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Environmental Gradients Impact Key Leaf Traits in Riparian Trees

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Introduction

Given the rising need to assess ecosystem health and function in a rapidly changing world, researchers have sought out innovative ways to classify ecosystem functioning. Trait-based approaches help address this challenge by improving the predictive power of ecology (McGill et al. 2006). These approaches have been essential in informing life history strategies, ecosystem function, forest productivity, community assembly processes, and restoration project efficacy (Cornwell and Ackerly 2009; Sandel et al. 2011; Adler et al. 2014; Durán et al. 2019; Šímová et al. 2019; Carlucci et al. 2020). The units of trait-based ecology are functional traits, which are organism level traits that impact survival, reproduction, growth, and/or ecosystem function (Violle et al. 2007). Despite the importance of functional traits, for most species there is still a question of how traits vary within a species (through environmental filtering and local adaptation or phenotypic plasticity) along environmental gradients, and how functional traits are mediated by trait-environment relationships at different scales.

The conditions under which intraspecific leaf functional traits are affected by local environmental factors and developmental stages can vary widely. The patterns seen in leaf traits may follow interspecific cross-continental LES trends, but at smaller scales results are inconsistent. The interactions between this study’s functional trait, specific leaf area, and its determinants have not been fully addressed by the literature (Poorter et al. 2009; Funk et al. 2017), and multiple local determinants of our studies leaf trait, are rarely measured *in situ*. In riparian ecology, there are only a handful of studies that incorporate intraspecific trait variation in water availability and urbanization measures, and none which incorporate it in SLA. Studies that do address intraspecific variability are typically done in greenhouse or garden experiments. In this research we explore both intra and interspecific variability in a functional trait *in situ*. The benefit of this type of research is assessing whether patterns seen in the lab or hypothesized in functional trait papers are observed in the environments where the species naturally occur.

Specific Leaf Area as a Functional Trait

Functional traits fall into two categories. The first is a “response trait”, which is correlated to aspects of the organism’s fitness in an environment, an example being body size. On the other hand, “effect traits” are traits that affect dynamic processes in the environment, for example, leaf nitrogen in nutrient cycling (Kearney et al. 2021). In this study, we examined a trait that can be both a response and effect trait. When a trait is both, it means understanding trait-environment interactions has implications for broader ecosystem processes, as well as organismal function, including its growth economics, or trade-offs among strategies.

In plants, a few key functional traits have been singled out to quantify whole-plant strategies, which are known as the “leaf-seed-height” scheme, and these traits are used to quantify strategies for growth, reproduction, and competition respectively (Westoby 1998). The growth trait in that scheme is specific leaf area (SLA): the ratio of light capturing area over the mass of carbon invested, or fresh leaf area over dry leaf mass. SLA is often used in the relative growth rate (RGR) equation. RGR is an important functional metric, since it generally determines how fast a plant can compete for light in an environment (Wright and Westoby 1999). In studies across continents on terrestrial plants, SLA often positively correlates to RGR and other key functions like mass-based photosynthetic capacity and mass-based leaf nitrogen content, while it negatively correlates with leaf lifespan (Poorter and Remkes 1990; Lambers and Poorter 1992; Wright et al. 2002; Diaz et al. 2004; Ruiz-Robleto and Villar 2005; Osone et al. 2008). Due to these correlations, SLA is often used as an easily measured trait indicative of overall growth strategy. The coordination of morphological, metabolic, and chemical leaf traits along an axis of fast to slow strategies, when displayed in leaf traits, is known as the leaf economics spectrum (LES). The LES suggests that leaf traits lie on a spectrum of slow to fast resource acquisition, which relate to environmental conditions and resource gradients (Wright et al. 2004).

When looking at SLA through the lenses of the LES, we see the carbon assimilated from photosynthesis is “invested” into a certain amount of light capturing area. A high SLA, where the leaf is thin with less carbon invested in relative area, has a short lived and resource exploitative strategy. This is also typically seen in areas with available resources and low stress (Wright et al. 2002; Diaz et al. 2004). High SLA leaves are generally short lived, as they typically lack structure and metabolites, and have high available N (e.g. Rubisco), making them more attractive to herbivores and susceptible to damage (Zirbel and Brudvig 2020). A lower SLA leaf, with more mass per unit area in the form of condensed cells, chlorophyll, lignin, and other metabolites, has a longer-lived leaf and a conservative strategy. Plants with low SLA are less likely to die in stressful environments (Greenwood et al. 2017), and low SLA leaves are typically found in stressful or low resource environments.

What defines a “high” or “low” resource environment is another question entirely. SLA has been associated with a wide array of stress tolerances along a suite of resource gradients that pertain to light, nutrients, and water, but the findings are mixed. This is likely due to the interplay between the compounds needed for photosynthesis and respiration, the total energy intercepted from light, and the anatomy of leaves processing it. Interspecific LES studies typically relate to temperature, precipitation, and sea level elevation gradients when discussing LES strategies, and trait changes are expressed as species turnover. It has been demonstrated that the overall trend in terrestrial species is an increase of species SLA means in high temperatures and high precipitation environments, which are thought of as high resource, low stress environments (Wright et al. 2002; Diaz et al. 2004; Fajardo and Piper 2011; Tian et al. 2016; Durán et al. 2019). Temporal effects such as season are important predictors of SLA as well, given the connection to leaf lifespan (Nouvellon et al. 2010; Dwyer et al. 2014). These effects are well studied on global scales, and among species. This provides a foundation for studying functional traits in ecosystems on local scales, and within species, where patterns are not as clear.

Determinants of Specific Leaf Area

There are many known local scale determinants of SLA variation. Light level is almost always the best predictor of SLA variation, and the effect is remarkably consistent among species and ecosystems (Poorter et al. 2009). Leaves that develop in more light generally have low SLA, with the opposite in shade (Shipley and Almeida-Cortez 2003; Milla and Reich 2007; Kwon et al. 2016; Celis et al. 2017; Zirbel and Brudvig 2020), which is also an effect seen within individual plant canopies (Hulshof and Swenson 2010; Legner et al. 2014). Although light is likely the main cause of canopy variation within individuals, it can covary with leaf nitrogen content as well (White and Scott 2006; Legner et al. 2014; Hikosaka 2016). This is attributed to the fact that, as SLA gets lower, leaf nitrogen per unit area (N_{area}) increases (Reich et al. 1999). Lower SLA and increased N_{area} allow for reduced leaf CO_2 concentrations and more efficient photosynthetic capacity per unit of leaf area, which is thought to be the mechanism behind increased water use efficiency in low SLA leaves (Cornwell and Ackerly 2009). This is especially useful in sunny leaves that experience water loss through transpiration. High N_{area} is likely only efficient in low SLA sun leaves because there is enough energy to process it, and without enough light its excess N becomes wasteful (Z. Liu et al. 2019).

While light is an important determinant of SLA, it is not the only one. Lower leaf cell area and number have been observed in plants grown in drought, and the increase in cell wall material makes for a sturdier, lower SLA leaf (Marron et al. 2003). The association of low SLA with drought conditions, water use efficiency, and the opposite effect of high SLA in high water availability situations is seen both within and among species (Reich et al. 1999; Nautiyal et al. 2002; Marron et al. 2003; Ackerly 2004; Poorter et al. 2009; Rossatto et al. 2013; Liu et al. 2017; Wellstein et al. 2017; Rosas et al. 2019). This is functionally displayed by lower tree mortality under drought conditions in conservative low SLA species (Greenwood et al. 2017). Additionally, a high SLA is thought to increase oxygen diffusion in submerged plants, and is to be an adaptation to flooding and submergence (Mommer et al. 2006; Jung et al. 2010; McCoy-Sulentic et al. 2017).

Thus, we might predict high SLA with high water availability environments. However, the evidence that water availability affects SLA is mixed (Funk et al. 2017, Wellstein et al. 2017). Intraspecific patterns are sometimes consistent with high SLA in high water resource environments (Nautiyal et al. 2002; Marron et al. 2003), but other studies find no effect or the opposite effect of intraspecific SLA variation when compared to interspecific SLA variation along precipitation and local hydrology gradients (Sandel and Low 2019; Emilio et al. 2021). Other studies simply find conflicting patterns to what would be expected with water availability in both intraspecific and interspecific variation (Griffin-Nolan et al. 2018; Alvarez-Maldini et al. 2020). Intraspecific responses of SLA to local water availability metrics are not well documented, leaving questions regarding the relationship between SLA and plant access to water.

In addition to water availability, there is a strong positive correlation between SLA and nutrient content (N and P), observed both within and among species (Wright et al. 2004; Ordoñez et al. 2010). This is thought to be why high SLA leaves are more prone to herbivory, as herbivores tend to prefer nutritious, high N content leaves, which also reduces leaf lifespan. Higher SLA is associated with high photosynthetic nitrogen use efficiency (PNUE). It is hypothesized that this is because lower SLA leaves have a larger investment of foliar N into cell walls, which leaves less N for photosynthetic enzymes (Hidaka and Kitayama 2009). It is also thought that the low chlorophyll content typically seen in high SLA leaves reduces internal shading in a leaf, which increases photosynthetic nitrogen use efficiency (Lambers and Poorter 1992). Ironically enough, this often means PNUE will decrease as N limitation increases. Since SLA is often correlated to leaf N_{mass} SLA is not only seen as a response trait, but also can be an effect trait capable of informing about broader processes like nutrient cycling. Yet, its use as an effect trait does depend on the other contexts in which SLA varies, because it is often seen interacting with other limiting resources. We see high N availability in the environment can decrease the effects of water stress (Iqbal et al. 2020), which could confound results seen in SLA when related to water. The breadth of potential interactions is large and understudied.

In addition to resource gradients, life history traits are known to impact SLA, such as plant size. Plant size is strongly correlated to age in plants, so it can be difficult to determine the mechanism. In one study, plant size was more important than all other environmental variables in its effect on lowering SLA (Z. Liu et al. 2019), but another study found no effect of plant size (Karavin 2013). To account for mechanisms of lower SLA in larger trees, it has been suggested that water potential differences between the top of a tree and the roots can lower the turgor pressure in leaves, which would lower SLA in taller trees and at the top of canopies (Nouvellon et al. 2010; Williams et al. 2017). This may be exacerbated by greater light exposure at the top of canopies as well since SLA is lower in sun leaves. There is also a potential ontogeny effect where growth slows down once maximum plant height is reached, and biomass starts accumulating in leaves and other organs of older (and presumably larger) trees, thereby increasing leaf mass and decreasing SLA (Karavin 2013; Gibert et al. 2016). Plant size has also been shown to have an influence on nitrogen content, SLA, and photosynthetic capacity (Liu et al. 2010). Plant size appears to be worth noting in the context of leaf trait variation, given its relationship to SLA, and the interactions with limiting resources.

Intraspecific Trait Variation

Intraspecific SLA variation at local scales often shows inconsistencies with LES patterns, as seen in the context of developmental stages and along resource gradients (Wilson et al. 1999; Ackerly and Cornwell 2007; Funk et al. 2017; Messier et al. 2017; Rosas et al. 2019; Carvalho et al. 2020). Within the LES, SLA has a notable amount of intraspecific variation in different study systems (Messier et al. 2017; Henn et al. 2018; Cochard et al. 2019). In one study, SLA intraspecific variation was found to be greater than leaf nitrogen content and leaf dry matter content (Garnier et al. 2001). So, the fact that SLA is correlated with important ecosystem and organism functional processes, in addition to its high intraspecific variability, makes SLA an interesting subject of study. We might expect that inconsistencies in intraspecific SLA variation may be explained by local predictors and the interactions among them.

Since SLA is used as a growth strategy trait, it also is a subject of interest in the context of invasion ecology, as a defining trait of invasive species has been thought to be fast, competitive growth rates (Lake and Leishman 2004; Grotkopp and Rejmanek 2007; Sandel and Low 2019). Invasive species have also been found to often have significantly higher SLA than native species (Lake and Leishman 2004), and this is thought to be a mechanism of invasive plant species success, as a high SLA is linked to a quick resource acquisition strategy. It has been suggested that successful plant invasions are comprised of species with greater intraspecific variability, and this is what allows invaders to overcome resource limitations as well as exploit resources when available (S. Liu et al. 2019). While invasives do tend to have faster resource strategies, it has also been shown they can converge on native conservative trait syndromes in stressful environments as well, indicating a large breadth of potential trait variance (Han et al. 2012). In some instances researchers have singled out phenotypic plasticity as an important mechanism of plant invasions success, as this would allow a species to respond to environment would overcome the founder effect and genetic bottlenecks (Z. Liu et al. 2019), which is supported by a meta-analysis on the topic, showing invasive species had greater phenotypic plasticity than non-invasive species (Davidson et al. 2011). In this study, we do not disentangle intraspecific variation mechanisms (phenotypic plasticity, genetic variance, or both), but it has been suggested SLA variation is comprised of similar amounts of genetic and plastic variance (Scheepens et al. 2010). Here, we examine overall intraspecific variation between a native and invasive tree species, with the prediction that the invasive will have a higher variance and mean SLA than a morphologically similar native species found in the same locations.

Riparian Systems and the Urban-Rural Gradient

Since higher levels of intraspecific variability can be found in environments with greater heterogeneity (Albert et al. 2010), riparian areas make for good model systems to explore intraspecific variability in SLA, as these systems are highly heterogeneous, with steep gradients of light, water availability, and nutrients. Better understanding the trait-environment dynamics in riparian systems is also important since they are essentially local biodiversity hotspots (Sweeney et al. 2004, Dolanc and Hunsaker 2017). In riparian systems, overbank flooding deposits phosphorus, so the local flooding regime is not only an indication of water availability, but also potentially nutrient levels (González et al. 2010). Riparian areas are also rare and endangered habitats, especially given how human development usually occurs near riparian areas (Fang and Jawitz 2019). Impervious surfaces from urban areas alone occupy a larger area than all herbaceous wetlands in the conterminous United States (Elvidge et al. 2004). In the context of riparian ecology, an urban-rural gradient makes for an interesting case study into how functional traits are affected by differing water and nutrient cycles.

Given our interest in heterogeneous environments, we might also expect a response of SLA in riparian corridors along an urbanization gradient. The impacts of urban and rural land use significantly alter conditions of light, nutrients, and water, so we expect these would impact SLA. There has been a growing research interest in urbanization impacts, likely because they are "living labs" to observe conditions of elevated CO_2, the heat island effect, increased precipitation, and in temperate climates, extended photosynthetic growing seasons (Idso et al. 1998; Pickett et al. 2001; McDonnell et al. 2008; McCarthy et al. 2010; Liu and Niyogi 2019; Wang et al. 2019). Agricultural areas have potential impacts on functional traits as well, given the effects of grazing, and pesticide and fertilizer inputs into the watersheds and soils (Poff et al. 2012). In urban and rural areas alike, groundwater depletion and river diversion permanently alters these riparian landscapes (Strange et al. 1999). Additionally, there are other riparian factors that come with urban areas, such as increased run-off, channel incision, and soil compaction, with those effects less common in rural and natural areas (Pickett et al. 2001; McDonnell et al. 2008; Solins and Cadenasso 2020). Both urban and rural land uses have been shown to degrade water quality (Mello et al. 2018), but other factors like urban wastewater treatment and N atmospheric deposition tend to increase nutrients N and P more so in urban watersheds when compared to rural (Hobbie et al. 2017; Tromboni and Dodds 2017; Wetherbee et al. 2022), although rural areas can have higher phosphorus (Duan et al. 2012). These urbanization effects could all potentially affect plant functional traits and influence growth strategies.

In the handful of plant functional trait studies that study an anthropogenic land use effect on SLA, most use interspecific species means and community weighted means (Brice et al. 2017; Kalusová et al. 2017; Cardou et al. 2020; Petersen et al. 2022). If these studies broke down trait tendencies, they found interspecific SLA had mixed responses, from increasing SLA with increasing urbanization (Song et al. 2019; Cardou et al. 2020), finding no effect (Kalusová et al. 2017), or even a negative effects (Petersen et al. 2022). Studies that incorporated intraspecific variability found the response of SLA to urbanization to be mixed, and species-specific. For example a study that found high convergence toward high SLA values, used soil P as an urban metric, so this is unsurprising given the relationship between SLA and nutrients (Dwyer et al. 2014). In another instance where intraspecific SLA increased with urbanization, they found there was an unexpectedly higher N soil concentration in more rural stands, but they still found a high SLA resource strategy within and among species in urban areas (Cochard et al. 2019). One attributed their findings of low SLA closer to roads as a function of air pollution stress (Zhu and Xu 2021), while another simply found a species-specific response to the urban-rural gradient among the 11 species they studied (Su et al. 2021). The literature lacks an apparent reason for why functional traits would vary in an inconsistent or species-specific manner along urbanization gradients.

The effects of local environmental gradients in riparian areas, including access to the water channel and light conditions, urbanization effects, plant size, and interactions among these SLA determinants are unresolved, especially so when looking within a species. For these reasons, we ask the following questions, and make the following predictions:

Questions and Predictions

1. Do we see similar patterns in an invasive and native species intraspecifically? Interspecifically?

We would expect both higher SLA and higher intraspecific variability in the invasive species, and potential interactions that reflect the different environmental tolerances of the species.

2. Do global LES patterns hold true on local scales, and how do environmental gradients and development stages interact?

We expect higher SLA in low light, closer to the water channel, and in smaller trees. We do not have an expectation for the urban-rural gradient given the mixed results of the literature. Given that nutrient, water, and light interplay, we might expect interactions at local scales in these factors, such as increased access to nutrients ameliorating water stress or one stressor exacerbating the impact of another.

Methods

Species Selection

We selected two co-occurring riparian species to represent different potential strategies in response to resource gradients. The first species was Russian olive (*Elaeagnus angustifolia* L.), a tree in the Elaeagnaceae family native to parts of Europe and Asia, but invasive in the North American West, where it is the fourth most frequent woody riparian plant, and can become the dominant species in riparian systems (Friedman et al. 2005; Nagler et al. 2011). Its current abundance compared with suitable habitat suggests Russian olive is experiencing invasion lag (Friedman et al. 2005; Collette and Pither 2015). Russian olive is both flood tolerant (Pearce and Smith 2001; Madurapperuma et al. 2013; Perry et al. 2018; West et al. 2020) and drought tolerant (Niinemets and Valladares 2006; Nagler et al. 2011). It can also resprout after damage and fix nitrogen via mutualisms with *Frankia* sp. bacteria in its root nodules (Katz and Shafroth 2003), which is likely part of what allows it to significantly alter available nitrogen in riparian areas (DeCant 2008; Follstad Shah et al. 2010; Mineau et al. 2011). Due to these abilities and tolerances, Russian olive sits in a unique category of a drought, shade, and waterlogging tolerant species. These tolerances are typically posited as fundamental tradeoffs among species and are rarely all present within a species (Niinemets and Valladares 2006). Hence, a species that ignores these apparently fundamental tradeoffs makes an interesting model to explore functional traits (Grubb 2016). To date, we have also not found a study explicitly on Russian olive SLA.

We paired our investigation of Russian olive with native peachleaf willow (*Salix amygdaloides* Anderss.), which is also a dominant riparian tree, and the sixth most abundant woody riparian plant in the Western US (Friedman et al. 2005), and as such provides resources and habitat for wildlife in riparian ecosystems (Kurz et al. 2013; USDA, NRCS 2022). Russian olive and peachleaf willow frequently co-occur in riparian ecosystems in the plains and arid west. The lifecycle of willows is closely linked to the river flow regime, because they rely on flood dynamics for dispersal (Karrenberg et al. 2002). The notable intolerance of willow species to shade, the preference for these species by native beavers, and most importantly, the permanent alteration of riparian flood patterns, have raised fears that invasive species such as Russian olive will replace native species (Howe and Knopf 1991; Gaddis and Sher 2012). Peachleaf willow serves as a species comparison for this study as it occupies a similar niche to Russian olive but is native, has fewer tolerances, and does not fix nitrogen.

Site Selection and Classification

We used population locations from a USGS survey (L. Reynolds, e-mail message., September 8, 2020) and iNaturalist (iNaturalist 2021) to find 12 sites with sufficient Russian olive, and peachleaf willow when possible, along the urban-rural gradient in Northern Colorado, USA (Fig 1). The study spanned from the edges of the forested foothills, into the Denver metropolitan area, to the rural eastern farm and grasslands. In each site, all Russian olive and associated peachleaf willow tree individuals were identified and geolocated using ArcGIS Collector, and each tree was classified into subgroups of approximate size (trunk diameter), sun exposure (shade versus sun), and position in floodplain (distance to the channel). We then used stratified random sampling of the subgroups to select ten Russian olive trees, so that the subgroups were as even as possible for each site and confounding variables were minimized by having different combinations of variables within a site (e.g., both large and small trees in shade and in sun at varying distances to channel). The closest associated peachleaf willow to a Russian olive individual was selected if present.

To quantify the urban-rural gradient, we used land use and land cover (LULC) categories from the USGS 2019 National Land Cover Database (Dewitz 2021). For each site, we calculated the percentage of each land use and land cover type within a 1000-meter buffer around the center of the site estimated from the center of all trees sampled. We also classified climate and sea level elevation variables for each site. We extracted monthly mean temperature and precipitation from the PRISM Climate Group (Oregon State University 2022 Mar 17) in the month

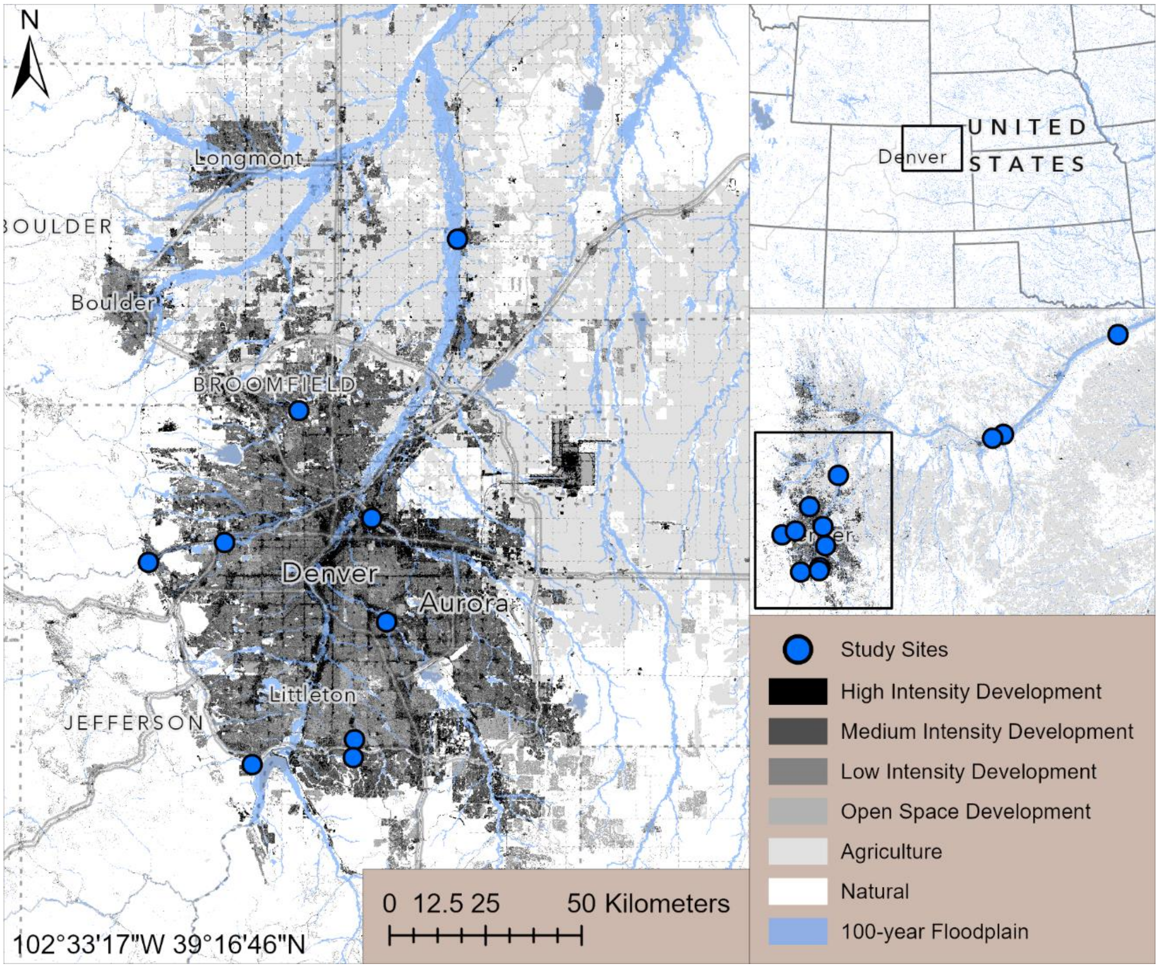

Figure 1: Study area extent with site locations and 100-year predicted floodplain zones; the "agriculture" category encompasses the hay & pasture and cultivated crop land use; the "natural" category encompasses the following land cover classes: barren land, mixed forest, deciduous forest, evergreen forest, shrub & scrub, herbaceous, woody wetlands, and emergent herbaceous wetlands.

and year when sampled. We recorded elevation above sea level at each site using the U.S. Geological Survey 1-meter digital elevation models (U.S. Geological Survey 2020 Nov 13). All landscape features were transformed into the WGS 1984 UTM Zone 13 projected coordinate system. Geospatial analyses were performed in ArcGIS Pro (Esri Inc. 2021).

Tree and Leaf Sampling

Methods from the functional trait handbook were followed with regard to selecting individuals and measuring leaf traits (Pérez-Harguindeguy et al. 2013), with exceptions for selecting only the most sun exposed trees, as we were interested sun exposure effects. We classified trees exposed to direct sunlight for most of the day as "sun trees", and trees in shade for most of the day as “shade trees”, as SLA is most affected by total irradiance over the course of a day (Poorter et al. 2009). For each of the 10+ trees selected at each site, we recorded a GPS point with a handheld Garmin GPS device, diameter at breast height (DBH, ~1.37 m), elevation above water channel, distance to water channel, and tree height. Russian olive and peachleaf willow are often multi-stemmed trees (Zhou et al. 2007; USDA, NRCS 2022), so when trees forked at 1.37 meters, the diameter below the fork was measured, and if the tree forked below 1.37 m, we measured up to 6 stem diameters at 1.37 m. We then calculated the diameter of multi-stemmed trees as the square root of the sum of all squared stem diameters (Magarik et al. 2020). We recorded distance to channel with a tape measure. In instances where foliage was impassable, we calculated the distance between tree GIS points and stream and river features from the National Hydrography Dataset (U.S. Geological Survey 2021). We measured elevation above channel with a Spectra Precision Laser (LL300), which had a vertical error of 10 cm. We measured tree height with a telescoping measuring pole. We also made a note of whether the tree was resprouting from a stump (presumably cut by invasive plant control crews). We obtained permission to sample tree material from city park authorities and Colorado Parks and Wildlife.

We sampled tree branches that were the most exposed to potential sunlight, and the least affected by within-canopy shading. We extracted branches with a pole pruner and took four branches from each tree. Two pairs of branches were taken from western and eastern cardinal directions, to control for the effects of the southern sun (Mediavilla et al. 2019). Within those directions, we sampled one pair from the upper canopy, and one pair from the middle canopy to evaluate canopy level effects. Branches were sealed in plastic bags and stored in field coolers and a lab refrigerator to reduce leaf water loss. Leaves were measured within 24 hours when possible. Three entire, new, fully expanded leaves were taken from the top of each branch. We measured fresh leaf area for both leaf and petiole on a Li-Cor LI-3100 Area Meter. Oven-dry leaf mass was gathered by drying leaves at 70°C for 72 hours and then measuring leaf weight with a precision scale.

Statistical Analysis

All statistical analyses were performed in RStudio (RStudio Team 2022) using R (version 4.2.1; R Core Team 2022). To address multicollinearity and create a single metric for the urban-to-rural gradient, we performed a principal component analysis (PCA). We used with the percentages of sixteen land use and land cover classifications and sea level elevation in the PCA (see correlation matrix, Appendix A). Variables were scaled and centered before running the PCA using the “scale.unit” option in the PCA function from the FactoMineR package (Lê et al. 2008). Development land uses and rural/natural uses loaded neatly on opposite sides of PC1 (Appendix B). Thus, we used PC1 as an urban-to-rural gradient.

To determine how leaf traits of different species that experienced the same environmental conditions differed, we addressed our question with a pairwise comparison of Russian olive and peachleaf willow. We used log transformed SLA in this analysis to better fit normality, and SLA values were averaged at the tree level. We ran a two-sided F-test to test for differences in variances, and a two-sided paired t-test to test for differences in means. We ran the var.test function for the homogeneity of variance test (ratio was set equal to 1) from the base R stats package. We used the t.test function with paired set to true, as the paired t-test, which was from the same package.

We collected leaf traits over the course of a season, in varying weather conditions. We know season and climate affect SLA, but we were interested in local effects and the urban-rural gradient. We isolated the climate and temporal effects by adding ordinal date (the number out of a 366-day year when collected), year, and precipitation/temperature at month of collection into a linear model with log transformed SLA as the response variable. We used the residuals from this model to test our main questions (Table 1).

To understand the sources of variation in SLA within and among species, we used model selection methods with linear mixed-effects models (LME) (Zuur et al. 2009). We used a grouped random effects structure in LME model. The unit level consisted of leaves, which were clustered in branches, and branches were grouped in trees. We excluded site from the random effects structure as almost all variation explained by site could be explained by the climate and date covariates. The categorical fixed effects in the model were tree sun exposure, branch canopy level, and species. The continuous fixed factors were diameter at breast height (DBH), distance to water channel, elevation above water channel, and the urban-rural gradient represented by PC1 (Table 1). DBH and tree height were highly correlated, but DBH was a better predictor of SLA in our dataset, so we used DBH in the final model as a measure of plant size. We did not include resprouting status in the final model as it explained a negligible amount of variability in SLA in preliminary analyses (not shown). We then created a “beyond optimal” model following the methods from Zuur et al. (2009), with all possible 3-way interactions among the remaining predictors to account for species-specific interactions and complex interactions. All continuous variables were transformed to z-scores using the base R scale function, and all categorical variables were converted to factors.

We analyzed 3-way interactions among the environmental gradients, tree sizes, and species, which allowed for interactions between species and multiple other interacting predictors. We then used backwards elimination model selection on the fixed effects using a model fit with maximum likelihood (ML) to avoid testing at the boundary. We ran the linear mixed effects models and model selection using the lmer and step functions respectively, in the lmerTest package (Kuznetsova et al. 2017). The final model was then fitted with restricted maximum likelihood (REML), and p-values were estimated with Satterthwaite’s approximations. This method produces acceptable type I error rates given the uncertainty of estimating degrees of freedom in mixed effects models (Luke 2017). Predicted values were visualized holding all other fixed and random effects constant using the ggpredict function in ggeffects package (Lüdecke 2018).

Table 1: List of variables that went into the linear model (LM) and linear mixed effects model (LME) as response variables, covariates, and predictor variables.

Variable	**Description**	**Data type**
Log(SLA)	Log transformed specific leaf area	Response in LM
Temperature	Monthly mean temperature at collection date	Covariate in LM
Precipitation	Monthly mean precipitation at collection date	Covariate in LM
Ordinal Date	Ordinal day of year when collected	Covariate in LM
Year	Year of collection	Covariate in LM
Log(SLA) Residuals	Residuals of covariate linear model	Response in LME
Species	Tree species	Predictor in LME
Sun Exposure	Light level of tree; sun tree or shade tree	Predictor in LME
Canopy	Canopy level; upper (top) or middle (mid)	Predictor in LME
DBH	Diameter at breast height (1.37m)	Predictor in LME
Elevation	Elevation above closest water channel	Predictor in LME
Distance	Distance to closest water channel	Predictor in LME
Urban-rural Gradient	PC1, including land cover classes and elevation above sea level	Predictor in LME

Results

A total of 155 trees and 1797 leaves were analyzed for the main linear mixed effects model. The pairwise data consisted of 70 trees (35 of each species) and 837 leaves.

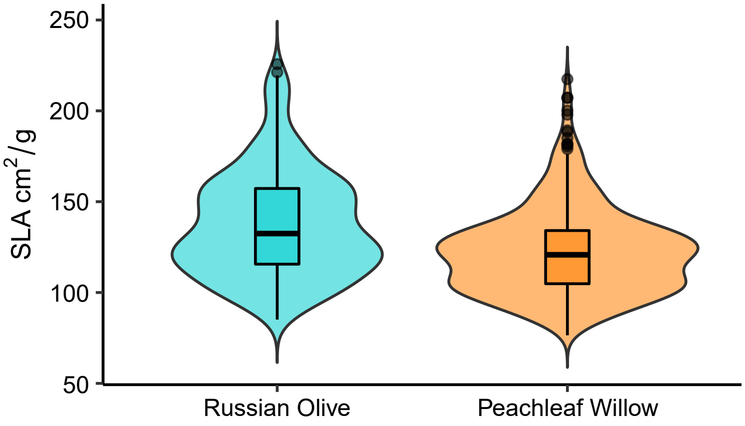

Figure 2: The pairwise distributions of observed SLA by species. Boxplots indicate median values and the interquartile range, and intraspecific variance within species is displayed in the violin plot. Pairwise tests used log transformed SLA tree means to avoid pseudoreplication and to better fit normality. The homogeneity of variance test showed SLA variances of the paired trees were not significantly different (F = 1.17, ndf = 34, ddf = 34, p-value = 0.647).

Pairwise Tests

Mean SLA (expressed in cm^2/g) for Russian olive was (M = 142, SD = 38.5, n (leaves) = 1380) and peachleaf willow was (M = 122, SD = 24.0, n (leaves) = 417). The paired t-test showed a significantly higher average for Russian olive, (t = 3.69, df = 34, p-value < 0.001), but the variances between species were not significantly different (Fig. 2).

Interactions Among Predictors

Among the seven predictor variables evaluated, all variables contributed to explaining SLA after accounting for variability due to date, seasonal climate (Appendix C), and significant interactions with other variables (Fig. 3). We found the conditional R^2 (with random effects) to be 89.2% and the marginal R^2 (only fixed effects) was 34.0% in the selected model. There was only one significant interaction with species, so both species are combined in the following reporting of results.

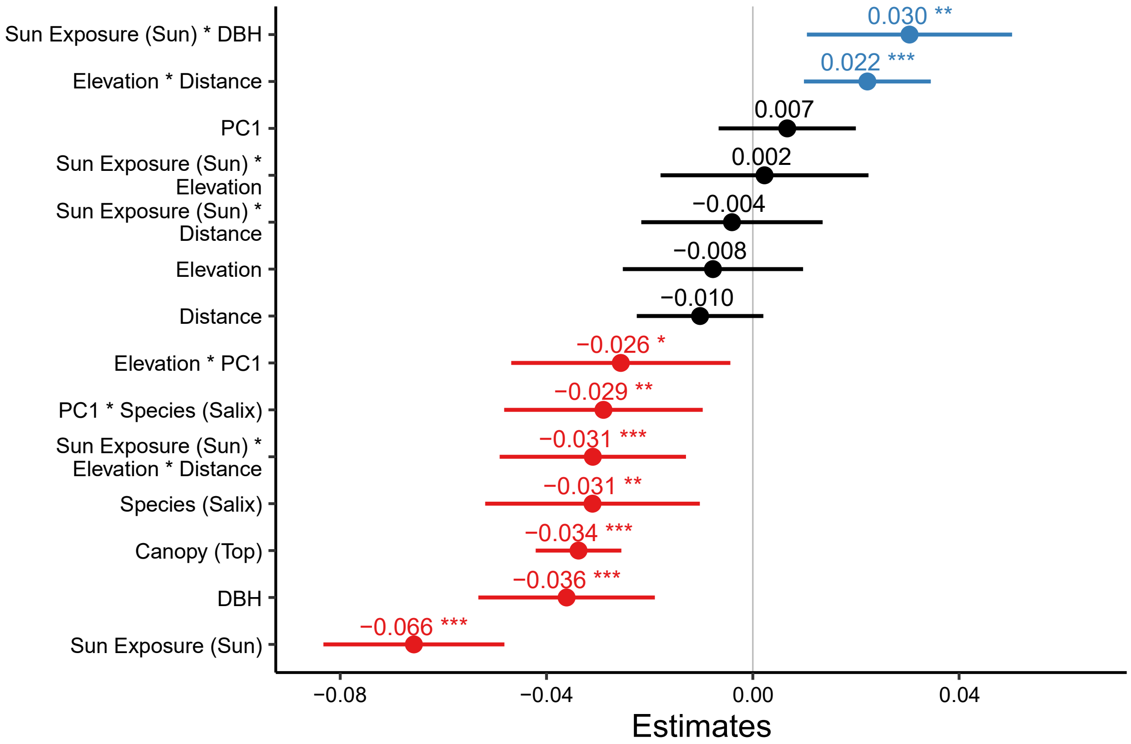

Figure 3: Parameter estimates to explain variance in SLA with the effect of covariates removed from the most parsimonious linear mixed effects model with fixed effects and interactions. No significance is denoted by black, significant positive estimates are blue, and significant negative estimates are red. Model fit with restricted maximum likelihood; significance of predictors and interactions estimated with Satterthwaite estimation of p-values: * p<0.05; **, p<0.01; ***, p<0.001.

Within trees, there was a significantly greater SLA for the lower light middle canopy leaves than for leaves collected from the top (Fig. 4). We also see that canopy position ("Canopy (Top)" in Fig. 3) had the highest predictor parameter estimate in the linear mixed effect model, as all other variables were involved in interactions with lower parameter estimates.

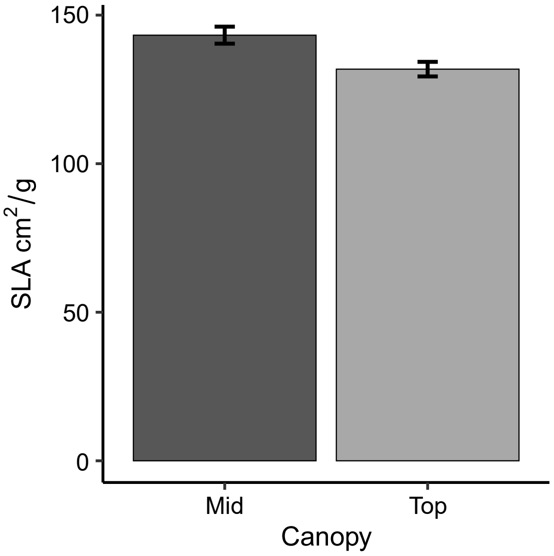

Figure 4: Observed untransformed SLA values for each canopy level with means and standard error bars calculated for averaged middle canopy (Mid) and upper canopy (Top) levels in each tree.

All subsequent interactions are graphed showing the lines of predicted values of the log(SLA) linear model residuals when holding

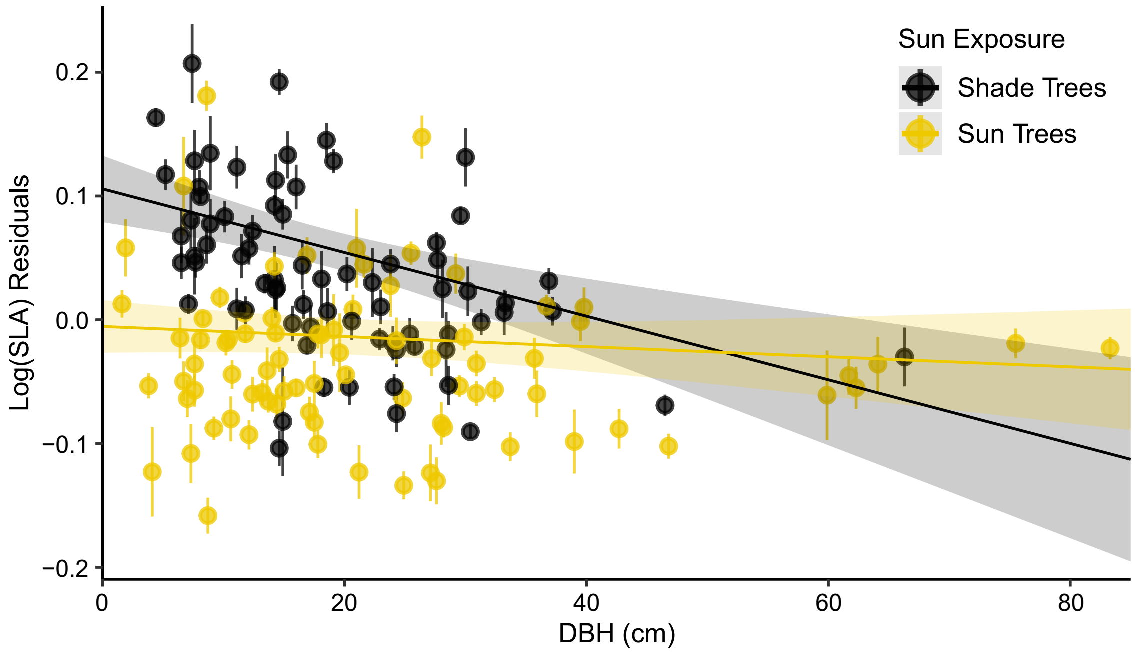

Figure 5: Marginal effects of diameter at breast height and tree sun exposure, where smaller shade trees have higher SLA than small sun trees, but the effect disappears in large shade trees.

all other fixed and random effects in the model constant. Error is shown as 95% confidence intervals. Marginal effects in the interactions are back transformed. The mean of all leaves within a tree are plotted as points with standard errors, given the values of the observed marginal effects and the log(SLA) residuals.

Tree sun exposure and DBH had the largest interaction parameter estimate in this model. This estimate is positive, despite sun exposure (in sun) and DHB both have negative estimates. This is due to a multiplicative effect that results in a positive estimate. In the interaction itself, there are higher SLA values for small shade trees, but as tree size increases, the values for SLA do not differentiate in the sun and shade (Fig. 5). The effect of tree size on sun trees appears to be much less than on shade trees, with only a slight downward slope.

There was an effect of the urban-rural gradient interacting with species. This was the only species-specific response in the model. At negative, more urban values, both tree species had similar predicted values for SLA, but the predicted values of Russian olive increased in more rural areas (Fig. 6a). Peachleaf willow SLA values did the opposite, and decreased with more positive,

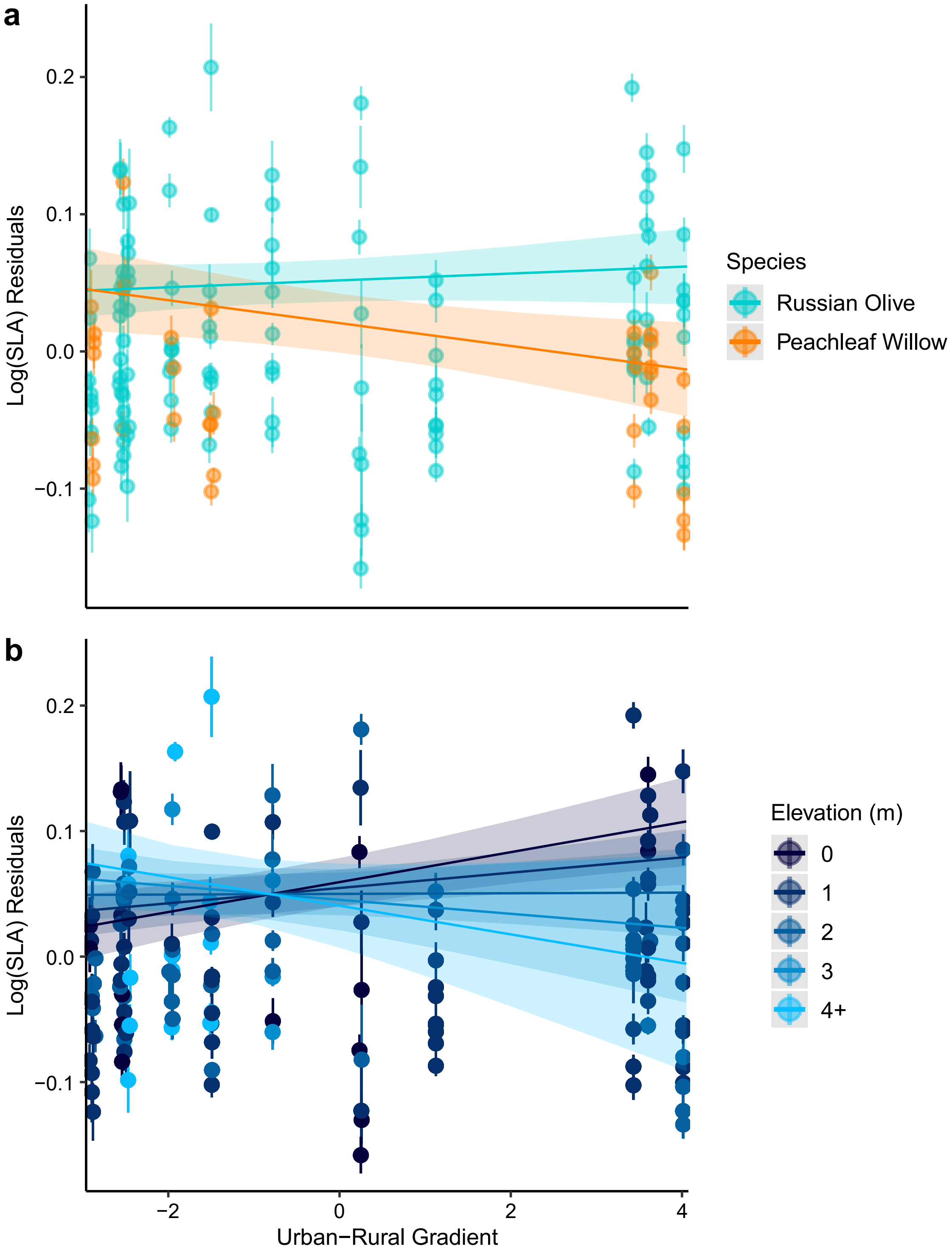

Figure 6: Marginal effects of the urban to rural gradient with a) the two tree species and b) elevation above the water channel. Urban areas are negative, and positive values are more rural. Peachleaf willow has a decreased SLA in rural areas, but Russian olive has a slight increase. SLA goes up with as trees grow close to the channel in rural areas, but SLA lowers at lower elevation in urban areas.

rural values. There was also an interaction between the urban-rural gradient and elevation above the channel. SLA increased in lower elevations above the channel in rural sites, but then decreased with lower elevations in urban sites (Fig. 6b).

Finally, there was an interaction between elevation above the channel, distance to the channel and tree sun exposure, which was the only three-way interaction seen in the model. There were two distinct patterns between sun and shade trees: in sun exposed trees, as trees grew further up and away from the channel, SLA decreased (Fig. 8), whereas in shaded trees, the opposite was seen. As trees grew further up and further away from the channel, SLA increased.

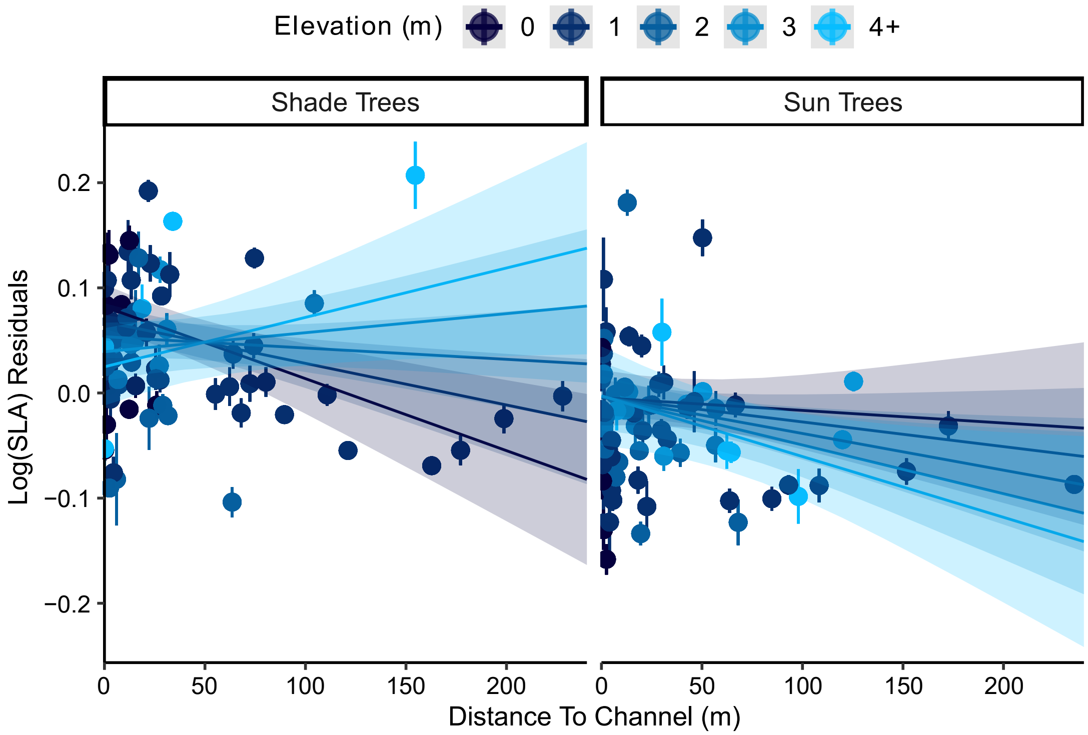

Figure 7: Marginal effects of distance to the water channel, elevation above the water channel, and sun exposure. SLA lowers in sun trees that are far away and high above the channel. A reversal of this pattern is seen in shade trees, where SLA increases higher up and further away from the channel.

Discussion

Light Effects

Canopy Level

We saw that light had the largest impact on SLA in this study; light was consistently found in interactions with the highest parameter estimates. Response to light was not different between our species, despite them having different relative shade tolerances. The overall pattern we observed both within and among individuals, where there was lower SLA in higher light, is consistent with the literature, and linked to improved regulation of water loss through transpiration (Poorter and Werf 1998; Shipley 2002; Marron et al. 2005; Poorter et al. 2009). In sun leaves, the reduction of leaf area along with higher concentrations of nitrogen per unit area, could allow sun leaves to continue photosynthesis at optimal rates while reducing water loss (Legner et al. 2014; Hikosaka 2016). This is likely driven by the stress of transpiration from direct light. There are potential interplays between nitrogen concentration within a canopy and water potential differences and the light levels that leaves are exposed to, but given the importance of light among trees, we expect it is also the main determinant of SLA differences within trees as well. The adjustment of phenotypic traits within individual genotypes in response to environment might be evidence for the potential role of phenotypic plasticity on within canopy SLA, especially in variable light situations, which has been documented in other studies (Avramov et al. 2007; Gratani 2014). For the among-tree interactions, we do not assert any mechanism of intraspecific variability, and it could be from phenotypic plasticity or local adaptation.

Floodplain Position & Tree Sun Exposure

In one of the more interesting interactions, we found that the effect of elevation and distance to the channel reversed in sun or shade. We may have seen this effect in part due to riparian tree’s proximity to and reliance on water from rivers and streams. Trees showed conservative, low SLA strategies in sunny trees further away from the water channel. That strategy is what we would expect given the water limitation further from the channel, compounded by direct sunlight and transpiration. What was unexpected is that the relationship reversed in shade, for both species. The explanation for the lowering of SLA in sun with increasing distance and elevation could simply be explained by evaporation. Soil moisture could be lower in the sun and therefore distance and elevation to water are better proxies of water availability in those conditions. The connection between low SLA and improved maintenance of relative water content may be a reason for why low SLA is seen in high light and low water availability conditions (Nautiyal et al. 2002). Alternatively, as we did not measure the degree of shade, and we might see more shaded areas further up and farther away from the channel in the urban and rural riparian forests. However, in our study areas, the sites tended to have open and scattered canopies, often with more trees closer to the channel, so we doubt this is the main explanation.

We could also be witnessing a tradeoff in strategies when trees are water limited but still in the shade. The advantage of maintaining high light capturing area in low light may be more important for SLA in this system than water limitation. It could be a mixture of scenarios where increased light reduces local soil moisture content, but the lower SLA allows those sun trees to photosynthesize at similar rates per unit leaf area as shade trees. We hypothesize that relative water stress is more pronounced in sun trees. The entire tree may exhibit a more conservative growth strategy if it does not have available water close by, and shade trees simply do not express water stress in SLA as much as sun trees.

Plant Size & Tree Sun Exposure

Response to light also appears to be plant size dependent, which to our knowledge, has not been documented *in situ*. Small trees tended to have higher SLA in the shade when compared to small trees in the sun, but the effect of shade lessened with increasing DBH. It has been shown that SLA decreases with plant size (Shipley and Almeida-Cortez 2003; Liu et al. 2010; Nouvellon et al. 2010; Lusk et al. 2011), either because leaves are simply higher in tall plants and are experiencing water stress due to wind and negative water potential values, or because of increased carbon accumulation from decreased growth rates in older trees. Our finding that there was almost no effect of plant size in sun trees, is consistent with an experimental study that found SLA decreased with age more drastically in low light conditions, but age had almost no effect at the highest light level (Shipley and Almeida-Cortez 2003). This finding could also be a result of our imperfect light metric, because young shade trees are more likely to truly be in the understory of the riparian forest, while larger trees, even if within shade, are taller and more sun exposed than younger trees. The results of Shipley and Almeida-Cortez (2003), which was a common garden experiment, shows support for the biological relevance of this effect. Interestingly, SLA has been found to also the best predictor of RGR in small plants and at low light levels (Lambers and Poorter 1992; Poorter and Werf 1998; Shipley 2002; Marron et al. 2005; Shipley 2006; Gibert et al. 2016). This illustrates how these trait-environment interactions may inform underlying trait-function responses. This is also interesting because, again, we see this effect regardless of species. Larger increases in plant size (and RGR) in small plants under shaded conditions have been documented in shade-intolerant species compared to shade tolerant species (Franceschini and Schneider 2014). This strategy allows shade-intolerant species to outcompete competitors and shade producers, which is a potential explanation for not finding a species effect in our light predictors. Interestingly, it has also been suggested that shade-intolerant species exhibit higher plasticity than shade tolerant species (Gratani 2014). Regardless, we see this effect in both a shade tolerant and shade intolerant species. It's been shown that trait-environment relationship between SLA and light availability has an effect on the establishment of plants in restoration projects, which means understanding the interaction of SLA and light with other variables has broader applications (Zirbel and Brudvig 2020).

Urban Effects

Species & Urban-Rural Gradient

Our two species generally behaved the same in response to the environment, despite their different evolutionary histories and physiological tolerances. We found only one interspecific interaction, which may point to a mechanism of invasion for Russian olive: its ability to fix nitrogen in the soil. The interaction showed that along the urban-rural gradient, peachleaf willow SLA decreased in rural areas, whereas Russian olive's SLA increased. The difference in these species' ability to fix N might point to the mechanism of the effect: urban nutrient pollution. In our study area's urban sites, urban air pollution and atmospheric N deposition can account for a upwards of 20% increase of nitrate in the South Platte River (Wetherbee et al. 2022), and increasing total N content in urban areas is a pattern common to watersheds in both this region (Dell 2016) and other urban areas (Duan et al. 2012; Hobbie et al. 2017; Tromboni and Dodds 2017). It is not surprising then, that a nitrogen-limited species such as peachleaf willow could match Russian olive's acquisitive SLA growth strategy in urban areas with high available nutrients but not in rural areas.

There are other potential factors that affect SLA along an urban-rural gradient, but none that would result in a divergence based on species. For instance, in our study system the urban-rural gradient could not be disentangled from sea level elevation, because urban land uses were at higher sea level elevations than rural. SLA tends to decrease with increasing sea level elevation at global scales, but this is mainly attributed to decreasing temperatures and increasing irradiance along elevational gradients (Midolo et al. 2019; Carvalho et al. 2020), and we did not see a decrease in both species. The total change in sea level elevation also only amounted to about 600 meters, so this would not be expected to be a significant determinant at this scale. One might also argue that higher levels of CO_2 in urban areas can increase the plant's photosynthetically active periods (Wang et al. 2019), and SLA is often correlated with high photosynthetic rates per unit mass. However, we would expect both trees to have increased SLA in areas with elevated CO_2, so this also would not explain the divergence. Furthermore, at least one study found no differences in productivity under elevated CO_2 conditions between invasive and non-invasive species (Hager et al. 2016).

This increase of Russian olive SLA in rural areas may point to another factor at play in our urban to rural gradient. Urban watersheds have more channel incision and built up riprap, which results in less overbank flooding (Solins and Cadenasso 2020). Overbank flooding is an important part of phosphorous deposition in natural floodplain systems (Noe and Hupp 2005; Tibbets and Molles 2005; González et al. 2010). In rural areas with less modified and incised channels, lower elevation might also be associated with higher phosphorous, which could also help explain why potentially P limited Russian olive's SLA increased in rural areas. We conclude that nutrient availability is the most logical explanation for the different responses between these species, with Russian olive potentially benefiting from increased access to P in rural areas, and peachleaf willow taking advantage of available N in urban watersheds.

Thus, our study may shed light on a key potential mechanism of species-specific leaf functional trait responses to urban-rural gradients in other studies. Since our study examined riparian areas with well-studied nutrient dynamics with a nitrogen fixing species and a non-nitrogen fixer, we have convincing evidence that higher SLA in urban areas is a result of nutrient pollution, although it must be acknowledged that we did not measure N in our study. Given the divergence of SLA along the urban-rural gradient in these species, the underlying N fixation of Russian olive, and the clear pattern of urban watershed nutrient pollution in this system, this result is compelling evidence that species-specific effect along the urban-rural gradient is the result of urban nitrogen pollution.

Elevation Above Water & Urban-Rural

We see another interaction with the urban-rural gradient and one of the floodplain position metrics, elevation above the channel. If we continue with our logic from the urban-rural gradient species response, we may also conclude this is also related to nutrient limitation and overbank flooding. While total leaf N_{mass} tends to increase with SLA, this interaction could also be explained with other effects of floodplain position and urbanization effects. As previously mentioned, overbank flooding increases phosphorous deposition, and overbank flooding is more likely in rural areas with less channel incision. In this interaction, a high SLA at low elevations in rural areas does make sense with the high acquisition strategy we might expect. In urban areas, this is reversed where higher SLA is seen higher above the channel. It might be that while there is less overbank flooding, that there are other benefits to nutrient pollution in urban environments. It has also been shown that available N in the environment can alleviate water stress in plants, which may also be a reason for the apparent reversal from conservative to acquisitive strategies high above the channel in urban areas (Iqbal et al. 2020).

Intraspecific and Interspecific Patterns

We had expected higher intraspecific variability in our invasive species, given that another study found significant differences in functional trait intraspecific variation between invasive and native groups (S. Liu et al. 2019), but in our paired comparison, there were not significant differences between the intraspecific variances of the two species. It should also be noted that to characterize intraspecific variation for an entire species, sampling needs to occur throughout the species' range, which was outside the scope of our study. We simply saw that within our study system, co-occurring riparian species did not have significantly different SLA variances. This may indicate intraspecific SLA variation does not account for species tolerances in the same environments. This was also corroborated by the lack of observed interactions between species and most environmental variables in our model. However, the lack of a difference in intraspecific variation between species in our test, does not necessarily mean that the two species do not differ in mechanisms of intraspecific variability. The variation that comes from genetic components via local adaptation, or phenotypic plasticity, is not accounted for in this study. Given that intraspecific variation is not a reliable indication of phenotypic plasticity (Henn et al. 2018), we also cannot rule out that this invasive species may still have more phenotypic plasticity potential than its native counterparts, since invasive species do tend to have higher amounts of phenotypic plasticity (Davidson et al. 2011). Further work on intraspecific functional trait variance would benefit from teasing these two mechanisms apart.

While variances were not different, our invasive, shade tolerant tree species did have a significantly higher SLA, which is consistent with other studies that have found this trend (Lake and Leishman 2004; Sandel and Low 2019). High SLA has also been associated with increased shade tolerance (Liu et al. 2016) , which may better explain differences in tolerances between the two species than interactions with light. It should be noted that our test of environmental interactions was also heavily weighted by the effects of Russian olive, which are overrepresented in the model with interactions. Although, the equally weighted pairwise tests still showed higher SLA for Russian olive, indicating it maintained a fast strategy in N limited settings, while peachleaf willow did not. The species-specific trait of N fixation could also be behind the mean SLA differences, as high N typically raises SLA (Sun et al. 2022). It has been suggested that mutualisms of microbial bacteria and fungi should qualify as a type of functional trait, and our results would bolster that argument. These associations could be crucial factors when assessing functional leaf traits and community assembly. The invasive and native statuses of organisms are arbitrary categories, so understanding underlying mechanisms on more universal scales will only help in the understanding and control of invasive species.

The higher overall SLA of Russian olive, especially in rural settings, also indicates the potential to alter nutrient cycling in communities, which has been documented in Russian olive habitat (DeCant 2008; Follstad Shah et al. 2010; Mineau et al. 2011). This is especially relevant given the literature suggesting Russian olive distributions are in a stage of incomplete dispersal, so controlling Russian olive in rural riparian systems, where its growth strategies are more competitive, may be important for practitioners. Matching species trait phenotypes to projected suitable trait-environment conditions can help inform restoration projects that wish to successfully recover native species, and not just remove invasive species, which can often happen (Gaddis and Sher 2012; Goetz et al. 2021). This requires knowing the range and intraspecific trait variability within an environment to understand niche breadth. On the other hand, the high SLA acquisitive strategy of peachleaf willow in urban areas means it can match the growth strategy of Russian olive in urban watersheds with high nutrient pollution, which would make it a competitive candidate for riparian urban parks. In urban areas, finding native species with ecosystem service benefits and trait phenotypes capable of overcoming anthropogenic filters shows the practical benefit of functional traits and this type of study.

Conclusions

The use of SLA as an indicator of fast versus slow strategies has been questioned due to its high variability and seeming lack of coherence with the worldwide leaf economics spectrum in smaller spatial scales (Wilson et al. 1999; Funk et al. 2017; Messier et al. 2017; Rosas et al. 2019). Yet, at the community level, SLA is one of the best predictors of ecosystem processes (Poorter et al. 2009), and conveys more information about leaf mechanical processes than its separate components (Reich 2014), so it seems important to understand how all of these attributes can be true. As Messier et al. (2017) points out, using leaf traits with confidence on local scales requires that they work consistently with the LES. From our findings, it might appear that local patterns conform to slow strategies in resource limited environments and fast strategies in resource rich environments, but only in particular contexts of interactions among light, water, plant size, and potential nutrient effects. Since this is an observational study, we cannot assert a cause for the SLA patterns, but we suspect that different resources and stressors accounted for different strategies within interactions. Light has the largest effect on SLA, and it potentially overrides the effects of plant size and water availability. We also found that our two species behaved similarly in their response to the interactions between light, floodplain position, and plant size. We would have expected more species interactions, given that SLA is thought of as a shade tolerance trait, and our two species had differing shade tolerances. High SLA may be more important for shade tolerance than intraspecific variance based on our findings. Understanding the relationship of functional traits and local environments is important to improve ecological predictions, because functional traits of plants and animals have been shown to be under selection pressure at least four times stronger than non-functional traits, where abiotic factors influence selection on functional traits more than biotic factors (Caruso et al. 2020). For this reason, understanding local sources of functional trait variance along environmental gradients will not only help us understand trait-environment relationships, but also potential trait-function relationships.

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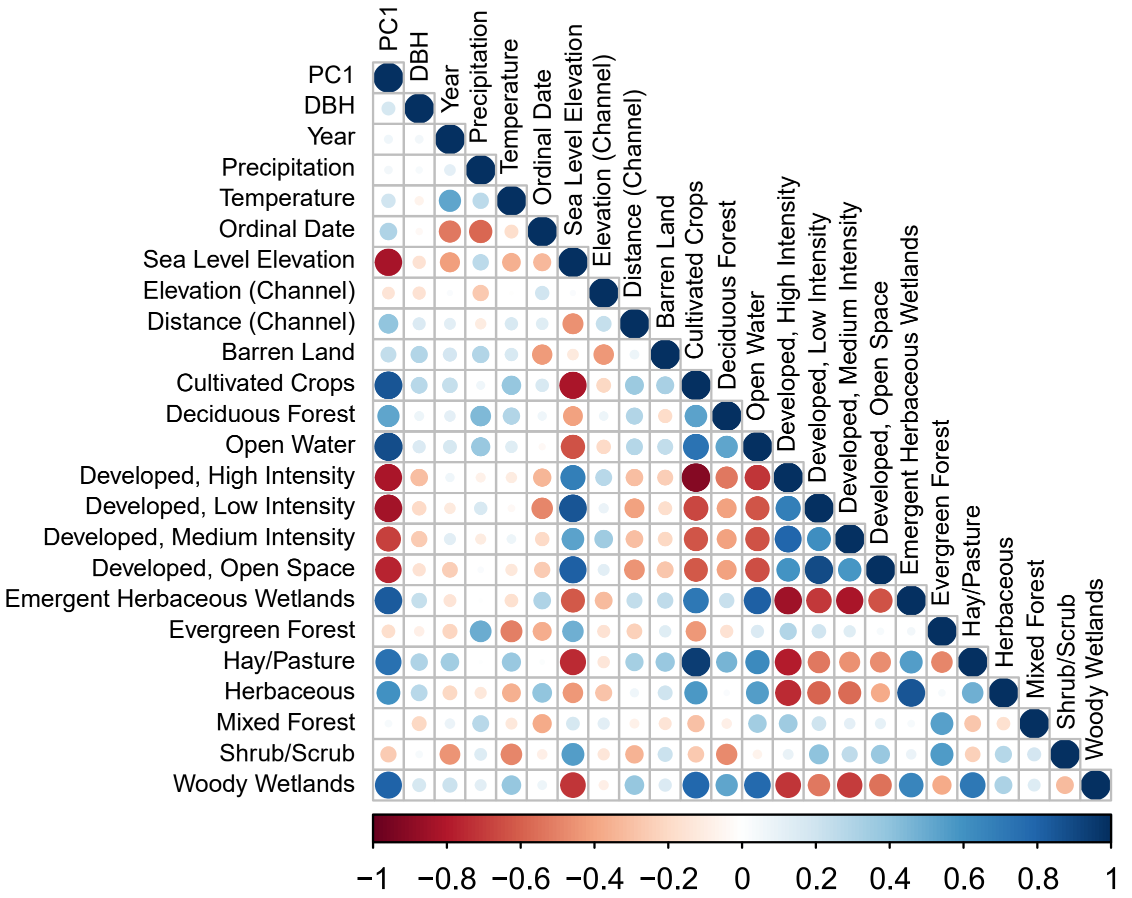
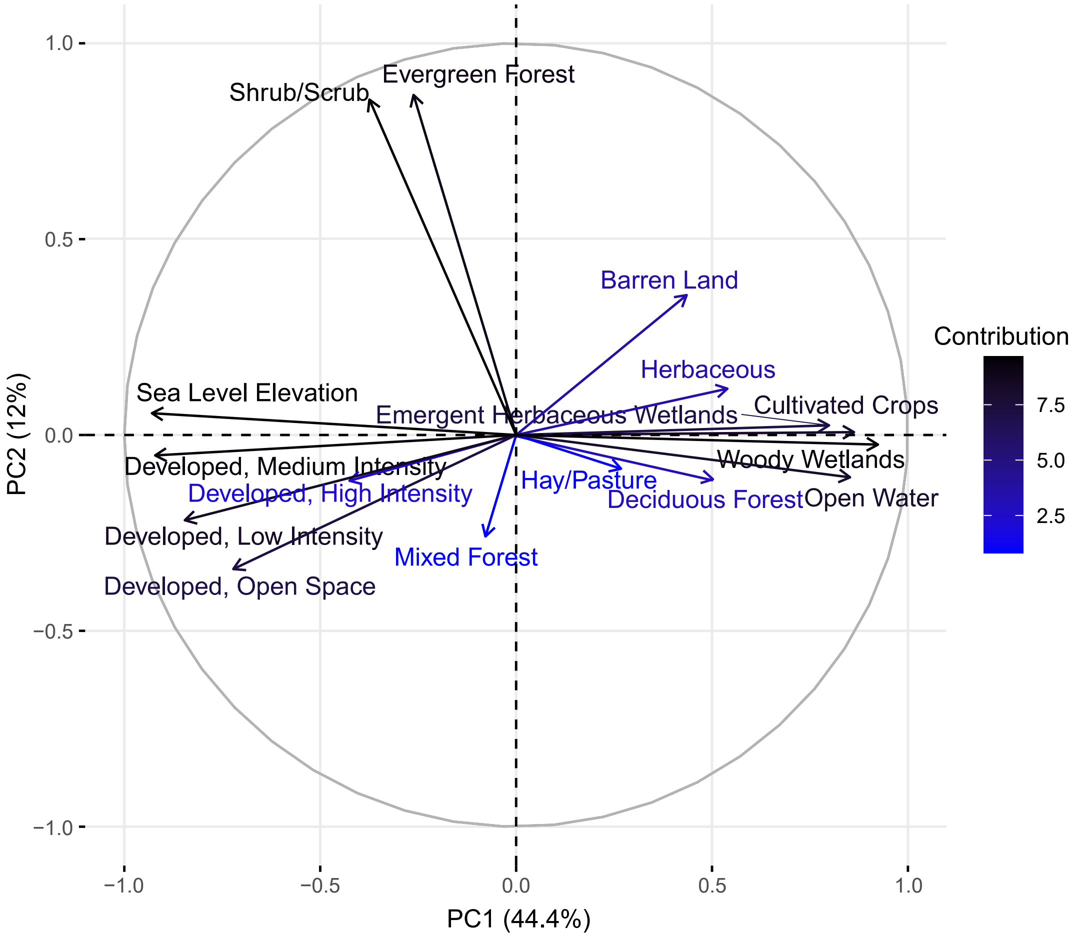
Appendix A



Appendix A: Correlation matrix with Spearman correlation coefficients for floodplain position (Elevation & Distance), plant size (DBH), the urban-rural gradient (PC1), climate and date variables, as well as correlated land classification and sea level elevation variables. High multicollinearity between sea level elevation and the site land classifications were accounted for in a principal components analysis.

All predictors in the mixed effects model, including PC1, DBH, Elevation (Channel), Distance (Channel), had correlation coefficients below 0.4 (Appendix A). Variance inflation factors for all predictors in the linear mixed effects model did not go above 5, which is the threshold for problematic collinearity (James et al. 2013).

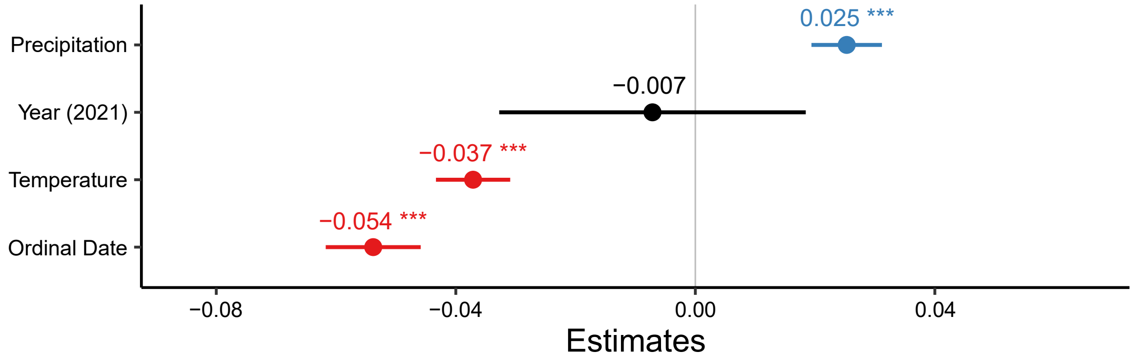
Appendix B



Appendix. B: The principal component analysis of the National Land Cover Database percentages at each site, along with sea level elevation from the U.S. Geological Survey 1-meter Digital Elevation Models. Contributions of variables to PC1 are weighted from largest (black) to lowest (blue). In PC1, on the negative axis, developed land uses accounted for 31.9% and sea level elevation accounts for 12.2% of variation. On the positive axis, woody and herbaceous cover accounts for 31.5% (except for mixed forests), and agricultural uses accounted for 11.5%.

PC1 explained 44% of the variability among sites, while PC2 only explained 12% (Appendix B). Elevation above sea level and the development land uses loaded on the negative side of PC1. Agricultural land uses, along with forests and herbaceous cover, loaded on the positive side of PC1, so PC1 was used as an urban-to-rural gradient.

Appendix C



Appendix C: Parameter estimates from the covariate linear model. There were significant positive effects of monthly precipitation, and significant negative effects of monthly temperature and ordinal date on SLA. No significance is denoted by black, significant positive estimates are blue, significant negative estimates are red; p-values: * p<0.05; **, p<0.01; ***, p<0.001.

We saw significant effects of precipitation, temperature, and ordinal date on SLA in the linear model (Appendix C). Precipitation had a positive effect on SLA, but ordinal date and temperature both had a negative relationship to SLA. The positive effect of precipitation is what would be expected, high SLA in wetter environments. Mean monthly temperature had a negative effect on SLA, which is not would be expected in global models, but considering this is an arid environment, hotter monthly temperatures translated to more stress. Ordinal date had the largest effect size, which is consistent with its importance in the literature. The main linear mixed effects model used the log transformed SLA residuals from the linear model as the response variable to control for the effects of these covariates.