

1 Introduction

Plant economic theory predicts that plants are under selection to maximize individual fitness by allocating limited resources to competing pools of growth, reproduction, and storage (Bloom, Chapin & Mooney 1985; Hinman & Fridley 2018). If so, plant populations that are exposed to frequent and predictable resource limitations or disturbances, should exhibit a more conservative growth strategy by actively allocating a higher percentage of their overall carbon gain (C) to non-structural carbohydrate (NSC) storage, rather than competing pools, relative to populations that are exposed to less frequent disturbances or resource limitations (Iwasa and Kubo 1997; Long et al. 2017). Cyclical disturbances that remove live biomass are likely a selective force that results in intraspecific variation in C allocation strategies across a single species. NSC reserves in perennial woody plant species can act as a ‘bank account’ to assist recovery/compensation after tissue loss (Kozlowski 1992; Hudgeons *et al.* 2007; Clarke *et al.* 2013). Common garden experiments using populations sourced across broad environmental gradients can be used to evaluate patterns of local adaptation (Richardson *et al.* 2014; Chaney, Richardson & Germino 2017; Lazarus, Germino & Richardson 2019), and in some cases selection within recently introduced species that result in variable C allocation patterns in response to climate.

Populations exposed to late-winter or spring cold temperatures are at risk from two different, potentially lethal, phenomena. The first risk is cell death in newly grown tissues due to freezing temperatures shortly after leaf flush. The second is the risk of freeze-thaw cavitation in xylem tissue (Sperry & Sullivan 1992; Pockman & Sperry 1997; Rodrigo 2000). These stressors should select for genotypes that are active C savers, rather than spenders. Allocation of a high percentage of photosynthate to C storage relative to other C pools could be adaptive because 1)

plants can mobilize NSC from storage pools in roots or woody stems for regrowth following dieback of sensitive aboveground tissues (Clarke *et al.* 2013), 2) soluble sugars in xylem sap reduce the risk of cavitation by lowering the freezing point (Regier *et al.* 2009) and 3) NSC could be used in reversing cavitation from freeze-thaw events through phloem loading of sugars or for growth of new xylem after cavitation (Nardini, Lo Gullo & Salleo 2011; Secchi & Zwieniecki 2012; Lintunen, Paljakka, Jyske, Peltoniemi & Sterck 2016). Conversely, populations from more arid sites where freeze events are rare or absent could also 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, Leuzinger, Philipson, Tay & Hector 2014). Studies on intraspecific variation in C allocation strategies among perennial populations are rare (but see 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).

Regardless of potential constraints on carbon uptake, increased C allocation to labile storage should result in fitness tradeoffs because C that is stored is not readily available for other immediate uses such as growth, reproduction, or defense (Baker 1974; Bloom *et al.* 1985; Chapin, Schulze & Mooney 1990; Long *et al.* 2017). There is however, some 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; Hoch, Popp & Körner 2002; Körner 2003; Hartmann & Trumbore 2016). Reviews and syntheses have indicated that the regulation of C storage processes is not well understood (Sala, Woodruff & Meinzer 2012; Furze *et al.* 2018; Hartmann *et al.* 2018), but some studies have categorized species as either carbon 'savers' or 'spenders' (Hinman & Fridley 2018). 'Spender' species are those exhibiting higher than average

growth and/or reproduction and lower total NSC concentrations, while ‘savers’ preferentially allocate carbon to storage (NSC) at the expense of the other uses. Although invasive plants are often considered to have higher growth rates and would be broadly categorized as ‘spenders’, Hinman and Fridley (2018) found that this was not a safe assumption: in their seasonal system some invaders had higher storage of NSCs in the spring compared to natives.

The *Tamarix* species complex in North America, comprised of 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. This invasion is predominately by *T. chinensis*, *T. ramosissima*, their F1 hybrids, and subsequent backcrosses (Gaskin & Schaal 2002). Hybrid individuals dominate low elevation desert riparian environments in their introduced range that experience extreme mid-summer heat and aridity, as well as high elevation riparian areas with harsh winters and late-spring freeze events (Friedman, Roelle, Gaskin, Pepper & Manhart 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, D’Antonio, Chen, Huang & Peng 2016; Oduor, Leimu, van Kleunen & Mack 2016). Using the large variation in climate conditions across the introduced range of *Tamarix*, we established a common garden experiment to test for interpopulation variation related to C allocation strategies in the *T. chinensis* X *T. ramosissima* hybrid complex (hereafter referred to as *Tamarix*). Heritable variation in plant traits that vary predictably across an 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 interpopulation variation in NSC storage? (2) is this variation among populations consistent with an allocation tradeoff towards growth or reproduction? and (3) is this variation correlated with exposure to either freezing temperatures or thermal stress? We tested the hypothesis that labile carbon storage, as simple sugars or starch as opposed to hemicellulose, would increase with environmental stress potential (freezing or cold stress) of source populations, but with the tradeoff of reduced allocation to growth and reproduction. Our overarching hypothesis gives rise to three inter-related predictions: 1) strong tradeoffs will be detected in C allocation strategies such that plants with high above ground growth rates and reproductive yields (i.e. flower production) will consequently have seasonally lower tissue concentrations of NSC, 2) genotypes sourced from cold climates that are regularly exposed to early growing season freeze events will display higher NSC storage in their stems, and 3) genotypes from low elevations will allocate a higher percentage of their labile carbon pool to soluble sugar during the growing season (spring, summer, fall), as opposed to osmotically neutral starch molecules, to maintain cell turgor through osmotic regulation as a consequence of local adaptation to thermal stress.

Materials and Methods

Common garden site and provenances

A *Tamarix* common garden was established 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 distribution of *Tamarix* in North America (Fig. 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 are classified by the National Resource Conservation Service as

“superstition sand” comprised of approximately 95% sand, and 5% clay. 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 (hereafter, *provenance sites*) locations, are provided in Table 1. *Tamarix* cuttings were collected from provenance sites throughout Arizona and SE Utah (Fig. 1). Sites were selected to represent an elevational gradient (45 – 1791 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 mm 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. 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 prior. Populations were planted in a randomized block design, with each population being represented once in eight blocks for a total of eight replications. For each population replicate, each of the 16 individuals were assigned a random location in a 4 x 4 planting arrangement with 2 m spacing between plants (Supplemental Fig 1). These populations, hereafter called P_g (garden populations), were selected to represent an elevation gradient, generally representing low (45 - 135 m), mid (135 - 1017 m), and high (1077 – 1791 m) elevation zones. We believe this represented a testable range for measuring foliage and flowering phenology, labile C storage, and biomass accumulation.

Carbon saving: non-structural carbohydrates

We sampled stem and root tissues to assess allocation to storage. All P_g genotypes were sampled on May 26th and October 21st, 2016 to assess correlations between provenance site and NSC concentrations across populations. Due to the large time commitment to measure NSCs, we selected a subset of three populations for the seasonal monitoring of storage, including one population each from a high-, mid- and low-elevation site. Stem and root tissues from these focal populations, hereafter P_f (Fig. 1) were collected on May 26th (Spring), July 22nd (Summer) and October 21st (Fall) in 2016 and February 26th (Winter) in 2017. Temperature ranges for the collection dates were as follows: Spring 16-31°C, Summer 31-45°C, Fall 21-36°C, Winter 12-21°C (Fig S2). Total precipitation between March 1st 2016 and March 1st 2017 was 86.9 mm, and all plots were flood irrigated to supplement precipitation and maintain soil moisture. At the start of sampling the trees were over 2 m tall. Mature second year stem samples (7-12 mm diam) were collected at breast height (1.37 m above soil surface) and coarse root tissue samples (5-10 mm diam) 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. Individuals were randomly selected for NSC analysis and six genotypes were sampled from three of the blocks (n=18 for each population).

For the NSC analysis, we used the methods described as best practices in Quentin *et al.* (2015), including using internal standards of glucose (Sigma-Aldrich G7528) and starch (Sigma-Aldrich S5926Fluka). Samples were placed on dry ice immediately after excising from the tree and microwaved within 24 hours to prevent enzymatic degradation. Samples were then oven dried at 60 °C for 48 hours 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, Swedesboro, NJ), and then fine ground with a dental amalgamator (Wig-L-Bug, Dentsply Rinn, Charlotte, NC). A sub-sample of 50 mg (± 1.5 mg) was used for extractions with the final weight recorded, for every 10th sample, a second sub sample was taken for internal quality control. All water-soluble sugars (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 was repeated three times. Total water-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 was evaporated and an enzymatic digestion using Alpha-amylase and amyglucosidase was used to degrade starches into glucose. The percent glucose was quantified using the PGO enzyme method at 525 nm (Chow and Landhäusser 2004). The percent glucose by biomass 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 carbon storage not accounted for in our extraction methods (e.g. hemi-cellulose 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. Secondary metabolites in *Tamarix* were not found to vary across a broad latitudinal gradient of source populations in a similar common garden study (Hussey, Kimball & Friedman 2011).

Relative risk of freeze-thaw events

We used linear regressions to analyze the risk of freeze events as predictors of carbon allocation. We defined freeze events as any day between January 1st and June 1st when the minimum temperature was below 0 °C and the maximum temperature was above 0 °C. *Tamarix* is a deciduous species that has shown differences in timing of leaf flush across its introduced range, as well as in common gardens (Friedman, Roelle & Cade 2011; Long *et al.* 2017). We chose January 1st as the start date to emphasize the importance of freeze events after new season growth could have emerged. 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 1992-2012 for all P_g sites using data from the PRISM Climate Group, Oregon State University (<http://prism.oregonstate.edu>, created 10 Jan 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.

Carbon spending: reproduction and growth

Flower phenology and output

Tamarix has small (<2 mm), perfect (bisexual) flowers that are on secondary racemes, each supporting an average of 50-60 flowers (Warren & Turner 1975; Gaskin & Schaal 2002; Andersen & Nelson 2013). *Tamarix* plants may support as many as 750,000 flowers, each producing small amounts of sucrose rich nectar to attract pollinators (Andersen & Nelson 2013). Bimonthly phenological observations were made from February 2016 until June 2016 on 12 individual plants from three randomly selected blocks from each of the P_g genotypes. These

individuals included those sampled for the NSC monitoring. 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 one hundred 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.

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 mean growth increments of each population during the growing season. Initial measurements were taken in late spring (May 25th 2016) and again in the fall (October 25th 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 oval where r is stem radius:

$$A_b = \frac{\pi r_1^2 + \pi r_2^2}{2} \quad (1)$$

Three representative stems were selected for repeat measurements and marked with paint pens at ten cm above the ground surface so that they could be re-measured 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; $\text{mm } d^{-1}$) were calculated according to (Lambers, Stuart Chapin III & Pons 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} :

$$BAI = \frac{A_{bf} - A_{bi}}{d} \quad (2)$$

Canopy volume was measured on May 25th, 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}; m³) was calculated using the radii of two widths (W₁, W₂) and half the max height (H) of the tree and the formula for the volume of ellipse

$$Vol_{can} = \frac{(4\pi)(H)(W_1)(W_2)}{3} \quad (3)$$

Statistical Analyses

Correlations were analyzed using linear regressions, and all comparisons were done with one-way ANOVA and post hoc analysis on stems and roots separately using Tukey's Honest Significant Differences using the 'stat' package in R (R Core Team 2017). The spring phenology was analyzed 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.

Tradeoff modeling

In order to aggregate the two different components of spending, 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 fall stems). The scale function generated z scores by

determining how many standard deviations an individual genotype was from the garden mean of each trait. Fall stems were selected to represent storage since we predicted higher storage of NSCs in stems to provide adequate carbohydrates to fuel regrowth after spring freeze events. Higher NSC concentrations in roots would be expected in populations exposed to disturbance events that remove all aboveground biomass (e.g. fires). Reproduction and growth were added together to determine an aggregate spending score.

Results

Carbon saving

Among the three P_f , NSC levels were dynamic throughout the year, but the total concentration of NSC (soluble sugars plus starch) of the high and mid elevation population were more abundant in root tissue than in stems across all seasons (Fig. 2). In the roots there were significant differences among populations (ANOVA $F_{11,104} = 12.84$, $p < 0.001$, Fig. 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 ($M = 176 \text{ mg g}^{-1}$, $SE = 6.35$) were nearly twice as high as those found in low elevation roots ($M = 90.14 \text{ mg g}^{-1}$, $SE = 11.49$). 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 (ANOVA $F_{11,104} = 23.24$, $p < 0.001$, Fig 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 that the time of year affected the composition of the NSC pool. In stems there was a significant change in the composition (ANOVA $F_{3,182} = 169.65$, $p < 0.001$, Fig. 3a), which was driven by a shift from soluble sugars to starch from summer to fall. The roots also showed a

247 significant interaction between season and pool (ANOVA $F_{3,182} = 12.37$, $p < 0.001$, Fig. 3b), but
248 lacked the marked shift in allocation from sugars to starch.

249 The highest risk site based on the PRISM climate data had an average of 42.2 freeze-thaw
250 days between January and June when the minimum temperature dropped below 0 °C at night
251 after being above 0 °C during the day. Across the nine provenance sites for the P_g , none of the
252 low elevation sites were at risk of exposure to freeze-thaw events, while mid elevations had a
253 low risk relative to the coldest site (0.07 - 0.19) and high elevation sites had the highest risk
254 (0.64 -1.00). For all populations we observed that the risk of freeze events at the provenance site
255 was positively correlated with NSC storage in fall stems (Fig. 4a), both as total NSC (Total NSC
256 = $103.64 + 24.78 \times \text{relative risk}$, $r^2 = 0.48$, $F_{1,7} = 6.50$, $p = 0.038$) and starch (Total starch = $64.75 +$
257 $21.47 \times \text{relative risk}$, $r^2 = 0.61$, $F_{1,7} = 10.75$, $p = 0.014$). We observed a similar, but slightly
258 weaker, trend in the fall root tissue for total NSC (Fig. 4b, Total NSC = $130.58 + 41.34 \times \text{relative}$
259 risk, $r^2 = 0.34$, $F_{1,7} = 3.6$, $p = 0.099$).

260 Ratios of starch to water-soluble sugars in the three P_f were found to vary across tissues
261 (ANOVA $F_{1,219} = 33.93$, $p < 0.001$, Fig 5), sampling date ($F_{3,219} = 184.65$, $p < 0.001$, Fig. 5), and
262 population source ($F_{2,217} = 24.35$, $p < 0.001$, Fig. 5). The highest starch to sugar ratio was found
263 in the roots of the high elevation population (10.39:1) and lowest in the stems of the low
264 elevation populations during the summer (0.092:1). No differences were detected between
265 tissues and source populations during the spring and summer, but differences were found in the
266 fall and winter. In the fall the high elevation population had a significantly higher ratio of starch
267 to soluble sugars in both roots and stems compared to the low elevation population (Tukey's
268 HSD $p < 0.0001$ and $p = 0.022$, respectively). During the winter there were no differences found
269 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).

Carbon spending

Flowering phenology and output

Flowering differed considerably over the spring among P_g source elevations ($F_{18, 135} = 3.8$, $p < 0.0001$, Fig. 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. Peak flowering dates were March 5th, April 2nd, and March 19th for low, mid and high elevations, respectively. At their respective peak flowering dates 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 February 4th to June 11th, 2016 (ANOVA $F_{2, 356} = 22.04$, $p < 0.001$). Unlike NSC accumulation, there was no relationship between number of racemes produced and the risk of freeze events at the provenance site (Fig. 6b; number of racemes = $201 - \text{relative risk} \times 201$, $r^2 = 0.12$, $F_{1,7} = 0.97$, $p = 0.36$).

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 risk of freeze events and both spring basal area (Fig. S3) and canopy volume (Fig. S4a). Basal area increments (BAI) also showed no relationship with relative risk (Fig. S4b).

293 *Tradeoffs in carbon allocation*

294 To visualize the tradeoffs between saving and spending of carbon we developed a
295 comparison of normalized scores encompassing growth, reproduction, and labile carbon storage.
296 Generating the normalized z scores allowed us to combine the different ‘spender’ metrics into
297 one variable to compare to storage. Although our method of using normalized scores does not
298 consider the relative carbon costs of the different pools it allowed us to evaluate how allocation
299 was prioritized by comparing individual scores to the average values of all the populations. Since
300 we only studied *Tamarix*, the carbon costs of specific tissues (e.g. flowers) should be similar
301 across all genotypes. We found the saver z-score was a predictor of the average of the spender z-
302 scores (spender z-score = $-0.057 - \text{storage z-score} \times 1.14$, $F_{1,7} = 16.07$, $r^2 = 0.70$, $p = 0.0051$, Fig.
303 7). The strategy exhibited by the different populations can be described by which quadrant they
304 occupy in a cartesian plane (Fig. 7). Populations occupying quadrant II were defined as spenders
305 since they have positive spending scores, and negative saver scores; while those in quadrant IV
306 were classified as savers since they exhibit the opposite scores. Populations in quadrant III could
307 still be considered spenders since they had less than average saver scores, assuming there is some
308 spender category that we did not account for in our analysis [e.g. herbivore defense (Herms and
309 Mattson, Jr. 1992)]. Quadrant I could only be occupied by populations that had higher than
310 average spending and saving rates, none of our population means existed in this space, but a few
311 individual genotypes did. In our study system, high elevation populations all occupied the saver
312 space of the coordinate plane, while mid and low populations were found in spender quadrants.

313

314 Discussion

315 Using a common garden design, we detected considerable differences among genotypes
316 in allocation to non-structural carbohydrate pools that can be predicted by source population's
317 exposure to freeze risk. Specifically, populations from colder environments allocated more
318 carbon to storage, but reduced carbon allocation to growth and/or reproduction. The variation in
319 the degree of 'bet-hedging', allocating carbon to storage instead of growth/reproduction, may
320 help to explain the wide-spread success of *Tamarix*, and other woody deciduous species, across
321 broad climactic gradients as populations adapt to local stressors (Gleason & Ares 2004;
322 Alexander 2013). More broadly, these results shed new light on the possible importance of active
323 NSC accumulation in long-lived woody taxa.

324 *Carbon saving: non-structural carbohydrates*

325 *Tamarix* genotypes showed an accumulation of NSC in the fall that is consistent with
326 patterns found in many winter deciduous species that accumulate or translocate carbohydrates in
327 storage organs prior to leaf fall (Hoch, Richter & Korner 2003; Hultine *et al.* 2015; Martinez-
328 Vilalta *et al.* 2016; Furze *et al.* 2018). However, we observed that the risk of freeze events at the
329 provenance site was positively correlated with increased NSC storage in both the roots and stems
330 in the fall (Fig. 4). This was consistent with our prediction that genotypes from cold
331 environments would maintain higher NSC concentrations, primarily as starch. These patterns
332 indicate that cold-adapted plants are storing labile carbon in response to freezes or other related
333 canopy dieback events (Hudgeons *et al.* 2007; Charrier & Ameglio 2011; Clarke *et al.* 2013;
334 Pratt *et al.* 2014). Likewise, populations of *Tamarix* from colder northern latitudes maintain
335 higher root to shoot ratios than those from warmer southern locations (Sexton, McKay & Sala
336 2002; Williams, Friedman, Gaskin & Norton 2014). Similarly, genotypes from the coldest

337 location in the present study had root area to leaf ratios that were at least 100% higher than non-
338 freeze-adapted genotypes (Bush et al. in revision), potentially amplifying the already higher per-
339 dry mass NSC concentrations in freeze-adapted genotypes.

340 Maintaining a high NSC storage may decrease mortality from disturbance regimes and/or
341 facilitate rapid regrowth following tissue damage (Dietze et al. 2014; Long et al. 2017). Greater
342 storage of NSC in the stems as well as roots could also be adaptive in high-elevation genotypes
343 to minimize freeze-thaw cavitation events, despite the risk of loss of stored NSC due to stem
344 breakage during the winter. The localized storage of NSC could provide osmotic gradients that
345 are necessary to refill embolized xylem vessels, specifically when starch stored in xylem
346 associated tissue (parenchyma) is degraded to simple sugars and loaded into the embolized
347 xylem (Brodersen, McElrone, Choat, Matthews & Shackel 2010; Nardini *et al.* 2011; Hartmann
348 & Trumbore 2016). Although it is unclear which response or mechanism (e.g. regrowth, tissue
349 repair, or osmotic regulation) may be driving selection in our study system, the differences in the
350 ratio of starch to simple sugars across the provenance sites may highlight the different adaptive
351 uses of NSC for regrowth versus osmotic regulation in relation to seasonal temperature
352 variations.

353 During the growing season (spring, summer, fall) we detected lower ratios of starch to
354 sugars, where osmotically active NSC (i.e. water-soluble sugars) play an important role in
355 osmotic regulation and drought tolerance at the cellular and tissue level (Regier *et al.* 2009). We
356 had originally predicted that the lowest starch to sugar ratios would occur in the most arid-
357 adapted populations (low elevation), and although these populations did have the lowest starch to
358 sugar ratio they were not significantly lower than the other population classes. Compared to a
359 recent synthesis on the dynamics of NSCs in terrestrial plants (Martinez-Vilalta *et al.* 2016),

360 *Tamarix* showed an atypical pattern of having larger relative pools of soluble sugars during the
361 summer (Fig. 3a,b) rather than in the winter as found in most temperate and boreal plants. In
362 combination with the reduced starch to sugar ratios in summer across all populations likely
363 reflects the necessity of osmoregulation to cope with the extreme aridity at our common garden
364 site and across the range of *Tamarix*. In all of our study populations the ratio of starch to sugars
365 decreased by nearly an order of magnitude from winter to summer, indicating that
366 osmoprotection against drought or heat may be more important for *Tamarix* than it is for
367 freezing, or that *Tamarix* relies on recovery after freezing rather than freezing protection. These
368 results do not conflict with the observed higher total allocation to NSC, specifically as starch
369 which is osmotically neutral, in genotypes exposed to freeze-related disturbances or stressors in
370 their source environments, which may provide energy for regrowth rather than osmoprotection.

371 No differences in carbon storage were detected among populations in the spring.
372 However, the results in spring could be have been masked by variation in phenology among the
373 populations, with net carbon uptake occurring only after early season use of stored NSC to
374 support spring growth of photosynthetic tissues (Richardson *et al.* 2013; Furze *et al.* 2018).
375 Compared to mid and high elevation populations, leaf flush and flower production occurred
376 earlier in the spring in low elevation populations, triggering earlier photosynthetic carbon gain
377 and greater sink strength (Long *et al.*, 2017). Low elevation populations were fully foliated by
378 late march, two months before the spring NSC collection period. Those populations were likely
379 no longer depleting their NSC reserves, but rather were actively acquiring carbon which may
380 explain the convergence of NSC concentrations among populations in May. Furthermore, some
381 genotypes from the low elevation sites never fully entered dormancy and instead maintained
382 green photosynthetic tissues throughout the winter, as opposed to the mid and high elevation

383 genotypes that had all fully senesced by mid-fall or winter (Long et al. 2017). This seasonal
384 pattern is likely why reductions in NSC concentrations were smaller from the fall to winter in the
385 low elevation populations than those from colder provenance sites.

386 Whether contrasts in labile carbon storage among populations was a consequence of
387 active regulation of carbon allocation or a consequence of passive regulation related to seasonal
388 changes in source/sink relationships is an open question. One approach to evaluate contrasts
389 between active versus passive labile carbon regulation is to compare seasonal patterns of growth
390 and NSC storage (Bansal & Germino 2008; Dietze *et al.* 2014). In the present study, NSC
391 storage increased from spring to summer in stems, and to a lesser extent in the roots. During the
392 summer, all of the plants had full canopies and growth and whole-plant respiration effluxes were
393 most likely near peak rates. These patterns, therefore, provide evidence that observed patterns of
394 NSC storage were likely governed by active regulation. However, we cannot rule out the
395 possibility that NSC storage was a passive process related to large population-level contrasts in
396 foliage phenology (Long et al., 2017) and subsequent contrasts in source/sink relationships.
397 Nevertheless, passive labile carbon regulation would still be under strong selection given the
398 tight coupling between source/sink relationships with leaf senescence, and coupling between the
399 timing of senescence and local adaptation to the arrival of autumn freeze events.

400 *Carbon spending*

401 Flowering phenology, basal area and canopy volume

402 Spring flowering differed among the low, mid and high elevation populations, but unlike
403 NSC accumulation, there was no significant relationship between number of racemes produced
404 and the risk of freeze events at a given provenance site (Fig. 5). Similarly, we did not find
405 significant relationships between freeze risk and growth patterns measured in the common

garden. These results may have been due to an apparent tradeoff between growth and reproduction. For example, mean canopy volume for the low “frost” risk sites ranged from 4.1 to 8.9 m³ and the reproductive output of those same populations ranged from 206 to 726 racemes per individual, but the population with the highest reproductive output also had the smallest canopy volume. We expected to find the strongest tradeoff between NSC storage and growth/reproduction as carbon is allocated to the various competing pools (Chapin *et al.* 1990; Kozlowski 1992; Dietze *et al.* 2014; Hartmann & Trumbore 2016), but tradeoffs have also been shown to occur between growth and reproduction (Obeso 2002; Banuelos & Obeso 2004; Climent *et al.* 2008; Capelli, Lauri & Normand 2016). One plausible explanation for why growth and phenology were not correlated at the population level is that strong tradeoffs were present between growth and reproduction, and genotypes from low elevations tended to have a relatively high growth rate or reproductive output, but rarely both.

Tradeoffs between labile carbon storage, growth and reproduction

Broadly, selection for savers could be a result of regular exposure to episodic disturbance that triggers the loss of aboveground tissues. Plants that are confronted with regular tissue damage from spring frost events, for example, benefit from having a “bank account” of labile carbon to regularly rebuild tissues (Iwasa & Kubo 1997). Alternatively, high concentrations of NSC could be associated with osmotically reducing the temperature freezing point of living cells and xylem tissues (Greer, Robinson, Hall, Klages & Donnison 2000). In the present study, high elevation populations all occupied the saver space of the coordinate plane, while all but one mid and low populations were found in spender quadrants (Fig. 7). This supports the hypothesis that populations from sites exposed to more frequent disturbances would preferentially store labile carbon (Bloom *et al.* 1985; Dietze *et al.* 2014; Long *et al.* 2017; Hinman and Fridley 2018).

Specifically, we found that more frequent exposure to freeze events at the source environments increased the amount of labile carbon storage with reduced commitment to aboveground growth and/or reproduction.

Closing a whole-plant carbon budget and thus evaluating tradeoffs between NSC storage and growth in mature woody plants is challenged by several factors. One challenge is quantifying belowground allocation, particularly in deeply-rooted species such as *Tamarix*. A separate study using the same common garden as the current study found that high elevation genotypes had considerably higher fine root area than mid- and low-elevation genotypes (Bush et al., in revision). As a consequence, tradeoffs between NSC storage and whole-plant growth may either be suppressed or amplified relative to tradeoffs associated with aboveground growth, depending on seasonal NSC storage in deep roots, which we found to be generally higher than in stems. Likewise, the strength of carbon allocation tradeoffs is in part, dependent on the capacity of photosynthetic tissues to deliver photosynthates to various sinks. Previous common garden studies have shown that large intra-specific differences in net photosynthesis can emerge among populations (Zhang, Marshall & Jaquish 1993; Grady et al. 2011; Kaluthota et al. 2015). In an earlier study conducted at the same *Tamarix* common garden, 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 highly plausible that low-elevations genotypes were operating with a significantly 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 carbon storage over growth in freeze-adapted genotypes.

Conclusions

We found considerable evidence for local adaptation in *Tamarix*, with different “saver” and “spender” populations due to tradeoffs between carbon storage and growth/reproduction. Genotypes exposed to higher frequency of freeze events maintained higher stores of NSC than those from less frequent freeze events when grown together in a common garden. The bet hedging strategy of allocating greater resources to storage 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 and 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 and Schaal 2002; Lee et al. 2017; Long et al. 2017). These factors combined with strong gradients in climate, late freeze disturbances, and large reproduction events (more than 750,000 flowers per individual during peak reproduction events [Andersen and Nelson 2013]) appear to have resulted in rapid population differentiation in expressed physiological traits related to carbon 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 disturbances such as fire and herbivory. 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 tradeoffs 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 carbon allocation strategies are under strong selection.

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Figure Legends

Fig. 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 location of Arizona within United States. Map colors represent mean annual temperature variation across Arizona. Source: Esri. “USA Mean Temperature” [basemap]. “USA Mean Temperature”. September 20, 2018: https://landscape3.arcgis.com/arcgis/rest/services/USA_Mean_Temperature/ImageServer. (downloaded November 18, 2019).

Fig. 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 water-soluble sugars (Glucose, Fructose and Galactose) and starch in stems (**a**) and roots (**b**) from focal populations (P_f) representing low, mid and high elevations ($n=8$ for each tissue x date x elevation source). Error bars represent the \pm standard error of the means. Letters denote significant groups identified by a posthoc Tukey’s HSD analysis across all elevation groups and seasons.

668 Fig 3. Concentrations of individual pools of starch and soluble sugars measured separately for
669 both the stems (**a**) and roots (**b**) in *Tamarix* occurring in an experimental common garden. Three
670 focal populations (P_f) representing low, mid and high elevations were analyzed over one growing
671 season ($n=8$ for each tissue x date x elevation source). Error bars represent the \pm standard error of
672 the means. Letters denote significant groups identified by a posthoc Tukey's HSD analysis where
673 the letters are significant groups across all elevation groups and seasons, but within the separate
674 pools.

675

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

685

686 Fig 5. Ratio of starch to sugar of fall root and stem tissue ($n = 24$ for each tissue x elevation
687 source) in *Tamarix* genotypes sourced across a broad climate gradient. Higher starch to sugar
688 ratios indicates increased allocation to storage. Error bars are \pm standard errors of the means, and
689 letters and numbers indicate significant groups identified by a posthoc Tukey's HSD analysis.

690 Numbers are the groupings across all tissue sampling and dates, and letters are the results from
691 within a date and tissue.

692

693 Fig 6. Reproductive output of *Tamarix* populations from different elevation groups. **a)** Seasonal
694 dynamics of reproductive output for low, mid, and high elevation groups. Each point represents
695 the mean of all individual genotypes observed for the three different populations per elevation
696 groups ($n = 144$ per elevation). Error bars represent the \pm standard error of the means. The same
697 individuals were measured at each of the time points. **b)** The log transformed total reproductive
698 output from February 4th to June 11th 2016 for all nine populations. Colors are the elevation
699 groups and shapes are different populations within groups. Points are the means of samples,
700 which were pooled samples of 12 individual genotypes from three different blocks ($n = 36$)
701 within the common garden, error bars represent the \pm standard error of the means.

702

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

712 Table 1. Origin of source *Tamarix* populations for the common garden in Yuma, AZ. Source
713 population sites are ordered from low-to-high elevation. Weather data was collected from the
714 PRISM Climate Group, Oregon State University (<http://prism.oregonstate.edu>, created 10 Jan
715 2018)

Name	Elevation (m)	Minimum Temperature (°C)	Maximum Temperature (°C)	Annual Precipitation (mm)	Longitude	Latitude	Elevation Group
CYM*	45	6.3	41.7	90	-114.485	32.823	Low
Garden^	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*	943	-1.9	38.0	332	-111.856	34.573	Mid
CAF	1017	1.3	36.6	449	-112.063	34.257	Mid
BEN	1077	0.1	36.3	348	-110.279	31.968	Mid
HNT*	1654	-6.4	33.3	247	-109.706	34.648	High
KKA	1747	-6.4	34.2	213	-111.076	36.612	High
KKH	1791	-7.6	32.4	216	-110.282	35.828	High

716 ^Common garden site *Focal Populations (P_f)

717

718