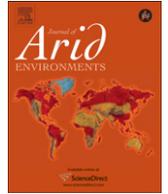




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Optimum seedling productivity in cottonwoods: A function of neighbor distance

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ABSTRACT

In most wind-dispersed species, young seedlings usually grow in clusters. Dense stands of seedlings are however not often recommended for most restoration sites due to poor stand growths. We evaluate the effect of varying neighbor distances on biomass (above ground) and survival of Cottonwood (*Populus deltoides*) seedlings. We used four different neighbor distances (5, 15, 25, and 35 cm) as treatments and planted seedlings in the field in hexagonal arrays. Each array had 31 equidistant seedlings. Bases on the position, seedlings were categorized as growing in the 'core' or the 'edge' in the array. Morphometric measurements of seedling, seedling biomass and survival were recorded. Seedling biomass was lower in treatments where neighbor distances were large, 35 cm or small, 5 cm. There was an optimum neighbor distance (15 cm) where seedlings had the greatest biomass accumulation. Morphometric comparisons of plants growing in different treatments showed that, seedlings had greater stem diameter and more leaves at the neighbor distance of 15 cm than at other distances. Seedling survival did not differ among the four treatment types but was significantly different based on the position of the seedling within an array, with greater survival in the core region than the edge.

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1. Introduction

Competition among plants is an important factor in controlling the structure and composition of plant populations and communities (Harper, 1977). Many plant competition studies have examined the effects of mean density on performance or yield in plant populations (deWit, 1960; Khan et al., 1975; Norrington-Davies, 1967; Schutz and Brim, 1967). Competition studies often assume that an average density provides an effective description of the state of the population without considering variation among individuals (Silander and Pacala, 1985). However, the fate of an individual plant is often contingent upon other plants in its immediate neighborhood (Pacala and Silander, 1990; Tyler and D'antonio, 1995).

Research in the past two decades (e.g., Goldberg and Werner, 1983; Pacala and Silander, 1985; Stoll and Weiner, 2000) has shown that size and number of neighbors primarily determine the outcome of plant interactions, whereas, type of neighbor (species identity) matters less. This theory is reinforced by the idea that all plants require only a few resources (light, water, space, and

nutrients), so species capable of acquiring these resources at a greater rate than others will eventually emerge as the superior competitor. Interactions among plant species are not strongly species specific (Goldberg and Landa, 1991). At a population level, this suggests that a species with greater maximum size is likely to out-compete smaller-sized species in the long term, irrespective of the per-unit-biomass (Stoll et al., 2002).

The dominant native woody species of riparian regions in the southwestern U.S. include cottonwood (*Populus fremontii*) and willow (*Salix* sp.) species. Cottonwood recruitment patterns are temporally irregular, varying to a large degree with the frequencies of El Niño years (Webb and Betancourt, 1992). They recruit in a consistent collateral spatial establishment pattern in high density narrow bands (typically 3–6 m wide) on sandbars (Rood et al., 2003) or freshly scoured areas on river floodplains (Taylor et al., 1999). Seedling density in these "recruitment sites" can be high, often reaching to 500–800 seedlings/m² (Bhattacharjee et al., 2006). However, the number of seedlings that survive the first and second years is often low (Rood et al., 2003; Taylor et al., 2006) unless there is sufficient moisture in the ensuing growing season (Bhattacharjee et al., 2008a; Stromberg, 2001).

Maximizing the density of cottonwoods recruited either in recreated floodplain sites or along active river floodplain through timed water release has been a goal of many riparian woodland restoration efforts (Friedman et al., 1995; Rood and Mahoney, 1995;

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Shafroth et al., 2002). However, increased recruitment does not necessarily result in greater seedling survival, and higher densities may have a negative impact on seedling survival (Augspurger and Kelly, 1984; Clark and Clark, 1984) and growth (Condit et al., 1992; Hubbell et al., 1990). Recruitment of seedlings in high densities therefore, may result in increased resource utilization and intraspecific competition (Bhattacharjee et al., 2006). An understanding of spatial interactions in cottonwood seedlings may enable planting of seedlings at densities (or planting distances) that are optimal for seedling survival and growth and potentially for long-term cottonwood forest establishment.

The relationship between plant competition and patterns exhibited at the population level can be addressed best by considering spatial orientation among plants. This is best accomplished either by using individual based models, IBM (DeAngelis and Gross, 1992; Houston et al., 1988) or the zone of influence models, ZOI (Czaran, 1998; Czaran and Bartha, 1989, 1992; Wyszomirski, 1986) or the ecological field or EF models (Alder, 1996; Walker et al., 1989; Wu et al., 1985). However, the use of these models have been criticized (Berger and Hildenbrandt, 2000) based on the fact that in the ZOI model, the division of resources in the overlapping zone is determined by the modeler and not by from the interaction of plants; and the FE model is far too complex to be universally applicable.

The “field-of-neighborhood” (FON) model was developed based on individual plants (Bauer et al., 2004) to model spatio-temporal dynamics of mangrove forests (Berger and Hildenbrandt, 2000). In the present study, we used a modified FON approach to evaluate the effect of different neighbor distances on growth and survival of newly recruited cottonwood seedlings. Instead of assuming several plants with overlapping zone of influence, in our study, we had seedlings growing at fixed distances without random overlap of the zone of influence. However, the central idea remains unaltered: plants do have a zone within which they are able to influence neighboring plants.

In this study, we evaluate the effect of varying distances between seedlings of cottonwood with regard to biomass accumulation and survival. The main objective was to determine the minimum distance between first-year cottonwood seedlings for optimal growth (greater biomass and survival in the first growing season). We hypothesized that there is a minimum interplant distance (D_{min}) requirement at which cottonwood seedlings grow without experiencing conditions of extreme competition for resources between neighbors. As the distances between cottonwood seedlings decrease (below the D_{min}), there is a decrease in overall growth (biomass) of seedlings and an increase in mortality. Most studies use seedling biomass as a measure of seedling health. However, in our study we compared morphological characteristics of the seedlings at different neighbor distances. This was done to account for the fact that seedlings growing in different neighbor distances may end up with the same biomass, but, morphologically, one (short with broad leaves) may be better suited to survive the existing environmental conditions than another (tall with narrower leaves).

2. Material and methods

2.1. Study site

The study was conducted at the Bosque del Apache National Wildlife Refuge (BDANWR) ($33^{\circ}48''$, $106^{\circ}53''$), a part of the Middle Rio Grande Valley (MRGV) in central New Mexico, U.S. The study was conducted in an impoundment along the Rio Grande at BDANWR (see Bhattacharjee et al., 2006). The impoundment was constructed within the historic Rio Grande floodplain west of the current channel.

Average annual precipitation at the refuge was 21.9 cm, with nearly 50% of the annual precipitation occurring during July, August, and September (Western Region Climate Center, from 1914 to 2003). Average daily maximum temperature from June through September was 23.6°C and average daily low temperature during this period was 13.2°C (Western Region Climate Center, from 1971 to 2000; data for 2001–2003 were not available).

2.2. Experimental design

A hexagonal arrangement of plants (Aguilera and Leuenroth, 1993; Aguiar et al., 2001) was used to estimate the minimum distance between cottonwoods to achieve the greatest biomass accumulation. This experiment was conducted in summer 2003 within the impounded area in a 30×30 m area cleared of all vegetation. To manipulate interplant distances, four sizes of iron frame templates were used so that seedlings in each hexagon were 5 cm, 15 cm, 25 cm, and 35 cm apart, respectively. Seven hexagons of a single size were arranged in a way where one hexagon was surrounded by six others. This arrangement allowed for equal intra-plant distance (Fig. 1), allowing uniform competition for space among plants. Each of these arrangements was termed an ‘array’. Each array (distance treatment) had five replicates. Arrays were positioned in a random manner within the 30 m^2 area. Within an array, we numbered plants from 1 through 31 (total number of plants per array). We further assigned specific positions to each plant, as occupying the “edge” zone, consisting of 18 seedlings, or the “core” zone, with 13 plants, (Fig. 1). All treatments had the same number of plants in each of the two zones, while their neighbor distances varied. Any plant that was in the core zone always had six plants as neighbors while the plants in the edge zone had either three or five plants, depending on their position in the array. This

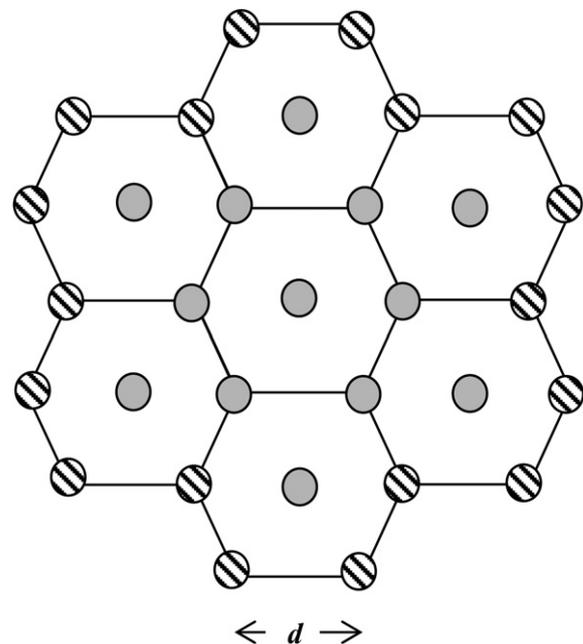


Fig. 1. Representation of a “ D_{min} ” plot used to study effects of interplant distances among seedlings of cottonwood on biomass accumulation. Where “ d ” is the distance between a plant and its neighbor. Circles represent position of plants in plots. Circles with the cross hatch represent plants that were not used for the biomass assessment, as they did not have the equal number of neighbors. They have been called “edge” plants. Circles that are shaded were used in the analyses for biomass estimation and have been called “core” plants. The values of “ d ” were 5 cm, 15 cm, 25 cm, and 35 cm.

experimental design had four treatments and five replicates per treatment.

For us to have access to newly recruited cottonwood seedlings, a separate impoundment adjacent to the one with the experimental plots, was flooded timed with natural seed rain of cottonwoods to create a “seedling bank”. Once the D_{\min} plots were established, about one-week-old seedlings were transplanted from the seedling bank to the experimental plots. Seedlings were cored out along with soil attached to the roots to keep fine roots undisturbed. The average height of seedlings at transplant was 4 cm. Seedlings were planted in the designated experimental plots during evening to avoid high daytime temperatures. Plots were watered twice a day during the first month to ensure seedling survival, after which watering frequency was reduced to once a day and finally to twice a week. Lack of precipitation and unusually high summer temperatures during 2003, made watering of the plants necessary.

2.2.1. Biomass estimation

After allowing plants to grow for three months, individuals from selected plots were clipped at ground level in October (before the plants shed their leaves with the onset of winter). Out of the five replicates for each treatment, one replicate was randomly selected from each treatment as a ‘sacrificial’ plot and all plants from the selected plots were clipped. Plants in the rest of the plots were left for future monitoring of the effects of neighbor distances on tree growth. Dead plants were not included in biomass estimation. Measurements of plant height, length and width of the largest leaf, stem diameter, number of leaves were taken for all the plants. Clipped plants were dried at 42 °C to a constant mass and weighed to nearest 0.001 g. The same measurements were taken simultaneously for the plants in the experimental plots. We developed nondestructive regression models for estimating seedling biomass for each treatment. Therefore, instead of using one model to predict biomass of plants for all treatments, four different models were developed and used to represent each treatment. Variables were selected based on Mallows’ $C_{(p)}$ (Littell et al., 2002). For estimating biomass of plants in different treatments, we used the following equations:

- Treatment: Neighbor distance = 5 cm
Model Fit: $C_{(p)} = 3.95$, $p = 4$, $R^2 = 0.95$
 $Biomass_{5\text{ cm}} = 2.88 + 0.05(\text{height}) + 0.53(\text{number of leaves}) - 0.27(\text{length of largest leaf}) + 0.34(\text{width of largest leaf})$
- Treatment: Neighbor distance = 15 cm
Model Fit: $C_{(p)} = 5.02$, $p = 5$, $R^2 = 0.87$
 $Biomass_{15\text{ cm}} = 2.02 - 0.08(\text{height}) + 0.16(\text{number of leaves}) + 0.40(\text{length of largest leaf}) + 10.41(\text{stem diameter}) + 0.22(\text{number of neighbors})$
- Treatment: Neighbor distance = 25 cm
Model Fit: $C_{(p)} = 5.00$, $p = 5$, $R^2 = 0.97$
 $Biomass_{25\text{ cm}} = 2.20 + 0.09(\text{height}) + 0.05(\text{number of leaves}) - 0.59(\text{length of largest leaf}) + 0.53(\text{width of largest leaf}) + 0.55(\text{stem diameter})$
- Treatment: Neighbor distance = 35 cm
Model Fit: $C_{(p)} = 4.03$, $p = 4$, $R^2 = 0.98$
 $Biomass_{35\text{ cm}} = 1.87 + 0.01(\text{height}) + 0.07(\text{number of leaves}) - 0.16(\text{length of largest leaf}) + 7.23(\text{stem diameter})$

2.2.2. Seedling survival

Plants in each array were numbered and their position marked to identify an individual plant in case of mortality. We monitored

mortality of seedlings in all plots during five sampling periods (beginning August through October). We marked the position and identification number of any seedling that died and removed it during each round of sampling.

3. Data analyses

The response variable biomass was evaluated for normality by using Shapiro–Wilk test and analyzing residuals and quantile–quantile plots (Kutner et al., 2004: 100–153) and was log transformed to meet assumptions underlying analysis of variance. We used a one-way analysis of variance (SAS[®] PROC MIXED, SAS/STAT 2004) to test for potential differences in end-of-season biomass of plants among treatments. In this analysis, biomass was the dependent variable and the varying neighbor distances (5, 15, 25, 35 cm) were independent variables. We also used a one-way multivariate analysis of variance (MANOVA) to test if height, number of leaves, length of the largest leaf, width of the largest leaf, and stem diameter varied as the distance between neighbors changed. We used multivariate multiple comparison method (PROC MULTTEST, Westfall et al., 1999:227–239) to test for simple effect differences among the above mentioned variables when MANOVA was significant (based on values of Wilks’ Lambda). To examine if there was a pattern in seedling mortality based on the position of a seedling relative to its neighbors (i.e., seedlings growing on the edge vs. the core region), we used a logistic regression (SAS[®] PROC GENMOD) with proportion of live plants in a plot as the dependent variable, and position of a seedling in a plot and different neighbor distances as independent variables.

4. Results

4.1. Seedling biomass as a function of neighbor distance

Seedling biomass varied ($F_{3,12} = 44.66$, $P < 0.001$) among distances between neighbors. Seedlings accumulated greatest biomass when the distance between neighbors was 15 cm. Seedling biomass declined when distance between neighbors increased to 25 or 35 cm or decreased to 5 cm (Fig. 2). When the distance between neighbors was 5 cm there was also lower biomass.

4.2. Effect of position in seedling survival

Survival of cottonwood seedlings was not different ($\chi^2_3 = 4.67$, $P = 0.19$) among the four interplant distances. However, position of seedling within a plot (edge or core) was important in determining

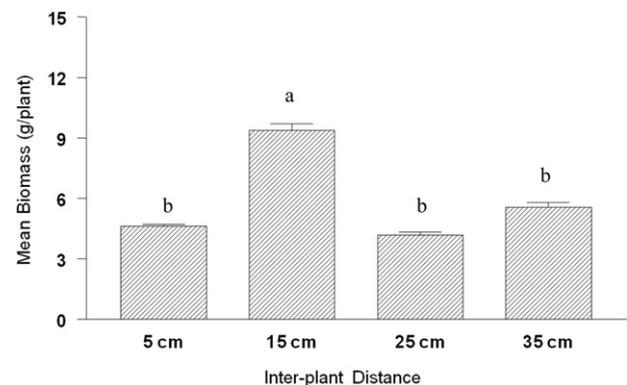


Fig. 2. Mean seedling biomass (per plant) at different D_{\min} treatments (5, 15, 25, and 35 cm) between neighboring plants. Different letters indicate differences ($P < 0.1$) among treatments.

($\chi^2_1 = 4.03, P = 0.04$) probability of seedling survival in cottonwoods. Seedlings had a slightly greater chance of survival (74%) when they were positioned in the core region and a lower chance of survival when on the edge (69%).

4.3. Effect of treatment on seedling morphology

Morphological characteristics (number of leaves, length and width of the largest leaf, diameter of stem) of seedlings differed among plants (MANOVA: Pillai's Trace, $F_{18, 27} = 1.97, P = 0.054$) growing in the four treatments. When the neighbor distance among seedlings was 15 cm, seedlings of cottonwoods had greater mean stem diameter than when the neighbor distance was 5 cm. Seedlings were shorter when the neighbor distance was 5 cm, compared to 15, 25, and 35 cm. Mean number of leaves was the lowest at neighborhood distances of 5 and 25 cm. Also, there is no significant difference in mean number of leaves between 15 and 25 cm distances (Fig. 3). The pattern of longer and wider leaves increases significantly from 5 cm to neighbor distances of 15, 25 and 35 cm. Between the 15, 25 and 35 cm distances, there was no monotonic trend in the leaf measurements (Fig. 4). Therefore, seedlings had wider and longer leaves when neighbors were at least 5 cm away, and thus, less clustered.

5. Discussion and conclusion

Biomass accumulation by cottonwood seedlings of the altered riparian habitats in southwestern US varied with distance to neighbors. Seedlings had lower biomass at relatively both large and small neighbor distances. At an estimated optimum 15 cm distance, seedlings had the greatest biomass. Cottonwood seeds are wind and water dispersed, which often results in their aggregation in seedling clusters. Seedling densities >500 plants/m² were observed in our study and by Taylor et al. (1999). Recruitment of seedlings in such high densities is usually followed by a low survivorship (88% mortality by the end of 3 years, Scott et al., 1999, and about 65% mortality in the first year of growth, see Bhattacharjee, 2005).

Seedling recruitment is an essential precursor to restoration of degraded riparian areas (Briggs et al., 1994), as other means, such as pole plantings are extremely cost and labor intensive (Taylor et al., 1999). Most riparian restoration efforts tested ways of recruiting high densities of seedlings (Rood and Mahoney, 1995; Shafroth et al., 2002; Sprenger et al., 2002; Taylor et al., 1999). The lack of

natural flooding events has reduced recruitment of seedlings (Howe and Knopf, 1991) and based on the low seedling survival during the first year, it may seem necessary to recruit the largest number of plants possible. This to an extent would be similar to episodic recruitment that would happen naturally in the event of a flood. However, the numbers of seedlings that make it to the stage of a mature tree are quite low (Taylor et al., 2006). Therefore, restoration efforts should foster recruiting seedling that are greater in biomass (with healthier seedlings more likely to grow into trees) with optimum densities for seedling survival and growth. Importance of seedling recruitment should be tied more to the performance of seedlings after recruitment. Measurements of seedling morphology also revealed that seedlings growing under conditions of reduced interplant distances had lower competitive ability (due to smaller leaf sizes, lower number of leaves per plant, and smaller basal diameter of the stem) even though mean height of seedlings did not differ among treatments.

Seedling mortality across treatments was also driven by location of the seedling within a plot. Seedlings in the edge regions had slightly lower survival than those in the core regions. This trend in survival supports findings by Stromberg (1997) who reported relatively higher cottonwood seedling survival when newly recruited seedlings were shaded by sweet clover during summer when temperatures were high. Further, if microclimate at the edge of an adult tree stand is hotter, drier, and more severe as compared to the interiors (Bruna, 1999, 2002, Benitez-Malvido, 2001; Camargo and Kapos, 1995; Kapos, 1989), then it is possible that a similar condition also occurs in a smaller scale. Plants on the edge may act as barriers and shield seedlings positioned in the interior from extremes of temperature and moisture stress, thus ameliorating adverse conditions for seedlings at the interior. Presence of neighbors is more likely to create favorable growing conditions by changing the microclimate (ambient temperatures and light quantity and quality, Menges and Waller, 1983) in the locale. Thus, when seedlings have neighbors relatively far apart, conditions become analogous to a seedling 'without' any neighbors and it is more likely to die due to severe environmental conditions.

It is evident that amassing resources by plants at the seedling stage is particularly important in determining their survival (Harper, 1977). For example, biomass in cottonwood seedlings was a function of seedling density. An increase in the neighbor distance from 5 to 15 cm resulted in increased seedling biomass; however, when neighbors were 25–35 cm apart there was a negative impact on biomass. Results of this study further suggest a nonlinear density-yield function, meaning seedling biomass increases with increasing neighbor distance, but may decrease after a certain neighbor distance is attained (Stoll et al., 2002).

The dependence of seedling survival on density (considered interplant distance in our study) can be applied to any habitat restoration program where the primary goal is to recruit pioneering tree species, to be followed by the natural ingression by other co-occurring species. The negative impact of high initial seedling density on seedling performance (biomass accumulation and survival) has also been reported in many studies from the tropics (Webb and Peart, 1999) to the boreal forests (Johnson et al., 2003). Our results support findings from other studies where effects of the presence of neighbors are not diffuse through a population but involve rather precise, quantifiable local interactions (Mack and Harper, 1977). Local crowding in plants is an important factor determining performance of individual plants (Mithen et al., 1984; Watkinson et al., 1983), and results of our study also indicate that differences in neighbor distances affect seedling fitness (biomass) in cottonwood seedlings during the first year of growth. Sprenger (1999:78–82) also reported increased competition and reduced biomass in cottonwoods seedlings growing at higher intraspecific

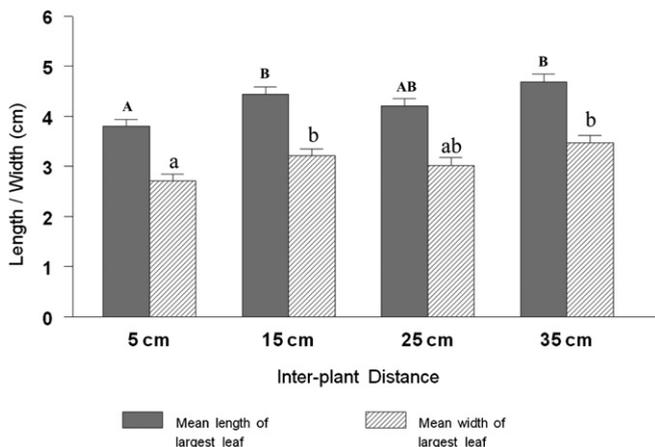


Fig. 3. Mean height, number of leaves per plant, and mean stem diameter at different interplant distances. Treatment means followed by either different lower or uppercase letters or numbers are different at $P < 0.1$.

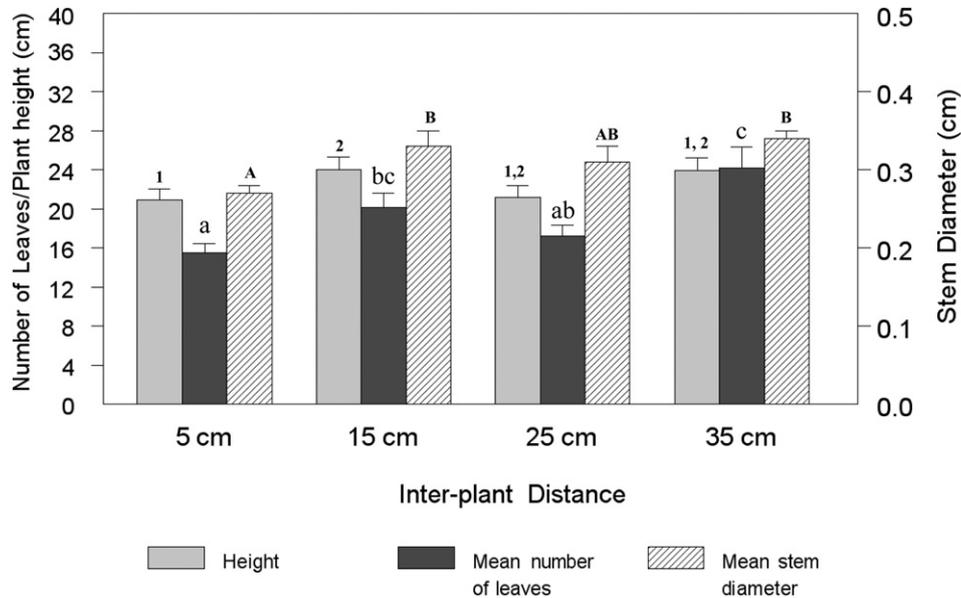


Fig. 4. Mean number of leaves per plant, and mean length and width of largest leaf at different interplant distances. Treatment means followed by either different lower or uppercase letters are different at $P < 0.1$.

densities (median biomass/plant at 20 plants/0.20 m² plot was 0.79 g against 17.54 g when there was one seedling in the plot). In this study, biomass per plant at a density of 4 plants/0.25 m² was about 16 g and about 10 g at the density of 40 plants per plot. Results of competition experiments conducted by Sher et al. (2000), Sher and Marshall, 2003) in the greenhouse also revealed that cottonwood seedling biomass decreased as density of seedlings increased. However, the present study and other studies mentioned above have worked with seedlings, and that no inference on optimal spacing for long-term success can be drawn from these studies as the optimal spacing changes continuously as seedlings grow into adult trees.

While restoration goals in most cases are driven by a additional factors not included in this paper, including hydrology, soil conditions and types, vegetation composition, to name a few, it is very important to be able to recruit the pioneering species first so that they can ameliorate conditions necessary for associated species to be recruited with time. Many land managers use simulated flooding to recruit native species and some consider higher densities as more successful than lower densities, without taking into account that initial high densities of cottonwood may lead to trees with lower DBH and hence low stand volume (Bhattacharjee et al., 2008b; Taylor et al., 2006). The results of our study have a tremendous practical value to managers who may not have high nurse tree density and who use seed bearing branches to establish low but effective plant densities. Further, for restoration sites where natural recruitment is not possible and “plant nurseries” are to be established, results from this study will provide a method for obtaining seedlings that will survive better and have optimum productivity (biomass accumulation) and therefore, aid in successful revegetation efforts. While our results are based on in-field experiments with cottonwood seedlings, the concept of optimum is seedling spacing is more global and may be used for any given species of interest, thus deriving species-specific D_{min} value, to be used by land managers.

For successful restoration of cottonwood in riparian areas, it is important to begin with a seedling cohort that is robust and has high survival, if the primary objective is to restore cottonwood forest as quickly as possible (Taylor et al., 2006). Obtaining high densities of seedlings alone may not result in healthy seedlings, due

to increased competition and reduced productivity. Therefore, low density recruitment of seedlings should be considered as potentially successful, following a few years growth. While it may be labor and time intensive to achieve equal distances among seedlings, it may be noted that hypothetically, if plants are grown at a D_{min} of 15 cm (as in our case for cottonwoods), in 1 m² area, one can pack or grow about 22 plants/m². This value is relatively close to an average of 19 plants/m², the density of cottonwoods obtained in a system where a slow water drawdown was timed with natural seed dispersal (Bhattacharjee et al., 2006) to restore cottonwood forests in the Bosque del Apache National Wildlife Refuge, in New Mexico. Therefore, in arid and semi-arid regions, where water is scarce and annual flooding events do not occur as often, carefully timed and well managed water drawdown can be used to obtain desired plant densities for successful restoration.

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