

Effects of drought-response genes of *Populus fremontii* on leaf litter quality and arthropod community composition in a riparian ecosystem

Introduction

Taking a broader view of riparian ecosystem restoration

In the context of climate change, biodiversity loss, resource extraction, and poverty, the activities of multidisciplinary groups like the Society for Ecological Restoration which promote the re-establishment of an “ecologically healthy relationship between nature and culture” (SER, 2015) are laudable and necessary. However, the practice of restoration is expensive, complex, and requires more than a “green thumb and a flair for old-fashioned natural history”: it requires the participation of ecologists and evolutionary biologists (Clewell and Rieger, 1997). For example, it is accepted that in dry-land ecosystems where droughts are expected to increase in frequency and intensity, riparian restoration can only be effective if the plant stock used is adapted to both current and future hydrologic regimes (for example, Landis *et al.*, 2006). To this end, large-scale, intraspecific screening methods for important drought adaptations like resistance to xylem cavitation are being developed for common riparian taxa like willow and cottonwood (Cochard *et al.*, 2007). Susceptibility to xylem cavitation (like many other aspects of drought response), can impact distribution, has the potential to influence competitive outcomes with other species (Pockman and Sperry, 2000), varies substantially among and within all cottonwood taxa (Rood *et al.*, 2003), and is heritable (Street *et al.*, 2006, Cochard *et al.*, 2007). Furthermore, susceptibility to cavitation in cottonwood is positively associated with aboveground biomass production, suggesting a trade-off between growth rate and xylem

Gregory Owens 2017-1-30 11:51 AM

Comment [1]: Whole paper is well written and easy to read. It doesn't use excessive scientific jargon or go off on tangents. All text works towards the central message.

Gregory Owens 2017-1-30 11:35 AM

Comment [2]: Starts off with the bigger picture and why we should care about the topic.

Gregory Owens 2017-1-30 11:36 AM

Comment [3]: Includes citations to back up statements.

weakness (Cochard *et al.*, 2007) that could result in a cline of cavitation vulnerability corresponding to a gradient in stream permanence.

The heritability of communities

It has been shown that some heritable traits of foundation taxa (like the production of tannins in cottonwood) can predictably impact community structure and ecosystem processes via “interspecific indirect genetic effects” (IIGEs) (Whitham *et al.*, 2006). Genetically distinct members of the same plant species have been associated with unique “community and ecosystem phenotypes” for which heritability can be quantified using tools derived from community statistics and quantitative genetics (Whitham *et al.*, 2012). Another example of an IIGE is the impact that leaf litter quality has on the community and ecosystem in which it is localized (Whitham *et al.*, 2012). The idea that the taxonomic origin of leaf litter impacts the consumer community is intuitive and relatively uncontroversial, particularly in light of the inherent structural and chemical diversity associated with litter (for example, Davies and Boulton, 2009 and Compson *et al.*, 2013). However, evidence that plant genotypes can shape communities of litter-associated arthropods is more limited, less conclusive, and the mechanisms by which it might operate remain unclear: importantly, they may not include differences in leaf litter chemistry (Crutsinger. *et al.*, 2008, and Madritch and Hunter, 2005).

Leaf litter as a source of water in dry-land riparian ecosystems

In terrestrial food webs, leaf litter functions as both a food source and a habitat in its own right, and its abundance and composition have been shown to impact arthropod abundance at more than one trophic level (Sabo *et al.*, 2005). In dry-land riparian food webs, trees also function as groundwater pumps, supplying scarce surface water to terrestrial arthropods through

Gregory Owens 2017-1-30 11:37 AM

Comment [4]: Important background information presented clearly and concisely.

greenfall (Sabo, 2008), thereby influencing their abundance (Allen *et al.*, 2014). Greenfall is the name given to the green-coloured leaf litter that is abruptly generated during periods of extreme drought, often as a result of xylem cavitation in a leaf's mid-vein (Street *et al.*, 2006). This is in contrast to the highly regulated process of senescence that occurs seasonally and during extended dry periods in drought-adapted plants, in which macromolecules (including chlorophyll) contained in the leaf are broken down and reallocated back into the plant body, culminating in controlled abscission of (usually yellow) leaves, triggered by increased ethylene production and sensitivity (Taiz and Zeiger, 2010).

Does susceptibility to xylem cavitation impact cottonwood litter-associated arthropod communities?

Here, I propose to investigate a) the existence of a cline of xylem cavitation vulnerability in genotypes of Fremont cottonwood (*Populus fremontii*) corresponding to a gradient in stream permanence, as represented by a cline in the ratio of green to total (green plus yellow) leaf litter generated during drought conditions in a common garden; b) the existence of differences in species richness and composition of litter-dwelling arthropod communities associated with these ratios; and (c) the heritability of both of these phenotypes. I predict that a) the ratio of green to total leaf litter will decrease in trees of drier origin, given the likelihood of a trade-off between growth rate and xylem weakness (Cochard *et al.*, 2007); (b) species richness of litter-associated arthropod communities will increase and change composition with the ratio of green to total litter, given the increased arthropod abundance observed by Allen *et al.* (2014); and (c) these phenotypes (leaf colour ratio and arthropod richness and composition) will cluster with specific tree genotypes when analyzed using non-metric multidimensional scaling, and will exhibit broad-sense heritability.

Gregory Owens 2017-1-30 11:43 AM

Comment [5]: Clear links between the different concepts introduced. It makes sense why one would affect the other.

Gregory Owens 2017-1-30 11:45 AM

Comment [6]: Hypothesis makes sense with background information and predictions are binary (e.g. "species richness will increase", not "I'll investigate species richness").

Methods

Study organism

Populus fremontii (Fremont cottonwood, see Figure 1 in Appendix I) is a drought and heat-tolerant riparian tree distributed in patches throughout the south-western United States and Northern Mexico (Little, 1971). As a foundation species with a fully sequenced genome and well-established connections between at least one phytochemical quantitative trait locus, a unique ecological community, and essential ecosystem processes, it is an ideal model organism for community and ecosystem genetics (Whitham *et al.*, 2006). Much is already known about its susceptibility and drought and xylem cavitation (Street *et al.*, 2006, Cochard *et al.*, 2007).

Common garden experiment

Five clones will be derived from each of five populations of *Populus fremontii* that span a gradient of stream permanence (from perennial to intermittent) along Sycamore Creek, the site of a long-term ecological study near Phoenix, Arizona (Jones *et al.*, 1997). These five source populations will represent five different genotypes. All clones will be planted in a common garden along an intermittent reach of the creek, which will be similar in flow permanence to the driest region from which the trees were sourced. 2.5m-high, lightweight fences made of large-gauge plastic mesh will be erected around trees to minimize spreading of leaf litter from beneath donor trees. Visual estimates of the ratio of green to total leaf litter under each tree will be made every week between May and August. Litter-associated arthropods will be collected from pitfall traps (one per tree) every two weeks, with traps being left out for forty-eight hours each time. They will be identified to species, and species richness will be calculated. Tree and arthropod data will be analyzed using non-metric multidimensional scaling, and broad-sense community

Gregory Owens 2017-1-30 11:47 AM

Comment [7]: Methods detail the key points, but don't get into the nitty gritty. Scope of the experiment is doable as an undergrad/masters student in a couple years.

heritability will be calculated as $H^2_C = \sigma^2_{\text{among foundation genotypes}} / \sigma^2_{\text{total}}$ as suggested in (Whitham *et al.*, 2006). Additionally, hydrographic data from gauge sites will be available to ascertain dates of lowest stream flow.

Gregory Owens 2017-1-30 11:47 AM

Comment [8]: Basic statistical analysis proposed.

Anticipated results

Trees sourced from reaches having the highest year-round surface flow (towards the perennial end of the gradient) are expected to generate the most greenfall (see Figure 2, Appendix I), and as a result, be associated with the highest richness of litter-dwelling arthropods (Figure 3, Appendix I). Leaf colour ratio and arthropod richness and composition will cluster with specific tree genotypes when analyzed using non-metric multidimensional scaling, and will exhibit broad-sense heritability. These results will be most striking for dates associated with the lowest streamflow.

Gregory Owens 2017-1-30 11:48 AM

Comment [9]: Anticipated results make sense based on background information given.

Discussion of significance

Because hydrology is a major factor controlling dry-land riparian ecosystem structure and function, human alterations to the hydrologic regime (such as groundwater extraction and dam construction) have the power to shape communities (Stromberg *et al.*, 2013). Likewise, the genetic provenance of the plant stock employed in ecosystem restoration could shape associated arthropod communities and beyond, in which case the input of ecologists and evolutionary biologists will add value to future ecological restoration projects.

Gregory Owens 2017-1-30 11:48 AM

Comment [10]: Discusses results in a broader context, linking back to why we care about the topic in general. What do we get out of your study in the end?

Appendix I: Figures

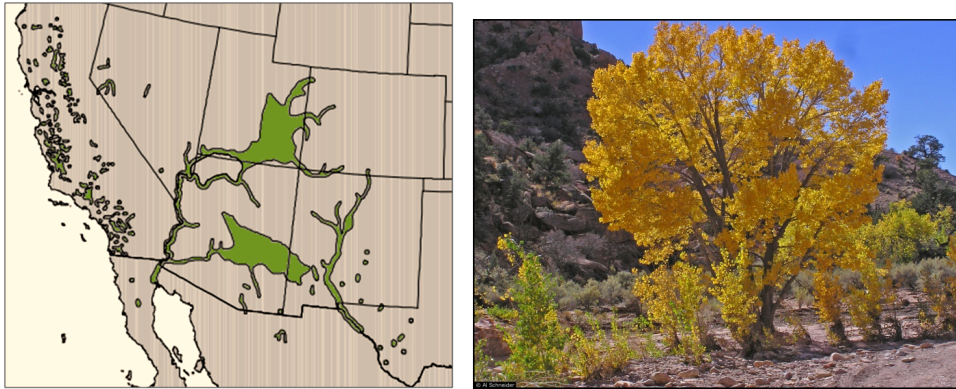


Figure 1 (left) Range of the riparian tree species *Populus fremontii*, which includes parts of the southwestern United States and northern Mexico, modified from Little (1971); (right) *Populus fremontii* (redorbit.com).

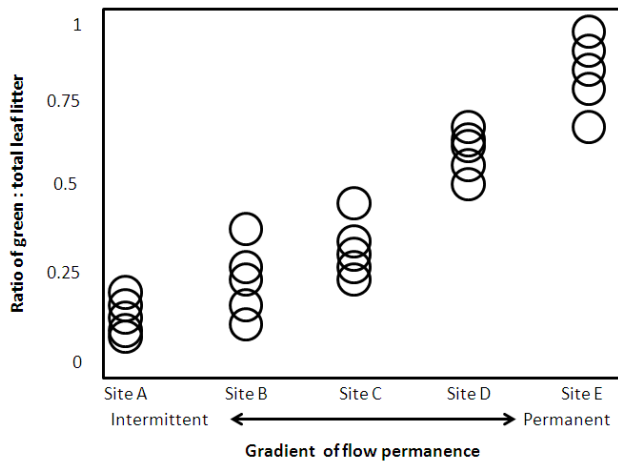


Figure 2 Predicted relationship between tree genotype (based on site of collection along a gradient of flow permanence, aka hydrologic provenance) and xylem cavitation susceptibility (ratio of green to total leaf litter produced during drought conditions in a common garden). Each circle represents the mean ratio of leaf colour generated by a single tree during the four-month period of observation.

Gregory Owens 2017-1-30 11:50 AM

Comment [11]: Figures are not mandatory, but in this case they provide a nice visual depiction of the predicted results to reinforce the text. Could also be used to visually show a complicated experimental design.

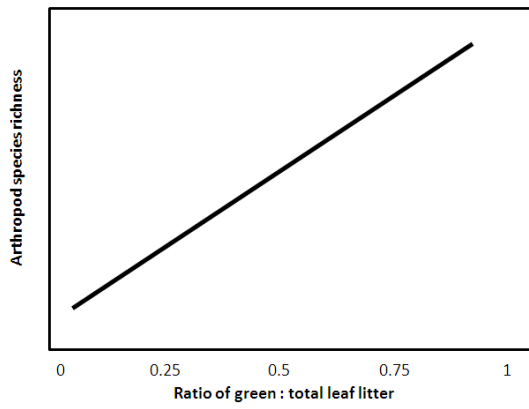


Figure 3 Predicted relationship between the ratio of leaf litter colour to arthropod species richness.

□ Site A ○ Site B △ Site C ♥ Site D ☆ Site E

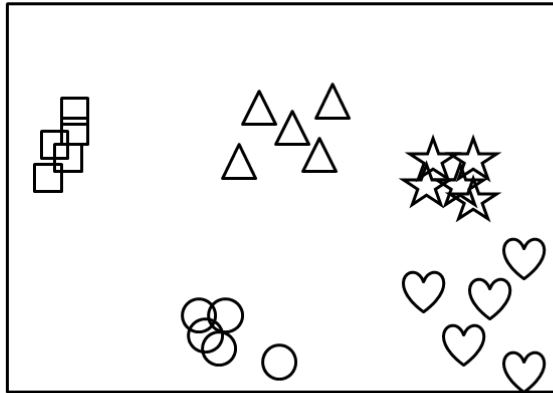


Figure 4 Predicted NMDS of tree genotypes (shapes) grouping according to arthropod community composition.

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Comment [12]: References in a consistent format and checked for errors.

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