ORIGINAL PAPER

Seedling competition between native cottonwood and exotic saltcedar: implications for restoration

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Received: 4 November 2007 / Accepted: 24 September 2008

Abstract Altered hydrology of southwestern United States rivers has led to a decline in native cottonwood (Populus deltoides). Areas historically dominated by cottonwood have been replaced by invasive saltcedar (Tamarix chinensis). Restoration of historic hydrology through periodic flooding of riparian areas has been a means of restoring native species. However, due to similarity in germination requirements of cottonwoods and saltcedars, flooding may create an unwanted increase in the number of saltcedar seedlings. Therefore, we evaluated competitive aspects of these co-occurring species in an extant riparian habitat in the arid southwestern US. We measured effects of competition between cottonwood and saltcedar seedlings and among cottonwood seedlings during the first growing season following seedling establishment in 360, 0.5 × 0.5-m plots at the Bosque del Apache National Wildlife Refuge, New Mexico. We used five interspecific density treatments and five intraspecific density treatments. Cottonwood seedling biomass

$Biomass_{cottonwood}$

Table 1 Models tested for varying seedling densities (X) of cottonwood (i) and saltcedar (j), with the response variable (Y, density or height of either species) in the Bosque del Apache National Wildlife Refuge, New Mexico, 2002

Model		Cottonwood		Saltcedar		References
		ΔAIC (Biomass)	ΔAIC (Height)	ΔAIC (Biomass)	ΔAIC (Height)	
Linear						
1	$Y_i = b_0 + b_1 X_j + b_2 X_i$	15.7	17.9	17.6	12.5	Sher et al. (2000)
2	$Y_i = b_0 + b_1 X_j + b_2 (X_i + 1)^{-1/2}$	7.1	6.3	6.5	6.0	This study
3	$Y_i = b_0 + b_1 X_j + b_2 (X_i + 1)^{-1}$	7.5	7.3	6.3	5.6	This study
4	$Y_i = b_0 + b_1 X_j + b_2 (X_i + 1)^{-3/4}$	7.5	6.8	6.4	5.9	Sher et al. (2000)
5	$Y_i = b_0 + b_1 X_j + b_2 X_i^{-1}$	22.7	24.3	7.9	6.5	Sher et al. (2000)
6	$Y_i = b_0 + b_1 X_j + b_2 X_i^{-3/4}$	8.8	9.4	7.5	6.6	This study
7	$Y_i = b_0 + b_1 X_j + b_2 X_i^{2}$	8.6	8.7	40.4	15.3	This study
8	$Y_i = b_0 + b_1 X_j + b_2 (X_i + 1)^{-1/2} + b_3 (X_i + 1)^{-1}$	1.5	1.4	2.6	1.5	This study
9	$Y_i = b_0 + b_1 X_j + b_2 (X_i + 1)^{-1/2} + b_3 (X_i + 1)^{-3/4}$	0.4	0.4	1.4	0.4	This study
10	$Y_i = b_0 + b_1 X_j + b_2 (X_i + 1)^{-1/2} + b_3 X_i^{-1}$	18.2	18.1	4.8	3.8	Sher et al. (2000)
11	$Y_i = b_0 + b_1 X_j + b_2 (X_i + 1)^{-1} + b_3 (X_i + 1)^{-3/4}$	0.0	0.0	1.1	0.1	This study
12	$Y_i = b_0 + b_1 X_j + b_2 (X_i + 1)^{-1} + b_3 (Xi + 1)^{-1}$	17.7	17.6	3.1	2.0	This study
13	$Y_i = b_0 + b_1 X_j + b_2 (X_i + 1)^{-1} + b_3 X_i^{-3/4}$	1.7	1.7	1.2	0.0	Sher et al. (2000)
14	$Y_i = b_0 + b_1 X_j + b_2 (X_i + 1)^{-3/4} + b_3 X_i^{-1}$	18.0	18.0	4.2	3.1	This study
15	$Y_i = b_0 + b_1 X_j + b_2 X_i + b_3 X_i^{2}$	12.4	12.4	0.0	18.7	This study
Non-linear						
16	$Y_i = W_i / (1 + C_i X_i + A_{ij} X_j)$	240.8[a]	108.0[a]	9,070.5[a]	1,717.2[a]	Shinozaki and Kira (1956)
17	$Y_i = X_i W_i / (1 + C_i X_i + A_{ij} X_j)$	249.2[a]	179.5[a]	10,077.9[a]	1,723.8[a]	Sher et al. (2000)

Note: b_1, b_2, and b_3 are density coefficients and C, A, and W are competition coefficients

[a] Model ΔAIC values were high and models were considered as bad fit

Table 2 Average model (based on the four selected models) for predicting biomass (g) and height (cm) of cottonwood (cw) biomass of saltcedar; reducing saltcedar biomass at higher densities.

Response surface analysis

Increases in saltcedar density from 0 to 25 plants/0.25 m^2 had no negative impact on biomass of cottonwood seedlings (Fig. 1a). Even at a cottonwood-saltcedar ratio of 3:5, biomass of cottonwood seedlings was not affected by competing saltcedar seedlings. Height of cottonwood seedlings, on the other hand was greatest at moderate densities of cottonwood and saltcedar (a mixed density of about 9–12 cottonwood seedlings and 10–15 saltcedar seedlings) (Fig. 1b).

Increases in cottonwood density beyond 7–8 seedlings/0.25 m^2 had a negative influence on biomass of saltcedar seedlings (Fig. 2a). Saltcedar biomass reached a maximum at about equal densities of cottonwood and saltcedar seedlings. From the response surface plane (Fig. 2a), when the density of cottonwood seedlings reached 15–20 plants/0.25 m^2, there was a sharp decline in biomass of saltcedar seedlings. However, a flat response surface plane (Fig. 2b) for predicting the height of saltcedar seedlings suggests that, at higher densities, neither cottonwood nor saltcedar seedling densities had any affect on saltcedar seedling height.

SE 1.14) at 4 plants/0.25 m^2 (Fig. 4). Overall, seedling survival differed (v^2_{4} 28:41, P \ 0.001) among treatments (Fig. 5). Survival of seedlings did not differ between densities of 4 plants and 10 plants/0.25 m^2. However, seedling survival at density of 20 plants/0.25 m^2 was the lowest among all treatments.

Discussion

In restored riparian areas, cottonwood seedlings can outcompete saltcedar seedlings in terms of biomass and height when natural hydrologic conditions are returned to a floodplain. The present state of saltcedar infestation in most river floodplains in the southwest

US is not due to superior competitive ability of saltcedars, but, altered floodplain hydrology, leading to unfavorable recruitment conditions for native cottonwoods. Cottonwoods evolved with the annual flooding cycles of the rivers and the absence of such events has led to altered riparian dominance. Because cottonwood seeds are liberated for only a few weeks each year, absence of annual floods in the recent past have resulted in little to no regeneration of cottonwood. Saltcedar liberates seeds for about 6 months and their seeds are viable for longer than that of cottonwood. Thus, saltcedar seeds may germinate following any precipitation event occurring during the growing season (Horton et al. 1960).

Competitive ability of native cottonwoods against invasive saltcedars

Overall, height and biomass of cottonwoods and saltcedars decreased as total stem density increased. Taylor et al. (2006) also reported height of saltcedar and cottonwood to be negatively associated with higher combined stem densities. Increased numbers of cottonwood seedlings resulted in lower saltcedar biomass (Fig. 3). Also, a higher ratio of cottonwood to saltcedar (15:25) in the treatments, reduced height of saltcedar seedlings. The predictive models for biomass and height suggests a greater influence of cottonwood seedling densities than saltcedar. Therefore, if historical riparian hydrological patterns are restored, cottonwood seedlings, being the superior competitor, will reclaim areas where cottonwoods once were the dominant canopy species (Taylor et al. 2006).

We appreciate help provided by the YCC crew (2002) and the fire crew at the Bosque del Apache National Wildlife Refuge for their help in fieldwork. We also thank Nancy McIntyre, Scott McMurry, and David Wester for their comments.

References

Agresti A (1990) Categorical data analysis. Wiley, New York

Attiwill PM (1994) The disturbance of forest ecosystems: the ecological basis for conservative management. For Ecol Manage 63:247–300. doi:10.1016/0378-1127(94)90114-7

Bhattacharjee J, Taylor JP Jr, Smith LM (2006) Controlled flooding and staged drawdown for restoration of native cottonwoods in the middle Rio Grande Valley, New Mexico. Wetlands 26:691–702. doi:10.1672/0277-5212(2006)26[691:CFASDF]2.0.CO;2

Bhattacharjee J, Taylor JP Jr, Smith LM, Spence LE (2007) The importance of soil characteristics in determining survival of first year cottonwood seedlings in altered riparian habitats. Restor Ecol (in press)

Burnham KP, Anderson DR (2002) Model selection and multimodel inference—a practical information-theoretical approach, 2nd edn. Springer-Verlag, New York

Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am Nat 122:661–696. doi:10.1086/284165

Connolly J (1986) On difficulties with replacement-series methodology in mixture experiments. J Appl Ecol 23: 125–137. doi:10.2307/2403086

Connor EF, Simberloffre6(o300767ksi(re6semWmixt,-505.4(Av2.714n:)-1s3iiy)-3366sema4]TJof)2Csfiodoi:Ehar16/0374-1127(94)90114-7

Scheiner SM, Gurevitch J (eds) (2001) Design and analysis of ecological experiments, 2nd edn. Oxford University Press, New York

Schumm SA, Lichty RW (1963) Channel widening and flood-plain construction along Cimarron River in southwestern Kansas: US Geological Survey Professional Paper 352-D. pp 71–88

Schutz WM, Brim CA (1967) Inter-genotypic competition in soybeans. I. Evaluation of effects and proposed field plot design. Crop Sci 7:371–376

Scott ML, Auble GT, Freidman JM (1997) Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. Ecol Appl 7:677–690. doi:10.1890/1051-0761(1997)007[0677:FDOCEA]2.0.CO;2

Scott WH, Wondzell MA, Auble GT (1993) Hydrograph characteristics relevant to the establishment and growth of western riparian vegetation. In: Morel-Seytoux HJ (ed) Proceedings of the 13th Annual American Geophysical Union Hydrology Days. Hydrology Days Publications, Atherton, California, pp. 237–246

Segelquist CA, Scott ML, Auble GT (1993) Establishment of Populus deltoides under simulated alluvial ground water declines. Am Midl Nat 130:274–285. doi:10.2307/2426127

Sher AA, Marshall DL (2003) Competition between native and exotic floodplain tree species across water regimes and soil textures. Am J Bot 90:413–423. doi:10.3732/ajb.90.3.413

Sher AA, Marshall DL, Gilbert SA (2000) Competition between native Populus deltoides and invasive Tamarix ramosissima and the implications for reestablishing flooding disturbance. Conserv Biol 14:1744–1754. doi:10.1046/j.1523-1739.2000.99306.x

Shinozaki K, Kira T (1956) Intraspecific competition among higher plants VII. Logistic theory of the C-D effect. J Inst Polytech, Osaka City University Series D Biol 7:35–72

Silvertown J, Charlesworth D (2001) Introduction to plant population biology. Blackwell Science, Oxford

Sprenger MD (1999) Restoration of riparian wildlife habitat in the middle Rio Grande Valley following historical river hydrographs. M.S. Thesis, Texas Tech University, Lubbock, Texas

Sprenger MD, Smith LM, Taylor JP (2002) Restoration of riparian habitat using experimental flooding. Wetlands 22:49–57. doi:10.1672/0277-5212(2002)022[0049:RORHUE]2.0.CO;2

Stoll P, Weiner J (2000) A neighborhood view of interactions among individual plants. In: Deikmann U, Law R, Metz JAJ (eds) The geometry of ecological interactions-simplifying spatial complexity. Cambridge University Press, Cambridge

Stromberg JC (1997) Growth and survivorship of Fremont cottonwood, Gooding willow, and saltcedar seedlings after large floods in central Arizona. Great Basin Nat 57:198–208

Stromberg JC, Patten DT, Richter BD (1991) Flood flows and dynamics of Sonoran riparian forests. Rivers 2:221–235

Stromberg JC, Fry J, Patten DT (1997) Marsh development after large floods in an alluvial, arid-land river. Wetlands 17:292–300

Taylor JP, Wester DB, Smith LM (1999) Soil disturbance, flood management, and riparian woody plant establishment in the Rio Grande floodplain. Wetlands 19:372–382

Taylor JP, Smith LM, Haukos DA (2006) Evaluation of woody plant restoration in the middle Rio Grande: ten years after. Wetlands 26:1151–1160. doi:10.1672/0277-5212(2006)26[1151:EOWPRI]2.0.CO;2

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton

Tyler CM, D'Antonio CM (1995) The effects of neighbors on the growth and survival of shrub seedlings following fire. Oecologia 102:255–264. doi:10.1007/BF00333258