populations, the ratio of starch to sugars decreased by nearly an order of magnitude from winter to summer, indicating that osmoregulation to maintain cell turgor against drought or heat may be more important for *Tamarix* than it is against freezing, at least at low elevations like our common garden site where freezing is rare. These results do not conflict with the observed higher total allocation to NSC, specifically as starch which is osmotically neutral, in genotypes exposed to freeze-related disturbances or stressors in their source environments, as the larger NSC pool may provide energy for regrowth rather than osmo-protection.

No differences in C storage were detected among populations in the spring. The results in the spring, however, are complicated by variation in phenology among the populations, with net C uptake occurring after early season use of stored NSC to support spring growth of photosynthetic tissues (Furze et al., 2019; Richardson et al., 2013). Compared to mid and high-elevation populations, leaf flush and flower production occurred earlier in the spring in low-elevation populations, triggering earlier photosynthetic C gain and greater sink strength (Long et al., 2017). Low-elevation populations were more than 50% foliated by early March, 2 months before the spring NSC collection period (Figure S5). Those populations were likely no longer depleting their NSC reserves, but rather were actively acquiring C which may explain the convergence of NSC concentrations among populations in May. Furthermore, some genotypes from the low-elevation sites never fully entered dormancy and instead maintained a small amount of green photosynthetic tissues throughout the winter only shedding those leaves as new leaves flushed, as opposed to the mid and high elevation genotypes that had all fully senesced by December (Figure S6). This seasonal pattern is likely why reductions in NSC concentrations were smaller from the fall to winter in the low-elevation populations than those from colder provenance sites.

Whether contrasts in labile C storage among populations were a consequence of active regulation of C allocation or of passive regulation related to seasonal changes in source-sink relationships is unclear. One approach to evaluate contrasts between active versus passive labile C regulation is to compare the seasonal patterns of growth and NSC storage (Bansal & Germino, 2008; Dietze et al., 2014). In the present study, NSC storage increased from spring to summer in the stems and roots, although to a lesser extent in the roots. During the summer, all of the plants had full canopies and growth and whole-plant respiration effluxes were most likely near peak rates. These patterns, therefore, provide evidence that the observed patterns of NSC storage were likely governed by active regulation. However, we cannot rule out the possibility that NSC storage was a passive process related to population-level contrasts in foliage phenology and subsequent contrasts in source-sink relationships, or from downregulation of growth in response to extreme summer temperatures (Sala et al., 2012). Nevertheless, passive labile

C regulation would still be under strong selection given the tight coupling between source-sink relationships with leaf senescence and coupling between the timing of senescence and local adaptation to the arrival of autumn freeze events.

4.2 | Carbon spending

4.2.1 | Flowering phenology, basal area and canopy volume

Spring flowering differed among the low, mid and high-elevation populations, but unlike NSC accumulation, there was no significant relationship between the number of racemes produced and the risk of freeze events at a given provenance site or between freeze risk and growth patterns measured in the common garden (Figure 6; Figures S3 and S4). It is of note that our low-elevation populations had the highest number of racemes, although we may not have seen the similar pattern if our common garden had been located at a high-elevation site. Despite this caveat, these results highlight an apparent trade-off between growth and reproduction in our experiment. If the populations from the low-elevation sites were producing more flowers due only to a home site advantage, then we should have found larger canopies and a greater number of racemes. This was not what was found within the populations from low freeze risk sites at our garden, where the population with the highest reproductive output had the lowest mean canopy volume among populations. We had expected to find the strongest trade-off between NSC storage and growth/reproduction as C is allocated to the various competing pools (Chapin et al., 1990; Dietze et al., 2014; Hartmann & Trumbore, 2016; Kozłowski, 1992), but we detected strong trade-offs between growth and reproduction, which have also been detected in other studies (Banuelos & Obeso, 2004; Capelli et al., 2016; Climent et al., 2008; Obeso, 2002). This provides one plausible explanation for why growth and phenology were not correlated at the population level, and genotypes from low elevations tended to have a relatively high growth rate or reproductive output, but rarely both.

4.3 | Trade-offs between labile carbon storage, growth and reproduction

Broadly, selection for savers could be a result of regular exposure to sublethal, episodic disturbance that results in the loss of above-ground tissues. Plants that are confronted with regular tissue damage from spring frost events, for example, benefit from having a 'bank account' of labile C to regularly rebuild tissues (Iwasa & Kubo, 1997). Alternatively, high concentrations of NSC could be associated with osmotically reducing the freezing point of living cells and xylem tissues (Greer et al., 2000), or competition at low-elevation sites could be selecting for plants that allocate more resources to growth (Chapin et al., 1987). In the present study, high-elevation populations occupied the saver space of the coordinate plane, while all but one

mid and low populations were found in spender quadrants (Figure 7). This supports the hypothesis that populations from sites exposed to more frequent sublethal disturbances would preferentially store labile C (Bloom et al., 1985; Dietze et al., 2014; Hinman & Fridley, 2018; Long et al., 2017). Specifically, we found that the amount of labile C storage was highest at locations with more frequent exposure to freeze events with reduced commitment to above-ground growth and/or reproduction.

Closing a whole-plant C budget and thus evaluating trade-offs between NSC storage and growth in mature woody plants is challenging for several reasons. One challenge is quantifying the below-ground allocation, particularly in deeply rooted taxa such as *Tamarix*. A separate study using the same common garden as our study found that high-elevation genotypes had considerably higher fine root area than mid- and low-elevation genotypes (Bush et al., 2021). As a consequence, trade-offs between NSC storage and whole-plant growth may either be suppressed or amplified relative to trade-offs associated with above-ground growth, depending on seasonal NSC storage in coarse roots, which we found to be generally higher than in stems. Likewise, the strength of C allocation trade-offs is, in part, dependent on the capacity of photosynthetic tissues to deliver photosynthates to various sinks. Previous common garden studies have shown that large intraspecific differences in net photosynthesis can emerge among populations (Grady et al., 2011; Kaluthota et al., 2015; Zhang et al., 1993), and an earlier study conducted at the same *Tamarix* common garden revealed that maximum net photosynthetic rates in mid-June were 42% higher in low-elevation genotypes relative to high-elevation genotypes (Long et al., 2017). Given that low-elevation genotypes had generally larger canopies and maintained significantly longer growing seasons, it is plausible that low-elevation genotypes were operating with a substantially larger pool size of photosynthates. However, despite the potentially larger pool size, the low-elevation genotypes maintained lower NSC concentrations throughout the year relative to their high-elevation counterparts, illustrating potential selection pressures to prioritize labile C storage over growth in freeze-adapted genotypes.

5 | CONCLUSIONS

We found strong evidence for local adaptation in *Tamarix*, with different populations displaying 'saver' or 'spender' strategies for C storage. Genotypes exposed to higher frequency of freeze events maintained higher stores of NSC than those from areas with less frequent freeze events when grown together in a common garden. The strategy of allocating greater resources to storage when stressful conditions are likely has been reported among plant communities across large taxonomic scales (Hinman & Fridley, 2018), but our study reveals that these patterns are predictable within species that span broad environmental gradients. The relatively short duration of site occupation by *Tamarix* in the western United States suggests that these physiological tactics can evolve over a

small number of generations. The introduction of multiple *Tamarix* species and subsequent hybridization, along with high rates of gene flow, has produced a massive hybrid swarm in North America with high genetic and apparent phenotypic diversity (Gaskin & Schaal, 2002; Lee et al., 2018; Long, D'Antonio, et al., 2021). These factors combined with strong gradients in climate, late freeze disturbances and large reproduction output (more than 750,000 flowers per individual during peak reproduction events, Andersen & Nelson, 2013) set the stage for rapid population differentiation in expressed physiological traits related to C allocation. Indeed, *Tamarix* appears to show similar levels of local adaptation as dominant co-occurring native woody species in expressed traits such as cold hardiness and foliage phenology (Friedman et al., 2008). The extent that individual *Tamarix* genotypes are 'savers' and 'spenders' may affect their resilience to increased cyclical disturbance events such as freezing, fire and/or herbivory that remove foliage but may not result in immediate mortality. However, increased resilience via greater allocation to storage is likely to co-occur with decreased allocation to growth and/or reproduction as a result of predicted trade-offs between competing pools. Although caution should be taken when implying adaptive significance to results collected from a single common garden with no reciprocal plantings in other climates, these results add to the growing body of evidence that C allocation strategies are under strong selection.

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AUTHORS' CONTRIBUTIONS

K.C.G., S.E.B., T.L.D., C.M.D. and K.R.H. designed the common garden; R.W.L. and K.R.H. designed the study; R.W.L. collected and analysed the samples and data; R.W.L. wrote the manuscript, and all the authors contributed to revisions.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.25349/D9RW3G> (Long, Dudley, et al., 2021).

ORCID

Randall W. Long  <https://orcid.org/0000-0001-9308-9996>

Tom L. Dudley  <https://orcid.org/0000-0002-3838-2230>

Carla M. D'Antonio  <https://orcid.org/0000-0002-0395-9650>

Kevin C. Grady  <https://orcid.org/0000-0003-3929-2461>

Kevin R. Hultine  <https://orcid.org/0000-0001-9747-6037>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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