INFLUENCES OF DROUGHT AND FLOOD STRESSES

ON RIPARIAN COTTONWOODS AND WILLOWS

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.

This thesis is dedicated to:

Marvin, Louise and Grant Amlin
and
Randal, Nikki, Benjamin and Jesse Holwerda

You all may be (are) crazy, but
I couldn't ask for a more terrific family.
Love always.

Abstract

Cottonwoods (*Populus* sp.) and willows (*Salix* sp.) are generally limited to riparian landscapes in semi-arid regions of western North America. Water availability is a major determining factor for the establishment, growth and survival of these plants. Willows generally occur closer to the stream and at lower elevations than cottonwoods, suggesting reduced drought tolerance and increased flood tolerance. In the present thesis project, three related studies were conducted to investigate this hypothesis. Firstly, tolerable rates of water table decline and the impacts of the corresponding drought stress were investigated by growing cottonwoods and willows under water table decline rates from 0 to 12 cm/d. Willow saplings responded similarly to cottonwood saplings, but willow seedlings were more vulnerable than cottonwood seedlings to rapid rates of water table decline. In the second study, willow saplings tolerated elevated water tables of 0 to 7.5 cm below substrate surface and the resulting flood stress for 152 days slightly better than cottonwood saplings. Finally, mature cottonwoods along Willow Creek, Alberta experienced water table decline from 1996 to 1998 due to water pumping in a nearby gravel pit; the water table recovered in 1999. The cottonwoods displayed physiological changes indicating drought stress in 1998 and recovered following restoration of the water table. This confirmed the cottonwoods' reliance on the water table as their primary moisture source. These studies indicate that the spatial separation of willows and cottonwoods may be particularly related to reduced drought tolerance of willows and these display only slightly increased flood tolerances. The studies confirm that both willows and cottonwoods are physiologically dependent on a sufficient riparian water table.

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When I first came to University, I never would have guessed that I could get my Masters of Science in my two favorite things: trees and water. There are many people I need to thank. Special thanks are extended to Stew Rood for supervising this project and tolerating the mood swings. Thanks are directed to John Mahoney, Cam Goater and Bob Rogerson, my thesis committee members, who provided direction to this "phantom" grad student. I thank the Gary Brown and Family, Alberta Infrastructure, Ron May and Alberta Environment for permitting this research on their lands. Thanks are also extended to the Natural Sciences and Engineering Research Council of Canada and Alberta Environment for funding.

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Chapter 1

Introduction

In semi-arid[1] areas of western North America such as the prairies of southern Alberta, willows (*Salix* sp.) and cottonwoods (*Populus* sp.) are the primary native woody plants. Both genera are generally restricted to streamside zones where they create riparian woodlands. These woodlands form an ecotone between the aquatic and terrestrial ecosystems, providing wildlife habitat and ungulate and rodent browse that are unavailable elsewhere in the prairie landscape (Viereck et al. 1993, Case and Kauffman 1997). Willows and cottonwoods also provide streambank stabilization and willows in particular, resist geomorphic changes along prairie rivers (Cordes et al. 1997). In these dry regions, willows and cottonwoods are not succeeded by other woody plants and consequently their ongoing establishment and survival are vital for healthy, functioning riparian ecosystems (Rood and Mahoney 1990, Cordes et al. 1997).

Not only do riverine zones provide important wildlife habitat, but they also supply many other resources of human interest. The river water is valued and often diverted for agricultural, industrial and commercial use. Floodplain substrates, especially sand and gravel, are mined for construction projects. Riparian woodlands may be cleared for agricultural use, grazed, or used for recreation. All these uses can contribute to cottonwood-willow forest decline (Rood and Mahoney 1990, Kauffman and Krueger 1984, Viereck et al. 1993).

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[1] In this thesis, semi-arid is operationally defined as a treeless landscape where annual potential evapotranspiration exceeds precipitation.

Water availability is often the principal determining factor in the growth and survival of cottonwoods and willows (Brunsfeld and Johnson 1985,Rood and Mahoney 1990, Kranjcec et al. 1998). Water is required for seed germination and seedling establishment (Johnson 1994) and to maintain growth and development throughout the life cycles of these trees and shrubs (Brunsfeld and Johnson 1985, Mahoney and Rood 1991). Cottonwoods and willows are phreatophytic. They obtain moisture directly from the water table or the adjacent capillary fringe. Consequently these genera require hydraulic connectivity to the water table throughout the growing season (Brunsfeld and Johnson 1985, Mahoney and Rood 1991, 1992). Any activities in the floodplain that impede access to water by willow and cottonwood roots, such as water table decline, or prevent water absorption, such as through flooding, can result in water stress and riparian woodland decline over time.

Riparian cottonwoods and willows have very similar phenologies and niche requirements (Johnson et al. 1976). Both genera release many small seeds with short viability periods (Johnson 1994) in spring during the recession or 'falling limb' of the river hydrograph (Mahoney and Rood 1998). Both genera are shade-intolerant (Johnson et al. 1976, McBride and Strahan 1984, Brunsfeld and Johnson 1985) and colonize fully exposed areas created by sediment deposition or scour provided by the flowing river. Willows tend to colonize finer substrates (Brunsfeld and Johnson 1985) and occupy lower elevations that are closer to the stream channel than cottonwoods, suggesting that willows have less drought tolerance and greater flood tolerance than cottonwoods (Stromberg et al. 1991, Busch et al. 1992, Brayshaw 1996, Stromberg et al. 1996, , Vadas and Sanger 1997, Everson and Boucher 1998, Shafroth et al. 1998).

Willows and cottonwoods often experience drought or flood stresses within the riparian zone. Drought stress can occur naturally in years with minimal precipitation that reduces stream flow and depletes the water table. Decline in water table elevations can also be artificially induced through river resource management including damming, flow regulation, floodplain mining or groundwater pumping. Flood stress can result from increases in stream stage due to extensive rainfall and snow melt, or localized flooding that can accompany riparian zone alterations such as reservoir development. Understanding the tolerance of willows and cottonwoods to these stresses should allow for the implementation of better management practices that will promote the continued survival of cottonwood-willow riparian forests. Other factors such as seed release dates and tolerance to flood water and ice scour may also influence the relative elevation of willows and cottonwoods along streams.

Considerable research has been conducted on the water relations and moisture needs of riparian cottonwoods (Kranjcec et al. 1998, Mahoney and Rood 1998, Rood et al. 1995, Scott et al. 1999, Stromberg and Patten 1996). Instream flow requirements (Stromberg and Patten 1996), tolerable rates of water table decline (Mahoney and Rood 1991, 1992) and the impacts of water table depletion (Scott et al. 1999) on cottonwoods have been partially determined. This knowledge has resulted in the development of riverine management tools such as 'recruitment box model', a cottonwood seedling establishment model based on survivable rates of water table decline at appropriate streambank elevations following seed release (Mahoney and Rood 1998). This model has been successfully applied to promote cottonwood establishment along a number of regulated rivers (Mahoney and Rood 1998, Rood et al. 1998, Kalischuk et al. 2000, Rood and Mahoney 2000). The determination of the tolerances of willows to drought and flood stresses and comparison to cottonwood tolerances should enable the refinement of this

recruitment model and other restoration tools, favoring the survival of willows as well as cottonwoods.

Of particular interest for the present thesis is the spatial separation of willows and cottonwoods in riparian areas. Chapters 2 and 3 investigate the hypothesis that willows are more flood tolerant and less drought resistant than cottonwoods by growing selected cottonwood and willow species and clones under varying drought and flood conditions in a controlled, greenhouse environment. Chapter 4 describes a third study that investigated the impact of prolonged water table depletion and subsequent water table recovery on mature riparian cottonwoods. A range of Salicaceae species are represented in this thesis; narrowleaf cottonwood, *Populus angustifolia* James, balsam poplar, *P. balsamifera* L., prairie cottonwood, *P. deltoides* Bartr., pussy willow, *Salix discolor* Muhlenberg, Drummond's willow, *S. drummondiana* Barratt, sandbar (or coyote) willow, *S. exigua* Nutt., and yellow willow, *S. lutea* Nutt were included in one or more of the studies.

This thesis will provide further understanding of the physiological impacts of drought and flood stresses on riparian willows and cottonwoods. This information will assist in the development of future river resource management practices that favor the establishment and maintenance of willows as well as cottonwoods.

Chapter 2

Comparative tolerances of riparian willows and cottonwoods to water table decline

Abstract: Cottonwoods (*Populus* sp.) and willows (*Salix* sp.) generally dominate riparian landscapes across western North America. To explore their relative tolerance to water table decline rate, rooted shoot cuttings of two willows, *Salix drummondiana* Barratt and *S. exigua* Nutt., were grown along with *Populus angustifolia* James and *P. balsamifera* L. in rhizopods, controlled growth devices that allow water table manipulation. Water table decline rates of 0 to 12 cm/d were delivered and plant growth and survival were monitored. In a second study, seedlings of *S. exigua*, *S. lutea* Nutt., *P. balsamifera* and *P. deltoides* Bartr. ex Marsh were exposed to water table decline rates of 0 to 8 cm/d. For cuttings and seedlings of both genera, gradual declines of 1 or 2 cm/d promoted growth, whereas more abrupt declines reduced growth and survival. The willow and cottonwood saplings were relatively similarly affected although the willow seedlings were slightly more vulnerable than cottonwood seedlings to abrupt water table decline. It is consequently recommended that along regulated rivers, stream stage recession in the late spring and summer should be very gradual (1 cm/d) through the low elevational zones to encourage willow recruitment.

Key Terms: drought tolerance, mortality, plant growth, *Populus*, recruitment, *Salix*, saplings, seedlings, survival, water table decline

INTRODUCTION

Willows (*Salix* sp.) and cottonwoods (*Populus* sp.) are the principal streamside shrubs and trees of riparian woodlands along most rivers in western North America. These woody plants contribute favorably to wildlife habitat and biodiversity of the riparian zones (Viereck et al. 1993, Case and Kauffman 1997). Both of these genera obtain moisture from the riparian water table that is partially provided by river water that infiltrates laterally into the streamside substrate. Along influent or hydrologically-losing streams (Gordon et al. 1992) that are typical of semi-arid regions, the riparian water table is generally at a similar elevation to the river stage and declines in river stage result in corresponding declines in water table elevation (Busch et al. 1992, Rood et al. 1995, Stromberg and Patten 1996). This hydrologic linkage is important since the decline of cottonwood forests downstream of some dams has been correlated to insufficient flows and abrupt water table declines due to river regulation by dams and offstream water diversion (Rood and Mahoney 1990).

Previous research has shown that water table decline rates that are similar to natural recession rates encourage the establishment of cottonwoods and this has provided a successful management tool for riparian conservation and restoration (Mahoney and Rood 1998, Rood et al. 1998, Shafroth et al. 1998, Rood and Mahoney 2000). To ensure the presence of willows along regulated rivers, tolerable rates of water table decline for those species need to be determined.

Willows and cottonwoods are closely related and share many ecophysiological similarities, including similar seed and seedling characteristics (Ware and Penfound 1949, Johnson et al. 1976, Krasny et al. 1988a, Johnson 1994, Brayshaw 1996).

Consequently, it might be expected that the two genera would have generally similar hydrologic requirements for seedling and clonal recruitment.

Across species, the distributions of streamside plants are partially determined by the depth to water table, rooting characteristics, substrate textures and hydraulic conductivities (Stromberg et al. 1996). Willows are often found in finer substrates (Brunsfeld and Johnson 1985) and typically occur at lower elevations and closer to the stream than cottonwoods (Figure 2-1) (Busch et al. 1992, Stromberg et al. 1996, Everson and Boucher 1998, Shafroth et al. 1998, Dixon and Johnson 1999). It might consequently be expected that willows would be less drought tolerant but more flood tolerant than cottonwoods. Van Splunder et al. (1996) concluded that differing drought resistances of *Populus nigra* and *Salix* species resulted in the zonation of these genera along the Rhine River; willows were considered to be less drought tolerant and accordingly situated closer to the stream. This prominent spatial differentiation between willows and cottonwoods might suggest that for recruitment, growth, and survival, riparian willows would require more gradual rates of water table decline than cottonwoods.

The present study investigated the relative tolerance of willow and cottonwood saplings (rooted cuttings) and seedlings to different rates of water table decline. This study should contribute to the understanding of the ecophysiology of these prominent and widespread riparian plants and the natural distribution of these shrubs and trees along streams. This knowledge should also allow dam operations to provide instream flow regulation that would conserve and restore willows as well as cottonwoods.
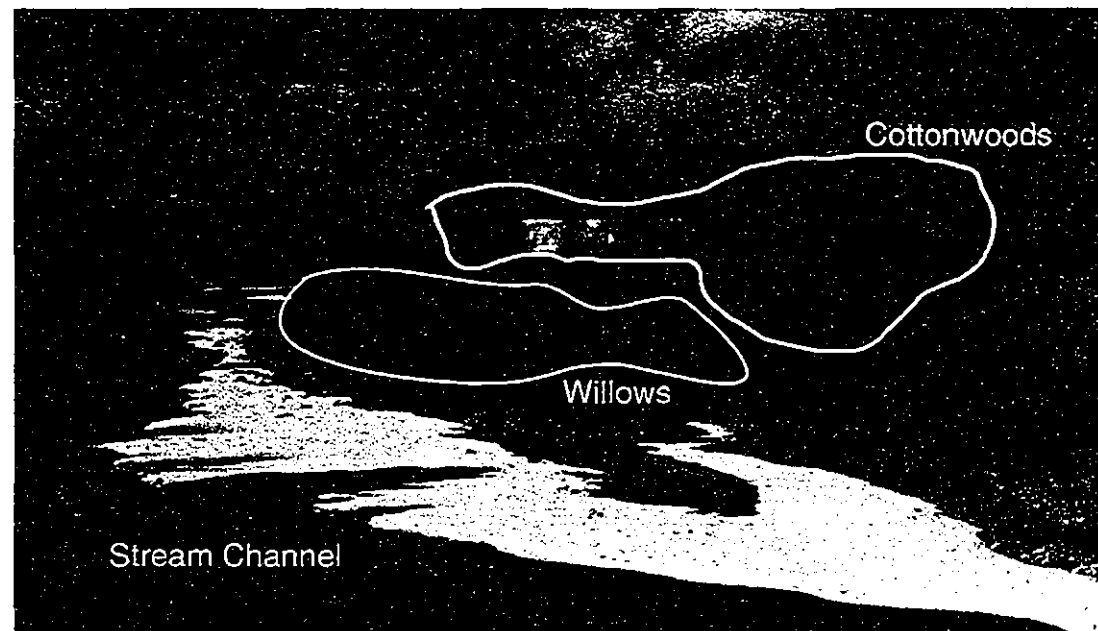
Figure 2-1: Leaf-less sandbar (or coyote) willows, *Salix exigua,* balsam poplars,

Populus balsamifera, and narrowleaf cottonwoods, *P. angustifolia,* along Willow

Creek, Alberta in early March 1999. The willows are closer to the stream and at

lower elevations than the cottonwoods. The Willow Creek Dam occurs behind

the cottonwoods and white ice and snow are visible in the foreground.

METHODS

Willow and cottonwood shoot cuttings and catkins were collected in 1999 from various riparian sites in southeastern British Columbia and southern Alberta, Canada (Table 2-1). The narrowleaf cottonwood, *Populus angustifolia* James, and balsam poplar, *P. balsamifera* L. (similar to the black cottonwood *P. trichocarpa* Torr. & A. Gray) cuttings were taken from clonal trees in the University of Lethbridge nursery that originated from cuttings of trees along the Belly and Oldman rivers, respectively. *P. balsamifera* seeds were collected from trees along Willow Creek and *P. deltoides* Bartr. ex Marsh seeds were collected along the Oldman River. The willow cuttings and catkins collected included Drummond's willow, *Salix drummondiana* Barratt, sandbar (or coyote) willow, *S. exigua* Nutt., and yellow willow, *S. lutea* Nutt..

Sapling Study

The cuttings were stored at 4°C until March 18, 1999, when they were cut into 10 cm lengths and soaked in water for five days. The *P. angustifolia* and *P. balsamifera* cuttings collected March 19, 1999 received no cool storage and were immediately cut into sections and soaked for 4 days. The flushing cuttings were then planted March 23, 1999 in rhizopods (Mahoney and Rood 1991, 1992), experimental devices including vertical growth tubes linked to a central water reservoir that allow the willows and cottonwoods to be subjected to different water table decline rates.

Table 2-1: *Populus* and *Salix* cuttings and catkins (seeds) collected in 1999 for use in the water table decline rhizopod studies.

Species	Location	Collected	Date
Populus angustifolia	University of Lethbridge nursery originally from Belly River, Alberta 49° 21' N, 113° 29' W	cuttings	March 19
P. balsamifera	University of Lethbridge nursery originally from Oldman River, Alberta 49° 35' N, 113° 56' W	cuttings	March 19
	Willow Creek near Stavely, Alberta 50° 7' N 113° 45' W (two groves)	catkins off tree and ground	June 23
P. deltoides	Oldman River near Taber, Alberta 49° 49' N 112° 10' W	seeds off ground	June 25
Salix drummondiana	Crowsnest Creek near Crowsnest Pass, Alberta 49° 37' N 114° 40' W	cuttings	February 15
S. exigua	Elk River near Fernie, BC 49° 28' N 115° 4' W	cuttings	February 15
	Pine Creek near Stavely, Alberta 50° 7' N 113° 45' W	cuttings	March 10
	Willow Creek at Chain Lakes Provincial Park, Alberta 50° 12' N 114° 11' W	catkins	June 29
	Willow Creek at Willow Creek Provincial Park, Alberta 50° 7' N 113° 45' W	catkins	June 29
	Oldman River near Taber, Alberta 49° 49' N 112° 10' W	catkins	June 25
S. lutea	Willow Creek at Chain Lakes Provincial Park, Alberta 50° 12' N 114° 11' W	catkins	June 29
	Willow Creek at Willow Creek Provincial Park, Alberta 50° 7' N 113° 45' W	catkins	June 29

The growth tubes of the rhizopods were filled with a base of 10 cm coarse gravel (Gordon et al. 1992) for drainage and then a 10:3 sand:fine gravel mixture with materials that had been excavated from along the Oldman River at Lethbridge, AB. Five saplings of a particular species were planted in each of the 15 growth tubes of each rhizopod. The rhizopods were set up in a University of Lethbridge (latitude 49° 47' N) greenhouse that was maintained at 23 ± 2°C. High-pressure sodium vapor lights provided 65 μmol/m^2/s photosynthetically active radiation (measured with a Li-Cor LI-1600 quantum sensor) for 16.5 h daily to supplement the natural light.

The water level in the central reservoir was maintained at 8 cm below the substrate surface for 7 days following planting to allow for sapling establishment; this water table depth coincided with the base of the cuttings. Subsequently, six treatments were applied: 0, 1, 2, 4, 8 or 12 cm/d water table decline.

Seedling Study

The willow and cottonwood seeds were stored in plastic bags with desiccant at 4°C following collection in June 1999 and sown in rhizopods January 15, 2000. Fifteen seeds of a species were positioned on the moist surface of each rhizopod growth tube (1 seed per 3 cm^2). Substrate and other growing conditions were similar to the sapling experiment. After sowing, the water levels were maintained at 5 cm below the substrate surface for 3 days with the surface misted with water twice a day. On the fourth day, treatments of 0, 1, 2, 3, 4 or 8 cm/d water table decline commenced.

Measurements

The saplings were harvested 35 to 37days after the treatments began. Shoot heights, shoot (leaves plus stems) dry weights, root lengths and root dry weights were measured. Shoot and root areas were determined with a Li-Cor (Lincoln, Nebraska) LI-3000 leaf area meter.

The seedlings were harvested 42 days after treatments began. Maximum number of seedlings established, seedling recruitment (the proportion of seedling survival) and shoot growth including shoot height and shoot dry weight were recorded. Fragility of the seedling roots prevented accurate measurements of root growth.

Two-way factorial ANOVAs were conducted on resultant data, considering the effects of water table decline rates (factor 1), and species (factor 2) and their interactions.

RESULTS AND DISCUSSION

Sapling Study

The variables of water table decline rate and species significantly affected shoot height, shoot area, shoot dry weight, root length, root area and root dry weight (Table 2-2). The interaction between water table decline rate and species was significant for all parameters except root dry weight.

Table 2-2: *F*-values and probabilities from factorial ANOVAs for shoot and root growth of *Populus angustifolia, P. balsamifera, Salix drummondiana* and *S. exigua* saplings grown in rhizopods for 35 to 37 days under water table decline rates of 0, 1, 2, 4, 8 or 12 cm/d.

Parameter Source of Variation	d.f.	*F*-value	p-value
Shoot Height			
Rate of water table decline (R)	5	38.6	***
Species (S)	3	37.8	***
R x S	15	2.844	**
Shoot Area			
Rate of water table decline (R)	5	66.0	***
Species (S)	3	174.6	***
R x S	15	4.7	***
Shoot Dry Weight			
Rate of water table decline (R)	5	88.9	***
Species (S)	3	161.9	***
R x S	15	10.5	***
Root Length			
Rate of water table decline (R)	5	23.7	***
Species (S)	3	30.2	***
R x S	15	3.6	***
Root Area			
Rate of water table decline (R)	5	21.7	***
Species (S))	3	17.1	***
R x S	15	2.2	**
Root Dry Weight			
Rate of water table decline (R)	5	11.8	***
Species (S)	3	12.7	***
R x S	15	1.2	0.26

** $p < 0.001$, *** $p < 0.0001$.

Root growth capacity of different species directly influences their survival of water table decline (McBride and Strahan 1984). Root elongation allows the phreatophytic willows and cottonwoods to continue to maintain contact with the receding water table. In the present study, all species demonstrated increased root elongation with gradual rates of water table decline of 1 and 2 cm/d (Figure 2-2). The faster rates of water table decline resulted in reduced root length in all species.

Some previous studies have shown cottonwoods to have a greater capacity for root elongation in the initial growing seasons than willows. McBride and Strahan (1984) found that cottonwood roots were three times as long as willow seedlings in the first growing season and Stromberg et al. (1991) reported that *Salix gooddingii* had a slower root growth rate than *Populus fremontii*. In our study, *P. balsamifera* had the greatest root elongation at the most extreme rates of water table decline of 4, 8 and 12 cm/d, but with the slower rates of decline, *S. exigua* exhibited the greatest root elongation. Overall, root growth was relatively similar across the two genera.

The willows and cottonwoods tended to display different root growth morphologies. The *Salix* species and particularly *S. exigua*, extended their roots into or near the saturated water table while the *Populus* roots remained in the capillary fringe well above the saturated zone. In a previous study, Stromberg et al. (1991) observed the same trend as *Salix* roots were found in the saturated groundwater zone while the cottonwood roots remained above the saturated substrate. This could indicate that willows require more moisture than cottonwoods, that willow roots have greater anaerobic tolerance, or both.

Figure 2-2: Mean (± 1 s.e.) shoot height and root length of *Populus angustifolia*

(n=9 per treatment), *P. balsamifera* (n=9), *Salix drummondiana* (n=10) and *S.*

exigua (n=33 to 35) saplings grown in rhizopods for 37 days under six water table

decline rates. Note the different y-axis scales.

Shoot elongation is another important growth parameter for willows and cottonwoods in riparian zones. Both genera are shade intolerant and must grow faster than surrounding vegetation to remain in bright sunlight. *S. drummondiana* and *S. exigua* tended to increase shoot height at the slower rates of water table decline of 1 or 2 cm/d (Figure 2-2). The greatest *P. balsamifera* shoot height was at the 0 cm/d treatment in which the water table remained 8 cm below the substrate surface. Shoot height was reduced with the faster rates of water table decline in all species investigated and this probably reflected drought stress that is known to particularly retard shoot cell elongation (Kozlowski and Pallardy 1997).

A comparison of growth proportions showed that with the faster rates of water table decline, *Populus* displayed decreased shoot height to root length ratios while ratios in *Salix* remained relatively unchanged. The cottonwoods may have allocated more resources to root growth with the increasing threat of drought while the willows apparently did not. With increasing rates of water table decline, water becomes a more limiting resource and greater resource allocation to enable water uptake may contribute to a greater ability of cottonwoods to survive faster rates of water table decline.

Root dry weight was promoted by the slow water table decline rates of 1 or 2 cm/d for all species (Figure 2-3). The faster rates of water table decline of 8 and 12 cm/d inhibited root biomass accumulation for all species. *P. balsamifera* had the greatest root weight at all rates of water table decline.
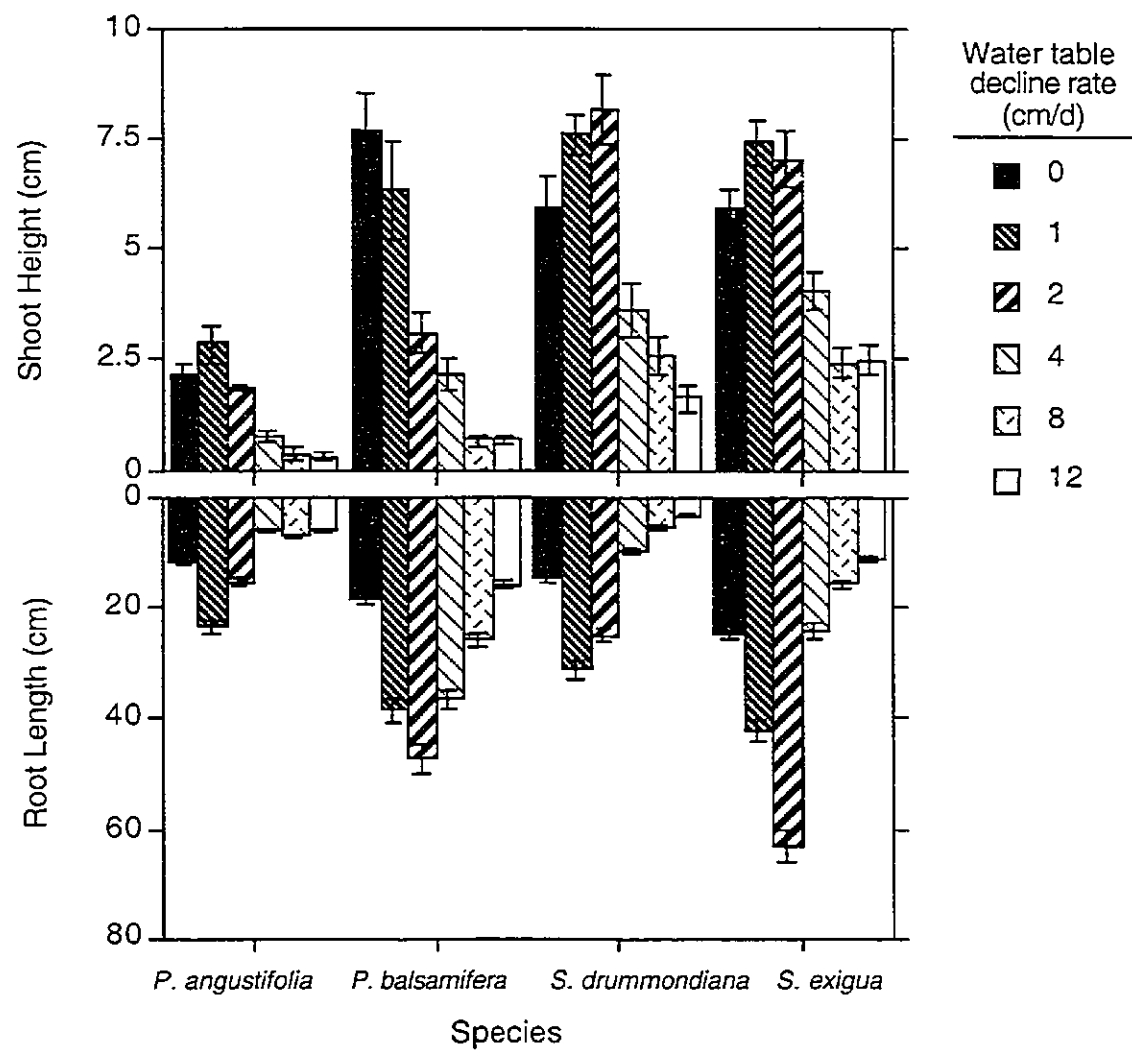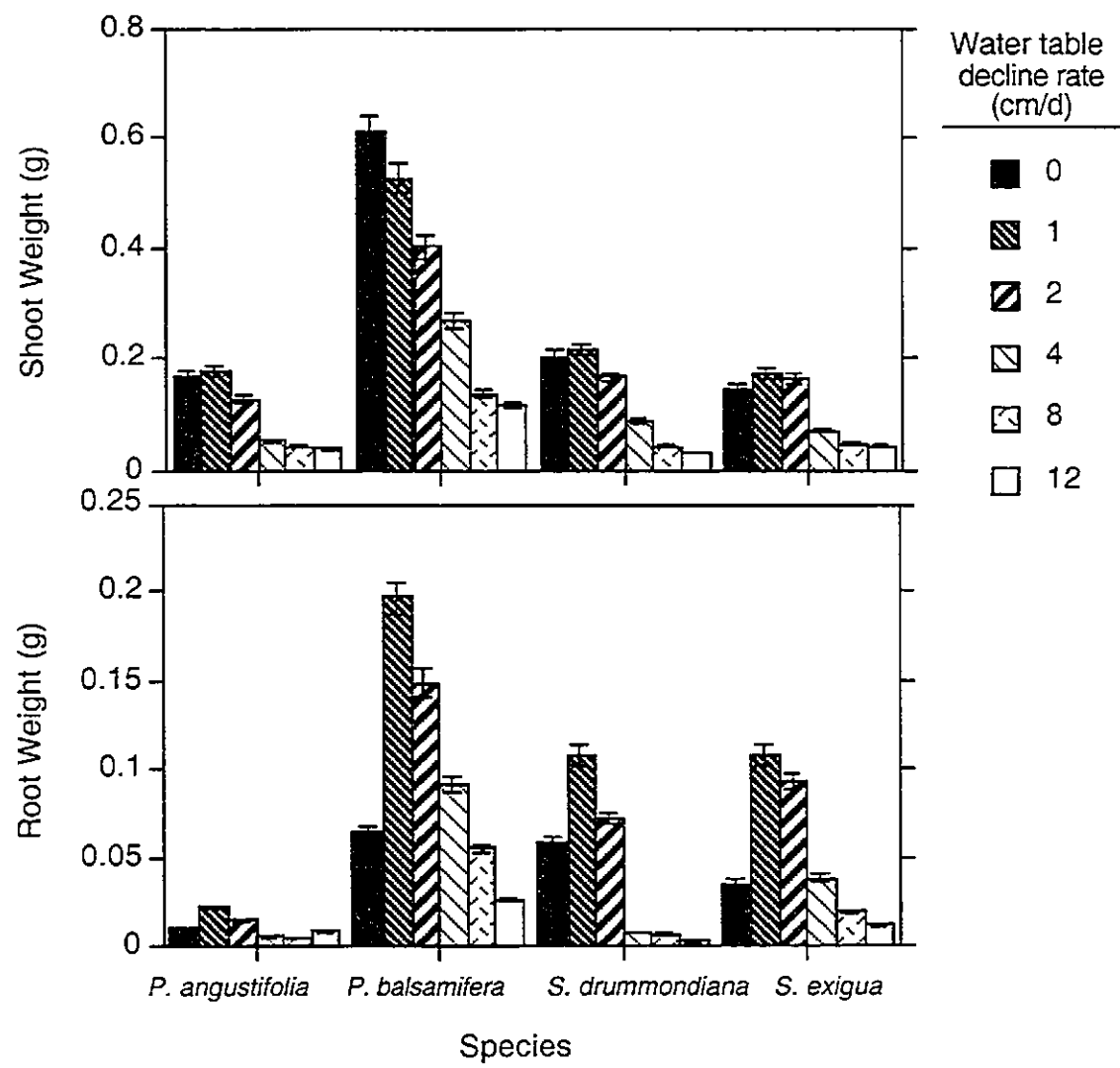
Figure 2-3: Mean (± 1 s.e.) shoot and root dry weights of *Populus angustifolia* (n=9 per treatment), *P. balsamifera* (n=9), *Salix drummondiana* (n=10) and *S. exigua* (n=33 to 35) saplings grown in rhizopods for 37 days under six water table decline rates. Note the different y-axis scales.

Lateral and adventitious roots are common in both cottonwoods and willows (Ware and Penfound 1949). In the present study *P. balsamifera* seemed to have the greatest lateral root growth at all decline rates as the differences in root dry weight between *P. balsamifera* and the other species studied was greater than the root length differences. The extra lateral roots may allow the cottonwoods to extract more moisture from the surrounding substrate as the water table declines rapidly while the willow roots tended to respond primarily by elongation of the tap root.

Shoot dry weights often increased with the slow decline rates of 1 or 2 cm/d but were reduced with faster decline rates (Figure 2-3). Shoot area and root area demonstrated similar patterns (data not presented). Generally, all of the growth parameters demonstrated promotion with slow rates of water table decline and reduction with faster rates of water table decline. This pattern has been seen in previous rhizopod studies with cottonwoods (Mahoney and Rood 1991, 1992).

Seedling Study

The seedling experiment provided additional information about the survival of the cottonwood and willow seedlings with different water table decline rates. The maximum number of seedlings established per growth tube by different species and the number of seedlings recruited (seedlings that survived to 42 days) under the different rates of water table decline were analyzed.

Riparian cottonwoods and willows share similar niche characteristics (Johnson et al. 1976) and it was expected that germination and establishment would be similar. Both cottonwoods and willows have large crops of small wind and water dispersed seeds with short periods of viability (Johnson et al. 1976, Krasny et al. 1988a, Johnson 1994, Brayshaw 1996). Cottonwood seeds are thought to have longer viability than willow seeds (Ware and Penfound 1949, Hosner 1957) although some researchers make no distinctions between the two genera (Stromberg et al. 1991, Johnson 1994). Germination of riparian cottonwood and willow seeds requires abundant moisture and is rapid (Krasny et al. 1988a, Stromberg et al. 1991, Johnson 1994). Consistent with these prior reports, germination proceeded in 24 to 48 hours in the present study.

The mean maximum number of seedlings (Figure 2-4) always occurred by the third day after sowing. For the first three days the water table had been maintained at 5 cm below the substrate surface and the surface was misted. The maximum number of seedlings varied across species (df=3, F=5.5, p=0.0019) and *P. balsamifera* and *S. lutea* averaged more seedlings than *P. deltoides* and *S. exigua*.
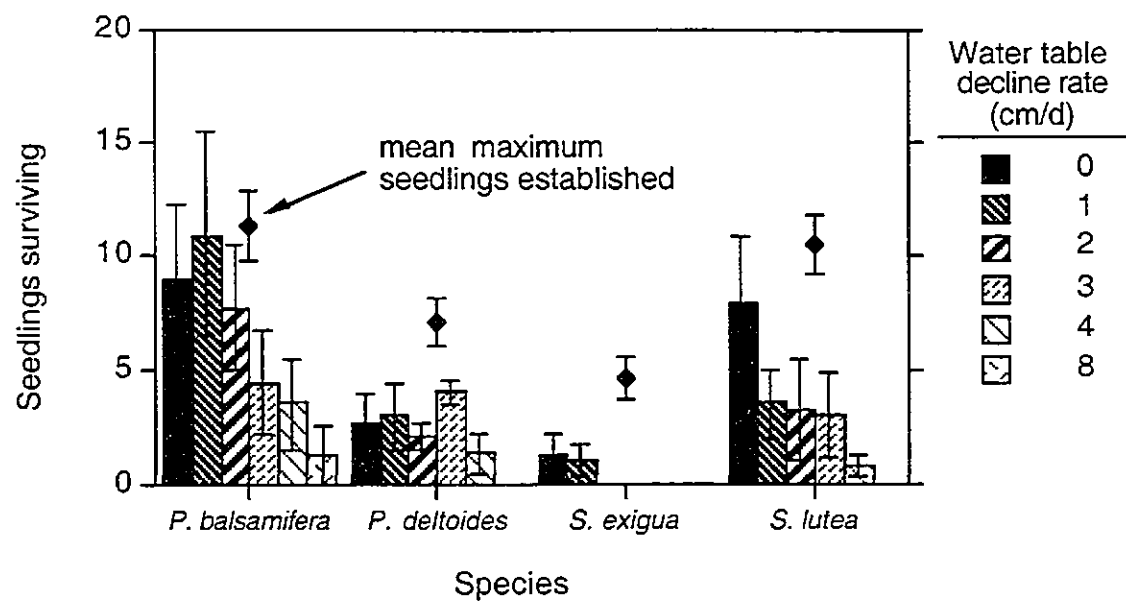
Figure 2-4: Mean ($\pm$ 1 s.e.) number of *Populus balsamifera, P. deltoides, Salix exigua* and *S. lutea* seedlings that established and survived 42 days of six different water table decline rates (n=15).

Seedling recruitment, the proportion of seedlings that tolerated the water table decline rates for 42 days, was significantly impacted by water table decline rate (df=5, F=10.4, p=<0.0001) and species (df=3, F=8.9, p<0.0001) (Figure 2-4). *P. balsamifera* seedlings were recruited under all treatments whereas *S. exigua* seedlings were recruited only under the 0 and 1 cm/d rates of water table decline. Of the seedlings that established prior to the initiation of the 8 cm/d decline rate, the *S. exigua* seedlings perished within 7 days, *S. lutea* seedlings died within 17 days but the *P. deltoides* seedlings survived over 24 days. These results suggest the increased vulnerability of willow seedlings to rapid water table declines as compared to cottonwood seedlings.

There are two probable explanations for the reduced willow survival with abrupt water table decline. The willow seedling roots may not have grown as quickly as the cottonwood roots and could not maintain contact with the declining water table and capillary fringe. Alternatively, some willow roots may have grown fast enough but these roots were still unable to absorb sufficient moisture to compensate for transpirational losses.

Seedling shoot growth parameters of height and dry weight were measured for the 0 to 8 cm/d decline rates (Figure 2-5). The pattern of growth promotion at the slower rates of water table decline was not as evident as in the sapling study but the 0 to 2 cm/d rates did tend to promote greater shoot growth than the 3, 4 or 8 cm/d rates. The factorial ANOVA indicated that shoot height was significantly influenced only by species (df=1, F=25.5, p=<0.0001), and shoot dry weight was influenced only by the interaction of species and rate of water table decline (df=8, F=3.4, p=0.001).
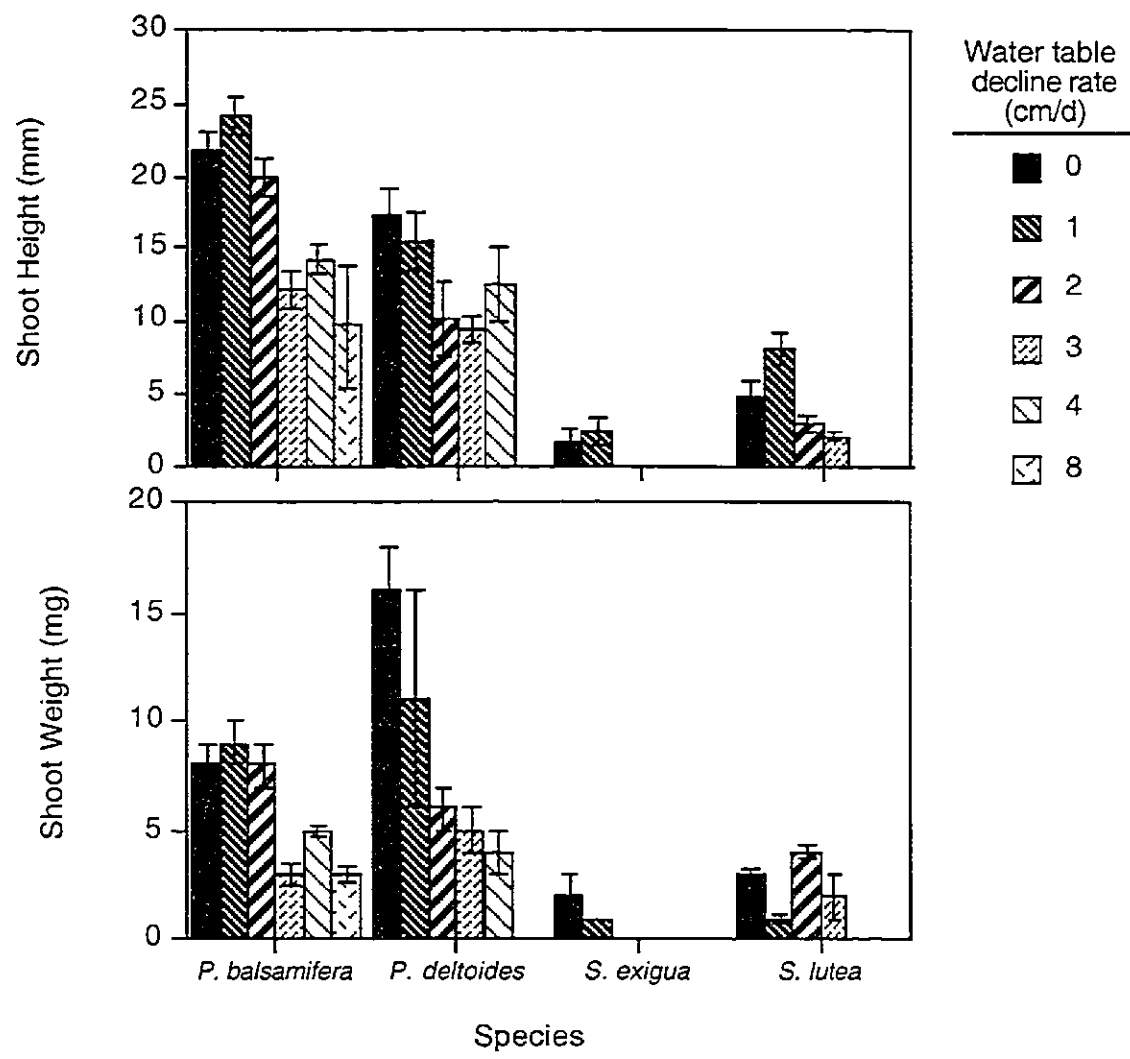
Figure 2-5: Mean (± 1 s.e.) shoot height and shoot dry weight of *Populus balsamifera* (n=5 to 44), *P. deltoides* (n=4 to 12), *Salix exigua* (n=4 to 5) and *S. lutea* (n=3 to 32) seedlings grown in rhizopods for 42 day under six different water table decline rates.

MANAGEMENT IMPLICATIONS

The willow saplings studied showed similar responses to water table decline rates as the cottonwoods, but the willow seedlings displayed reduced tolerance to rapid water table decline rates as compared to cottonwood seedlings. The *Populus* saplings and seedlings behaved similarly to cottonwoods and alders investigated in previous rhizopod studies (Mahoney and Rood 1992, Barsoum and Hughes 1998, Segelquist et al. 1993), with abrupt water table decline reducing growth. Optimum growth for both the cottonwoods and willows was achieved with gradual water table decline rates.

However, in contrast to cottonwoods slightly slower rates of water table decline of 1 cm/d may be beneficial to willow seedling recruitment along regulated streams. Mahoney and Rood (1998) developed the 'recruitment box model' for the establishment of cottonwood seedlings based on streamside elevation, seed release dates and tolerable water table decline rates of 2.5 cm/d. Because each of these parameters appears to be distinct for both cottonwoods and willows, this model should be modified to enable the establishment of willow seedlings along with cottonwood seedlings (Figure 2-6).

An elevational offset of the willow recruitment box from the cottonwood recruitment box (Figure 2-6) would reflect the observed differences in their respective elevational zones (Figure 2-1). The upper elevational band for cottonwoods was described as the point where the seedlings would not perish from desiccation (Mahoney and Rood 1998). To prevent desiccation, root growth must maintain contact with the declining water table. The present study determined that willow seedlings could not tolerate water table decline rates of 2.5 cm/d, the rate

tolerable for cottonwoods, but require slower rates of 1 cm/d to avoid drought stress. This lower tolerance to desiccation prevents willow seedlings from establishing at as high an elevation above the late summer stage as cottonwoods. The upper elevational limit of 100 cm depicted in Figure 2-6 was determined using the estimate of Cordes et al. (1997) that willows occur 50 to 80 cm in elevation below the prairie cottonwoods along Alberta's Red Deer River. Field measurements of the elevational differences between willows and cottonwoods should be conducted along additional rivers to confirm or refine these elevational parameters.

In Mahoney and Rood's (1998) model, the lower elevational limit of cottonwood seedling establishment is defined by physical scouring of seedlings by water or ice. Cottonwood seedlings are able to germinate and establish below the recruitment band, but there is a high probability that these seedlings would be scoured away in the following years when streamflows increase or ice drives occur. Willow seedlings also establish close to the stream but seem better able to tolerate the physical stresses at these lower elevations. Willows spread clonally through root and shoot suckers and also propagate through plant fragments to a greater extent than cottonwoods (Ware and Penfound 1949, Uchytil 1989, Ottenbreit and Stanforth 1992, Johnson 1994). This clonal capacity may provide increased tolerance to mechanical abrasions at lower elevations. Willows are also more pliable than cottonwoods and might consequently less likely to be sheared by ice or dislodged during high streamflows than the more rigid cottonwoods. Based on their increased clonal reproduction and pliability, willows are probably better able to survive in the low elevation zones from which cottonwoods are excluded.

Figure 2-6: The 'Recruitment Boxes' for riparian cottonwoods and willows defined by the establishment elevation (Recruitment Band) and seed release periods for each genus (top), survivable rates of water table decline (middle) and stage hydrograph requirements (bottom) for both genera. These figures are modified and expanded from the cottonwood recruitment box model by Mahoney and Rood (1998).
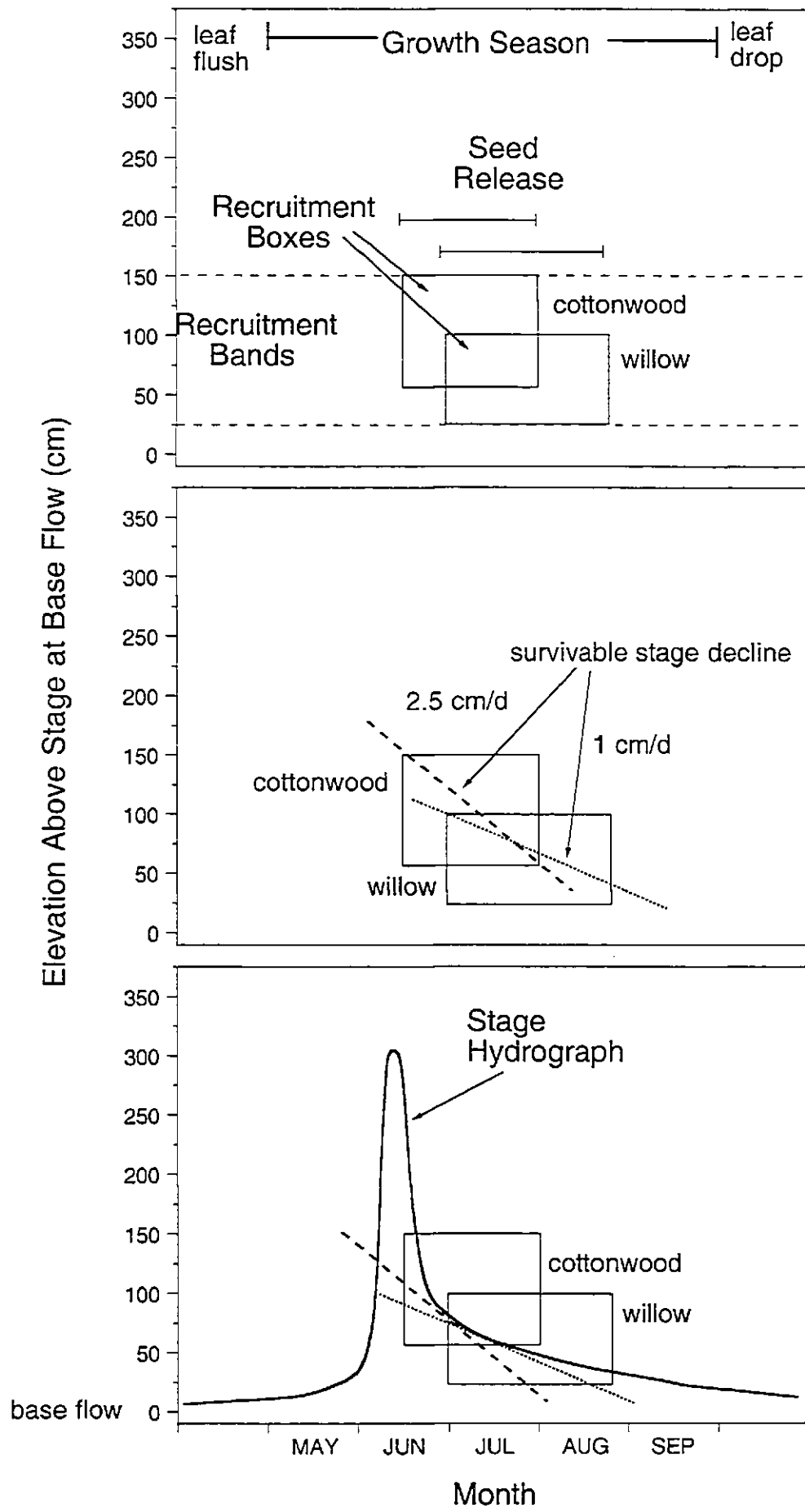
Nadine M. Amlin - Influences of drought and flood stresses on riparian vegetation

In the present revision of the recruitment box model, the period of seed release for willows is delayed relative to cottonwoods (Figure 2-6). This is based both on our observations of willows and previous reports that willows tend to release seeds later in the growing season than cottonwoods. In the Sonoran riparian forests, *S. gooddingi* released seeds later than *P. fremontii* (Stromberg et al. 1991). Along the Tanana River in Alaska, black cottonwood seeds were released from June 16 to June 30 while sandbar willow seeds were released from July 1 to July 30 (Krasny et al. 1988a). Peachleaf willows along the Platte River, Nebraska, released seeds later than prairie cottonwoods, June 8 to 22 compared with May 16 to June 1, respectively.

This revision of the recruitment box model should assist with river flow regulation for the conservation and restoration of riparian woodlands with benefits to both cottonwoods and willows. By instituting the 1 cm/d water table decline tolerated by willow seedlings during the seed release periods of willows when river flows are lower, willow seedlings should establish. As seen in Figure 2-6, willow recruitment is offset from cottonwood recruitment and both willows and cottonwoods could be established during the same recruitment event. Ramping the river stage by 2.5 cm/d at the higher elevations will promote cottonwood seedling establishment. Subsequently, slowing stage decline to 1 cm/d at the lower elevations should promote willow seedling establishment. It might be further anticipated that other recruitment box coefficients would exist for other riparian plants. The appropriate ramping rates could be determined by rhizopod studies, and it would be expected that the typical river stage ramping (gradual recession) patterns of unregulated rivers would enable the establishment and survival of riparian plant species.

Chapter 3

Comparative tolerances of riparian willows and cottonwoods
to elevated water tables

Abstract: Willows (*Salix* sp.) and cottonwoods (*Populus* sp.) are often subjected to flooding within their native riparian zones. This study investigated the relative tolerances of willows and cottonwoods to one component of flooding, elevated water tables. Three willow species, *Salix discolor* Muhlenberg, *S. exigua* Nutt. and *S. lutea* Nutt. were grown for 152 days along with three cottonwood species, *Populus angustifolia* James, *P. balsamifera* L. and *P. deltoides* Bartr. in 10 cm tall pots with four water table depths of 0 (flooded), 2.5, 5 or 7.5 cm below the substrate surface of standing water. Growth characteristics, survival and apparent transpiration (Ts) were monitored. Because willows generally occur closer to the river channel and at lower elevations than cottonwoods, it was expected that the willows would be more tolerant of the prolonged elevated water tables. The willows and cottonwoods were both highly tolerant of the elevated water tables, but continued Ts under the shallow water table conditions suggested that some willows are more flood tolerant than cottonwoods. With deeper water tables (reduced flooding) the cottonwoods had increased root growth, but shoot growth and survival were not significantly different between the two genera. Insufficient nutrition also limited growth of both cottonwoods and willows in the study.

Key Terms: cottonwoods, elevated water table, flood tolerance, plant growth, *Populus, Salix,* saplings, survival, willows

INTRODUCTION

Flooding is a common disturbance in riparian areas where willows (*Salix* sp.) and cottonwoods (*Populus* sp.) typically occur (Naiman and Decamps 1997). The waterlogged substrates produce many negative effects on plants including low oxygen levels that result in physiological changes such as reduced permeability of roots to water, metabolic and biosynthetic changes, accumulation of toxic compounds and increased pathogenic and fungal infections (Kozlowski 1982, Dionigi et al. 1985, Barrick and Noble 1993).

In environments where flooding is common, plant species are likely to be distributed at least partly based on their tolerance to inundation (Dionigi et al. 1985, Crawford-Zimmerman 1999, Denneler et al. 1999). In riparian zones, those species better able to tolerate waterlogged substrates and the physical stresses of flood flows are located near the stream channel and at low elevations where flooding is more frequent (Boggs and Weaver 1992). Willows are generally situated closer to the stream channel and at lower elevations than cottonwoods (Busch et al. 1992, Stromberg et al. 1996, Everson and Boucher 1998, Shafroth et al. 1998) and previous studies have found that some willow species have greater tolerance to inundation than cottonwoods (Hosner 1960, Pereira and Kozlowski 1977).

In semi-arid regions of western North America such as the prairie region of southern Alberta, willows and cottonwoods are the principal woody species and provide rich habitat for birds and other animals in riparian areas. As streams are dammed, flood frequency, timing, magnitude and duration are altered. This can affect the establishment, growth and survival of willows and cottonwoods. To conserve these species, their susceptibility to flooding should be determined.

The present study investigated the relative tolerance of willows and cottonwoods to elevated water tables, one component of flooding stress. It was expected that willows would be more flood tolerant than cottonwoods since riparian willows typically colonize lower sites that are closer to the stream channel. It was hypothesized that willows would demonstrate increased flooding tolerance through increased growth, survival and transpiration, as compared to cottonwoods grown in conditions if elevated water tables.

METHODS

Willow and cottonwood cuttings were collected from various riparian sites in southwestern Alberta and northern Montana in May 1999 (Table 3-1). The *Populus* saplings included one clone of prairie cottonwood, *P. deltoides* Bartr. (POd), one clone of balsam poplar, *P. balsamifera* L. (POb), and two clones of narrowleaf cottonwood, *P. angustifolia* James, (POa1 and POa2). The *Salix* clones included pussy willow, *S. discolor* Muhlenberg. (SAd), three clones of sandbar (or coyote) willow, *S. exigua* Nutt., (SAe1, SAe2, SAe3) and two clones of yellow willow, *S. lutea* Nutt.,(SAl1 and SAl2). For data presentation, the *Populus* clones are organized by probable drought tolerance. POd is considered the least flood tolerant as it colonizes higher elevation sites along streams (Gom and Rood 1999) and POa more flood tolerant. The *Salix* clones are presented alphabetically.

Table 3-1: *Populus* and *Salix* cuttings collected in 1999 for use in the elevated water table flooding tolerance comparison studies.

Species	Code	Location	Collected
Populus angustifolia	POa1	University of Lethbridge nursery originally from Belly River, Alberta	May 7
	POa2	49° 21' N, 113° 29' W	May 11
P. balsamifera	POb	University of Lethbridge nursery originally from Oldman River, Alberta 49° 35' N, 113° 56' W	May 11
P. deltoides	POd	University of Lethbridge nursery originally from Oldman River, Alberta 49° 41' N, 112° 51' W	May 7
Salix discolor	SAd	Crooked Creek near Waterton Park, Alberta 49° 08' N, 113° 47' W	May 11
S. exigua	SAe1	Oldman River at Lethbridge, Alberta 49° 47' N, 113° 07' W	May 7
	SAe2	Crooked Creek near Waterton Park, Alberta 49° 08' N, 113° 47' W	May 11
	SAe3	Wetland fringe near Waterton Park, Alberta 49° 07' N, 113° 47' W	May 11
S. lutea	SAl1	Teton River near Great Falls, Montana 47° 55' N, 111° 45' W	May 8
	SAl2	Crooked Creek near Waterton Park, Alberta 49° 08' N, 113° 47' W	May 11

POa1, POd and SAl1 were stored at 4°C for 2 or 3 days previous to soaking, while the other clones received no cool storage. Following the collection of shoot cuttings, they were soaked for 24 hours to promote adventitious root growth, except for POa2 and POb that were soaked for 2 hours. The flushing saplings were planted on May 11 and 13, 1999. The saplings were planted in 10 cm (height) X 15 cm (diameter) pots filled with a 10:3 sand:gravel substrate mixture with these materials have been excavated from the streamside zone along the Oldman River in Lethbridge, Alberta. Five saplings of one clone were planted in each pot and 20 pots were placed in each of four one metre diameter tubs with 2.5 cm deep standing water. The tubs were placed in the University of Lethbridge greenhouse (latitude 49° 47' N) that was maintained at $23 + 2°$ C. High-pressure sodium vapor lights provided 65 $\mu mol/m^2/s$ photosynthetically active radiation (measured by a Li-Cor LI-1600 quantum sensor) delivered for 16.5 h daily to supplement the natural light. On Day 0, 25 days after initial planting (June 7, 1999), the flooding treatments began by elevating the water table to 0, 2.5, 5 or 7.5 cm below the substrate surface with standing water. Two pots (10 saplings) of each clone were subjected to each water table depth. Two tubs supplied the 2.5 and 7.5 cm water table depths and two tubs supplied the 0 and 5 cm water table depths with the two treatments provided by placing pots on the tub bottom or on 5 cm bricks.

The tubs were adjusted daily to ensure constant water depths. The water was changed periodically, with 6 to 41 days between water changes. To promote cottonwood and willow growth 12 and 64 g of fertilized with chelated micronutrients (Plant Products 28-14-14 Calgary, AB) were added to each tub on day 47 and 50, respectively. On days 116, 119, 121 and 138, plants in one of the 2.5 cm / 7.5 cm flooding depths tubs (Tub 3) were sprayed with 0.02% pyrethrins and 0.2% piperonyl butoxide to control insects.

Shoot heights were measured weekly from day 0 to day 101, after which measurements were only collected during harvests. On day 69, apparent transpiration (Ts) measurements were taken with a Li-Cor LI-6400 gas exchange system (Lincoln, Nebraska). The transpiration rates of one clone of each species was determined for saplings at the water table depths of 0 and 7.5 cm below the substrate surface. 'Apparent' Ts recognize that the artificial cuvette condition may influence the gas exchange pattern. Relative patterns across treatments should be valid but absolute water flux rates may be disturbed.

In September, on Day 115, the first of two harvests occurred. One-half of the saplings of each clone were randomly selected and harvested with an attempt to minimally disturb the roots of those saplings not harvested. Shoot height, shoot area (leaves and stems) and shoot dry weight data were collected. A second harvest in November, on days 150 to 152, collected the remaining saplings. Shoot height, shoot area, shoot dry weight, root length, root area, root dry weight were measured. Area measurements were collected using a Li-Cor LI- 3000 area meter (Lincoln, Nebraska). 250 mL of substrate from each pot was weighed wet, oven dried and reweighed to determine the moisture content. Shoot growth, root growth and transpiration rates were analyzed with two-way factorial ANOVAs, investigating the significance of effects due to water table elevation (factor 1), clone (factor 2) and their interactions.

RESULTS AND DISCUSSION

The comparative results of the September and November harvests were very similar and only the November harvest data will be reported. The September harvest data are presented in Appendix A. Comparative analyses showed no differences between the two *Populus angustifolia* clones (POa1 and POa2) or between the three *Salix exigua* clones (SAe1, SAe2 and SAe3) and these clones have been grouped by species, labeled POa and SAe, respectively.

Depth of water table significantly affected the percentage water content (df=3, F=7.307, p=0.0002). However, a Fischer's PLSD post-hoc test revealed that only the water table 7.5 cm below the substrate surface was significantly different from the three other water table depths (p<0.0001 to p=0.0046). Soil moisture at the water table depths of 0, 2.5 and 5 cm below the substrate surface were not significantly different from each other.

All cottonwood and willow saplings survived the water tables at all depths for the duration of the experiment. However, sapling growth varied and water table depth, clone and their interaction significantly influenced root length, root area and root dry weight (Table 3-2). The *S. lutea* clone SAl2 generally had the greatest root area and root dry weight, while *P. deltoides* and *P. balsamifera* clones displayed the longest roots, with the roots extending for up to 1 m into the standing water (Figure 3-1). No willow roots extended beyond the pot.

Table 3-2: Factorial ANOVAs for shoot growth, root growth and apparent transpiration rates of *Populus deltoides, P. balsamifera, P. angustifolia, Salix discolor, S. exigua* and *S. lutea* saplings grown for 152 days (69 days for apparent transpiration) under water table depths of 0, 2.5, 5 and 7.5 cm below substrate surface.

Parameter Source of Variation	d.f.	F-value	p-value
Shoot Height			
Depth of water table (D)	3	1.7	0.17
Clone (C)	6	16.6	***
D x C	18	1.2	0.28
Shoot Area			
Elevation of water table (E)	3	4.5	**
Clone (C)	6	44.5	***
E x C	18	1.8	*
Shoot Dry Weight			
Depth of water table (D)	3	1.9	0.13
Clone (C)	6	36.0	***
D x C	18	1.5	0.10
Root Length			
Depth of water table (D)	3	15.3	***
Clone (C)	6	19.0	***
D x C	18	5.5	***
Root Area			
Depth of water table (D)	3	10.0	***
Clone (C)	6	23.7	***
D x C	18	2.0	*
Root Dry Weight			
Depth of water table (D)	3	12.1	***
Clone (C)	6	23.7	***
D x C	18	2.2	**
Apparent Transpiration			
Depth of water table (D)	1	0.9	0.34
Clone (C)	5	3.1	*
D x C	5	3.4	**

* $p<0.05$, ** $p<0.01$, *** $p<0.0001$.

Figure 3-1: Mean ($\pm$ 1 s.e.) root length, root area and root dry weight of *Populus deltoides* (POd), *P. balsamifera* (POb), *P. angustifolia* (POa), *Salix discolor* (SAd), *S. exigua* (SAe) and *S. lutea* (SAl1 and SAl2) saplings grown for 152 days under four water table depths (n=2 to 15).

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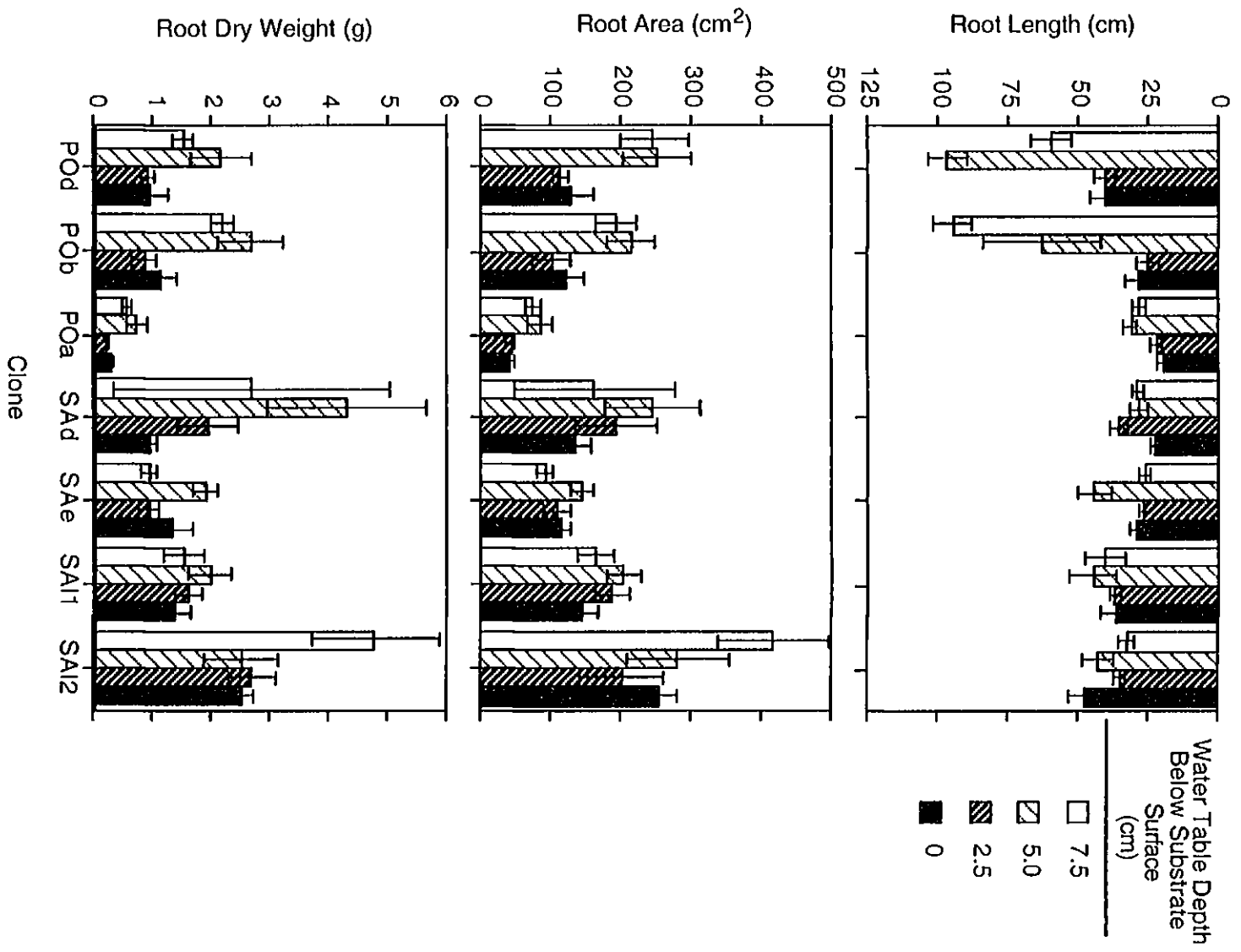
The shallow water table depths of 0 and 2.5 cm decreased root length, root area and root weight in the *Populus* clones only. Willow root growth was not significantly influenced by flooding depth with the exception of increased SAl2 root dry weight in the 7.5 cm treatment (Figure 3-1).

Both willows and cottonwoods produce adventitious roots when flooded (Armstrong 1968, Gill 1975). The ability to form adventitious roots is probably related to floodplain distribution. Species that grow in more frequently inundated sites produce significantly more roots (Krasny et al. 1988b). Willows tend to be flooded more often, and it was consequently expected that the willow species would demonstrate increased adventitious root growth relative to the cottonwoods. However in this study, the willows showed little increase in root growth at any of the water table elevations and displayed less root growth with the shallower water table treatments than *P. deltoides* and *P. balsamifera*.

It was expected that shoot growth would decrease with the shallow water tables, a flooded condition (Barrick and Noble 1993). Water table depth significantly influenced shoot area (Table 3-2) (Figure 3-2). The other shoot growth parameters of shoot height and shoot dry weight were not consistently affected. Even though cottonwoods displayed increased root growth with deep water tables of 5 and 7.5 cm, there was no corresponding increase in shoot growth. The willows did not demonstrate increased shoot growth overall compared to cottonwoods as had been expected.
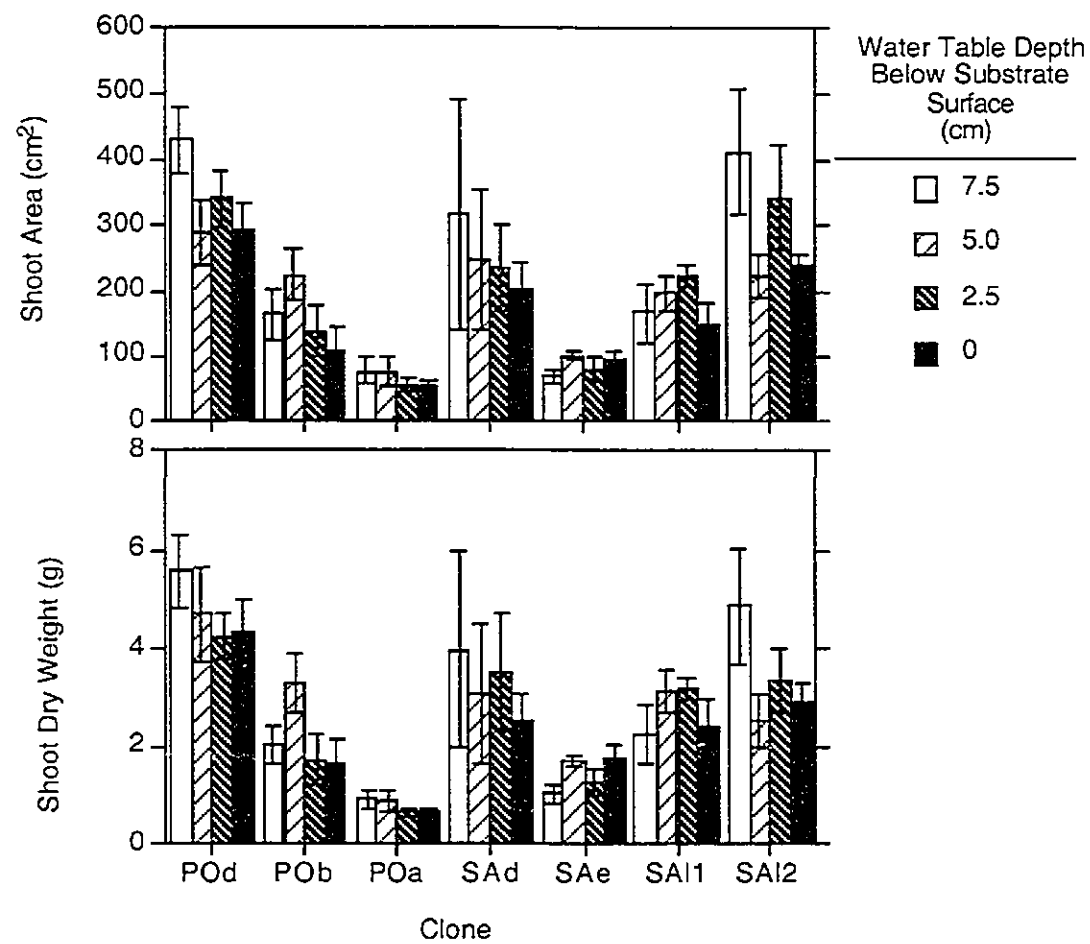
Figure 3-2: Mean (± 1 s.e.) shoot area and shoot dry weight of *Populus deltoides*
(POd), *P. balsamifera* (POb), *P angustifolia* (POa), *Salix discolor* (SAd), *S. exigua*
(SAe) and *S. lutea* (SAl1 and SAl2) saplings grown for 152 days under four water
table depths (n=2 to 15).

The rate of shoot elongation, the percentage of total elongation that occurred between each height measurement, showed no difference between the cottonwoods and willows and was similar at all water table depths (Figure 3-3). The rapid growth increase from Day 50 to 75 followed the addition of fertilizer. The riparian substrate that the saplings were grown in apparently had insufficient nutrient enrichment and the dramatic growth promotion indicated that nutrient deficiency was limiting growth.

Flooding is generally considered to decrease transpiration (Ts) rates since stomatal closure is rapidly induced (Pereira and Kozlowski 1977, Kozlowski 1982). It was expected that both the cottonwoods and willows would reduce Ts rates in the flooded, shallow water table, treatment and that the willows would be less affected than the cottonwoods. Clone and the interaction of water table elevation by clone did significantly influence Ts rates (Table 3-2). However, most clones maintained similar Ts rates at the 0 and 7.5 cm water table depths (Figure 3-4), indicating considerable flood tolerance of both genera.
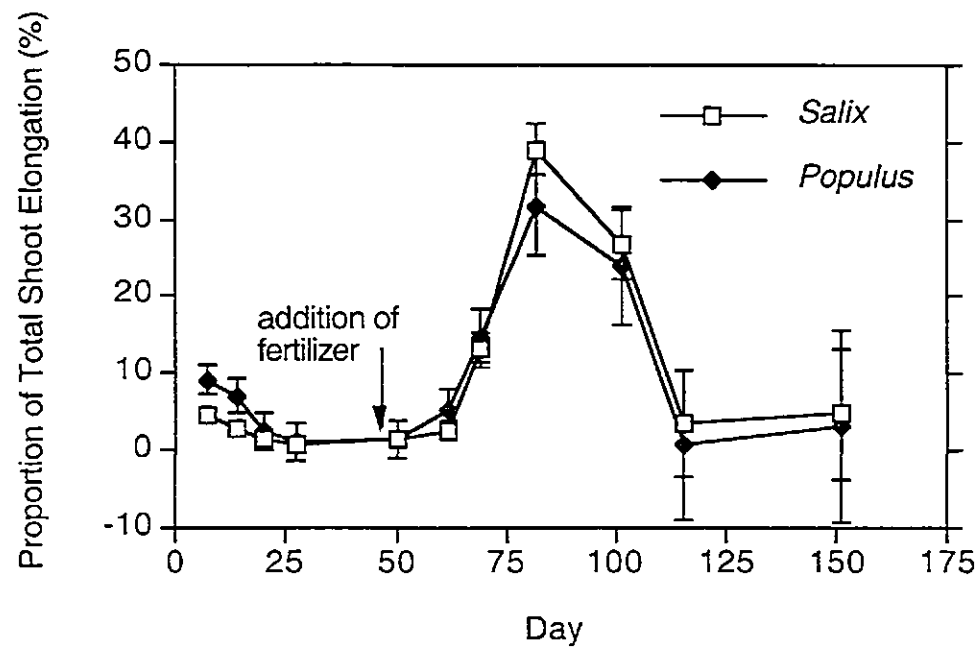
Figure 3-3: Mean (± 1 s.e.) proportion (%) of shoot elongation at each

measurement of total shoot elongation of and *Populus* species (n=63), *P. deltoides,*

P. balsamifera and *P. deltoides* and *Salix* species (n=192), *S. discolor, S. exigua*

and *S. lutea,* grown at different water table depths of 0, 2.5, 5 and 7.5 cm below

substrate surface.
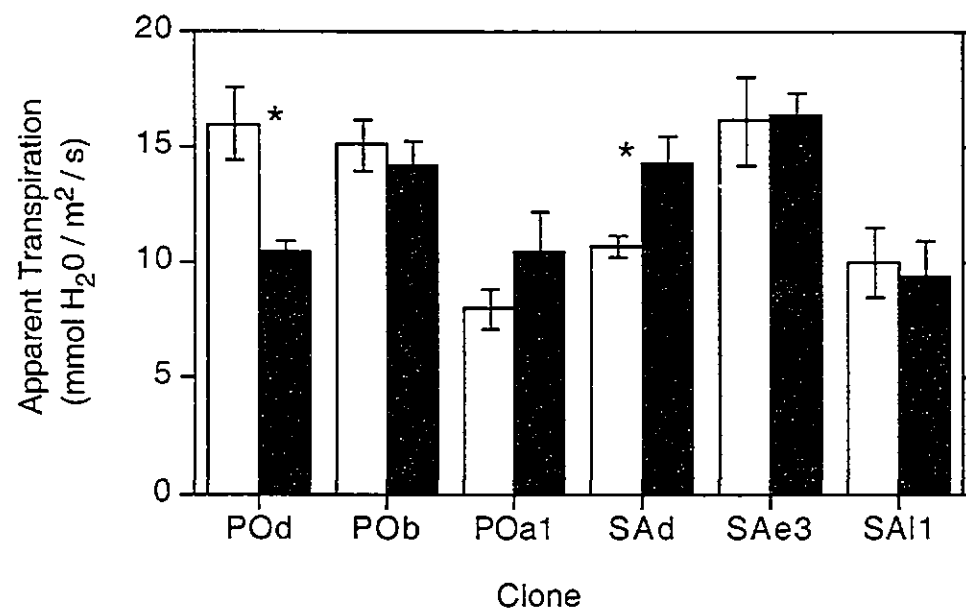
Figure 3-4: Mean ($\pm$ 1 s.e.) apparent transpiration (Ts) rate of *Populus deltoides*

(POd), *Populus balsamifera* (POb), *P. angustifolia* (POa1), *Salix discolor* (SAd), *S.*

exigua (SAe3) and *S. lutea* (SAl1) saplings grown for 69 days under two water

table depths, 7.5 (□) or 0 (■) cm below the substrate surface (n=4 to 13).

* $p < 0.05$.

For individual clones, only Ts rates of the pussy willow, *S. discolor,* and the prairie cottonwood, *P. deltoides,* were significantly influenced by water table elevation. The pussy willow Ts rate was significantly greater with the flooded 0 cm water table depth compared to the 7.5 cm depth. The prairie cottonwood, *P. deltoides,* showed an opposite pattern with Ts rate being significantly reduced by the flooded treatment of 0 cm depth (Figure 3-4). This finding supports the hypothesis that willows are more flood tolerant than cottonwoods as the increased flooding depth improved the pussy willow's Ts, while the deep flooding retarded the Ts of the prairie cottonwood, the cottonwood expected to be the least flood tolerant.

CONCLUSIONS

Generally, all of the cottonwood and willow clones studied tolerated the elevated water tables of 0, 2.5, 5 or 7.5 cm below substrate surface. There was no mortality but growth was influenced in both genera. The increased Ts rate of *S. discolor* coupled with the decreased Ts rate of *P. deltoides* at the flooded 0 cm water table depth suggests slightly greater flood tolerance of willows.

The rapid increase in shoot growth following the addition of fertilizer indicates that insufficient substrate nutrition may have masked possible differences in flood tolerance. It is unclear but possible that insufficient nutrition may be similarly limiting in natural riparian conditions.

Chapter 4

Stress and recovery of riparian cottonwoods accompanying
water table changes along Willow Creek, Alberta

Abstract: Gravel was excavated from the floodplain along Willow Creek, Alberta from 1996 to 1998 to provide materials for the construction of a new dam. The gravel pit was situated between Willow Creek and a grove of riparian cottonwoods (*Populus balsamifera* L. and *P. angustifolia* James). To permit gravel excavation, the gravel pit water table was lowered 5 m through water pumping and drainage ditches. Following the water table decline the trees in the grove adjacent to the gravel pit (drought-affected) displayed decreased petiole xylem water potential (Ψ_{xp}), increased leaf diffusive resistance (Rd) and precocious leaf senescence and abscission compared to trees in a nearby nonaffected grove. In 1999 the pit was refilled with excavation spoil and the water table recovered. Subsequently, the Ψ_{xp}, Rd and leaf senescence and abscission were restored trees in the drought-affected grove to levels similar to those in the nonaffected grove. Although annual branch growth increments varied across years, trees in the drought-affected and nonaffected groves had similar increments from 1994 to 1998, during and following the period of water table decline. This study demonstrated the vulnerability of riparian cottonwoods to drought due to water table decline and confirmed their physiological reliance on the riparian water table.

Key Words: cottonwoods, diffusive resistance, drought, *Populus*, riparian, water potential, water table decline

INTRODUCTION

Riparian cottonwoods and other phreatophytes depend on the water table as their principal water source (Busch et al. 1992, Mahoney and Rood 1992, Busch and Smith 1995, Kranjcec et al. 1998). In semi-arid regions such as the prairie regions of southern Alberta, the riparian water table is generally supported by water flowing laterally from the adjacent stream into the floodplain alluvium. The water table is therefore generally at a similar elevation to the adjacent river stage and gradually slopes downward with increasing distance from the channel (Busch et al. 1992, Rood et al. 1995, Stromberg and Patten 1996). The river stage and the depth of the water table naturally change seasonally and across years. Regulation of river flow with dams and diversions or interruption of the flow from the stream to substrate can alter the timing, frequency, magnitude and duration of water table changes and consequently affects the availability of water for riparian vegetation (Rood and Mahoney 1990).

Previous studies have demonstrated the dependence of cottonwoods on access to the riparian water table (Zhang et al. 1999). Cottonwoods generally grow in floodplains no more than 4 m above the riparian water table with part of the root system at least seasonally below the water table (Rood and Heinze-Milne 1989, Rood and Mahoney 1990, Busch et al. 1992, Scott et al. 1997, Stromberg et al. 1997). Additionally, diurnal water table fluctuations have been correlated with woody riparian vegetation transpiration response curves (Busch et al. 1992). Scott et al. (1999) demonstrated that sustained water table decline of more than one metre resulted in leaf desiccation, branch sacrifice (Rood et al. 2000), crown dieback and 88% mortality of *Populus deltoides* subsp. *monilifera* along an ephemeral stream in Colorado within 3 years. Willms et al. (1998) found water to be the

principal limitation to cottonwood branch growth during periods of low river flows, and Tyree et al. (1994) determined that cottonwoods are particularly vulnerable to drought-induced cavitation and shoot dieback. These studies demonstrate the vulnerability of cottonwoods to drought and the physiological dependence of cottonwoods and willows on the riparian water table.

The Pine Coulee Project is a water management project in southern Alberta and includes an offstream reservoir for water storage. The dam that creates this reservoir was constructed with materials partially excavated from a large gravel pit in the Willow Creek floodplain from 1996 to 1998. To permit gravel excavation, the water table within the gravel pit was lowered five meters by water pumping and drainage ditches. It was hypothesized that the cottonwoods separated from Willow Creek by this gravel pit would be drought stressed (designated as the 'drought-affected' grove) and that this would be indicated by particular physiological changes related to plant water status and flux. It was also expected that the trees in the drought-affected grove would display physiological recovery following water table recovery after the gravel pit was refilled.

METHODS

Study Site

The Pine Coulee Water Management Project is located in the Rocky Mountain foothills of southwestern Alberta (50° 7' N 115° 4' W) about halfway between the cities of Calgary and Lethbridge. Figure 4-1 is an aerial photograph of the study site in 1993 and provides the location of the gravel pit and the drought-affected and nonaffected groves prior to gravel excavation.
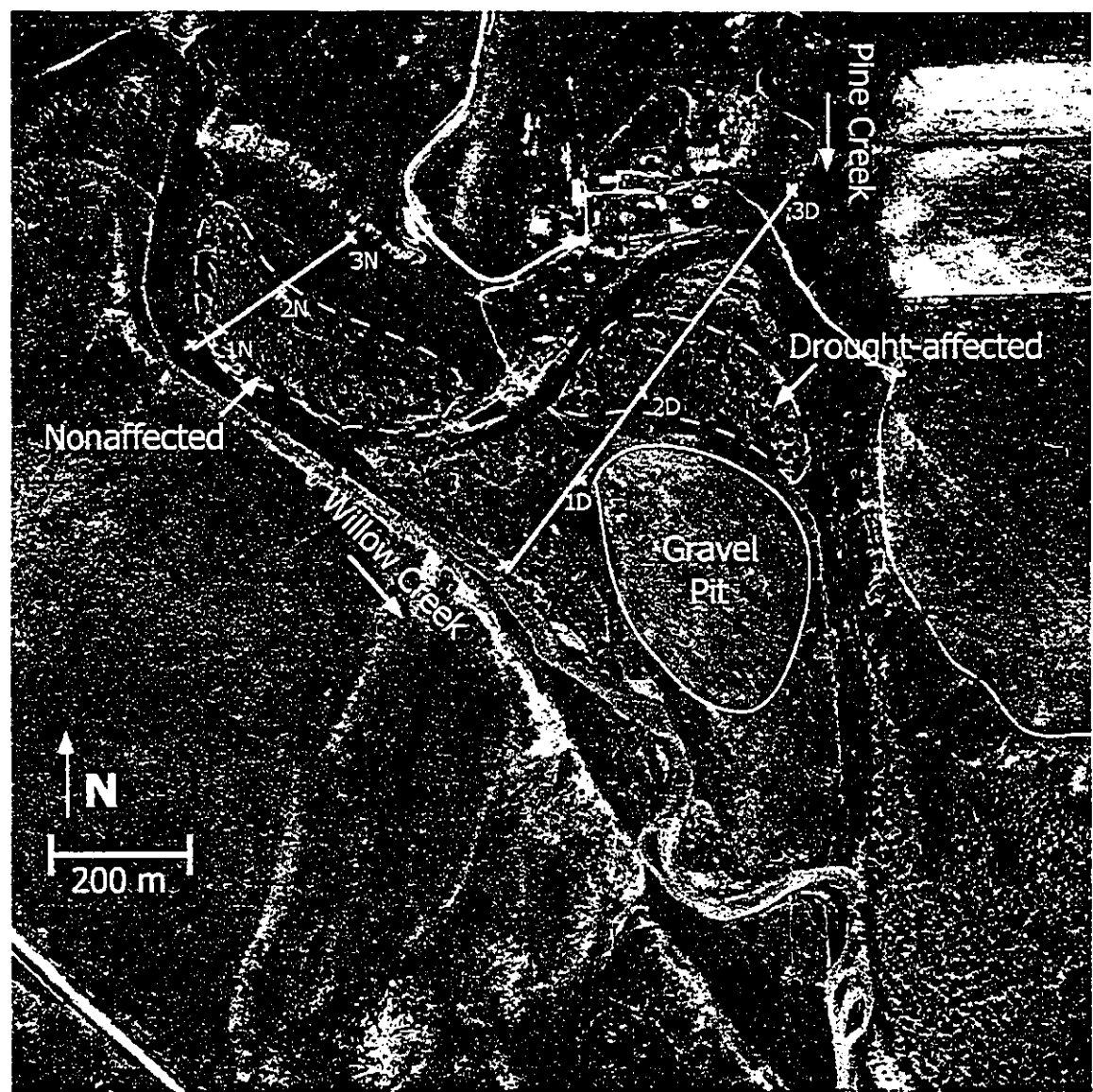
Figure 4-1: An aerial photograph of the study site at the Pine Coulee Project along Willow Creek, Alberta, showing the grove affected by gravel extraction in the gravel pit (Drought-affected) and the Nonaffected grove in 1993 prior to gravel extraction. The 'x's along the transect lines indicate test wells and stream stage measurement locations relevant to the two study groves.

To investigate the water tables within the two groves, test wells were positioned along transects perpendicular to Willow Creek in June 1999 (Figure 4-1). Surface elevations of Willow Creek and water table elevations were measured throughout the summer of 1999 and the slopes of the water tables were determined. The wells were designated N for the nonaffected grove and D for the drought-affected grove and numbered from Willow Creek. Well 3D was at a Water Survey of Canada gauging station along Pine Creek (05AB045). Other elevations were corrected to this benchmark.

Physiological Water Relations

In August and September 1998, petiole xylem water potentials (Ψ_{xp}), leaf diffusive resistances (Rd), leaf senescence and abscission and annual branch growth increments were analyzed from 22 cottonwood trees in the drought-affected grove and 18 trees in the nearby nonaffected grove (Figure 4-1). The cottonwoods were balsam poplars, *Populus balsamifera* L., narrowleaf cottonwoods, *P. angustifolia* James and a few interspecific hybrids (Rood et al. 1986). The trees studied were randomly chosen from those trees that had leaves that could be reached with a two meter tall stepladder. Water pumping and gravel excavation began in 1996 and the water pumping stopped and the gravel pit was refilled with excavation spoil in late fall 1998 after the 1998 measurements. The trees were revisited in August 1999 to analyze the same physiological characteristics as in 1998.

Data were collected between 10:00 and 16:00 daily because cottonwoods generally demonstrate maximum transpiration during this period (Blake et al. 1984). Measurements alternated between the drought-affected and nonaffected groves. The Rds of ten leaves per tree were determined using a Li-Cor (Lincoln, Nebraska)

LI-1600 steady state diffusion porometer on the abaxial leaf surface, the dominant surface for foliar transpiration in poplars (Blake et al. 1984). Five of these leaves were harvested and Ψ_{xp} were measured immediately using a PMS Instrument Co. (Corvallis, Oregon) Scholander-type pressure chamber . Leaf senescence and abscission were estimated visually as a percentage of total leaf cover for each tree periodically in September 1998. Photographs were also taken September 5, 1998 and September 23, 1999.

Annual branch growth increments from 1994 to 1999 were measured on five branches from each of ten trees within the drought-affected and nonaffected groves ($\pm$ 0.1 mm). The annual branch growth increment was represented as a percentage of the total branch growth over the six years.

For both 1998 and 1999, the Ψ_{xp} and Rd measurements were analyzed in two separate groupings. The early measurements of August 31, September 1 and 2, 1998 (Julian days 243, 244 and 245) were analyzed separately from the late measurements of September 7, 8 and 15, 1998 (Julian days 250, 251 and 258). In 1999, the measurements of August 4, 6, 9 and 10 (Julian days 216, 218, 221 and 222) were analyzed separately from the measurements of August 17, 18, 20 and 21 (Julian days 229, 230, 232 and 243). The Ψ_{xp} and Rd data were analyzed with two factor ANOVAs considering the grove, drought-affected or nonaffected (factor 1), measurement date (factor 2) and the interaction of the two factors. The correlation of Ψ_{xp} and Rd measurements was investigated through linear regression.

RESULTS AND DISCUSSION

Study Site

The water table elevations within the drought-affected and nonaffected groves demonstrated slightly different patterns (Figure 4-2). In semi-arid regions, water generally flows from the river into the floodplain alluvium to create the water table. The water table under the drought-affected grove demonstrated this pattern as it sloped downward away from the stream with a slight increase associated with Pine Creek. Due to this hydrology, the gravel pit would have interrupted the flow of water from Willow Creek into the sand and gravel substrate that the drought-affected trees are rooted in. Lowering the water table in the gravel pit should subsequently lower the water table under the drought-affected grove. The hydrology of the water table under the nonaffected grove was somewhat different with apparent localized flow into the stream (Figure 4-2).
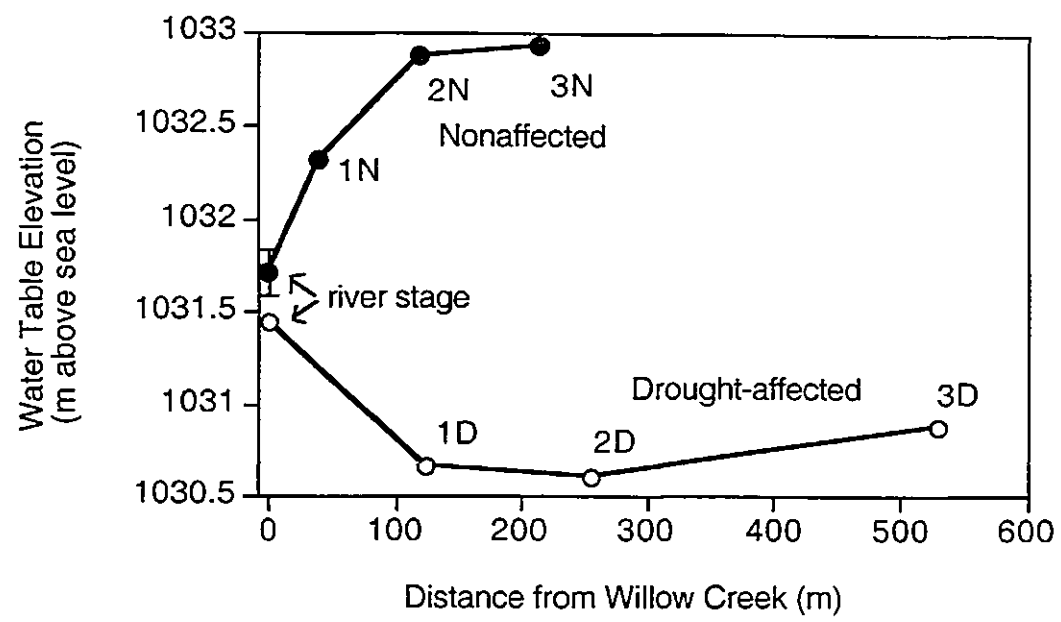
Figure 4-2: Mean Willow Creek stage elevations and water table elevations under the drought-affected and nonaffected groves in June through August 1999 at the Pine Coulee Project along Willow Creek, Alberta. The water table under the drought-affected grove was lowered from 1996 to 1998 due to gravel extraction and water pumping. Except for the river stage near the nonaffected grove, the standard error was smaller than symbol size (n=6 to 8).

Physiological Water Relations

It was expected that Ψ_{xp} would be more negative in the drought-affected grove while the water table was suppressed in 1998. It was also expected that Ψ_{xp} would be restored in 1999 following water table recovery. Over the two years, the drought-affected grove tended to have more negative Ψ_{xp} (df=1, F=3.2, p=0.075), and the measurement date (df=3, F=14.2, p<0.0001) and the grove x date interaction (df=3, F=8.9, p<0.0001) were highly significant. In early September 1998, the drought-affected and nonaffected groves were not significantly different from each other (Figure 4-3), while in mid-September, the drought-affected grove displayed significantly more negative Ψ_{xp}. In 1999, there were significant differences between the two groves in early and late August. The drought-affected grove had significantly more negative Ψ_{xp} in early August but the pattern had reversed by mid-August (Figure 4-3). This recovery may have reflected a rebound in water status following branch sacrifice that occurred during the earlier period of stress (Scott et al. 1999, Rood et al. 2000). With the restoration of the water table, the physiologically pruned trees would have had a more favorable balance of water uptake versus transpiration.

In some previous cottonwood studies, drought-stressed cottonwoods have had decreased water potentials, while in other cases, there as been little change in water potential. In Colorado, declines greater than one meter lowered the Ψ_{xp} of *Populus deltoides* spp. *monilifera* (Scott et al. 1999). Pezeshki and Hinckley (1982) found that leaf water potential of cottonwoods did not decrease below -0.9 MPa during prolonged drought as the stomata remained closed, maintaining the water potential. In the present study, it appears that other factors besides water table decline were affecting the Ψ_{xp} to create the differences between the two groves in 1999.

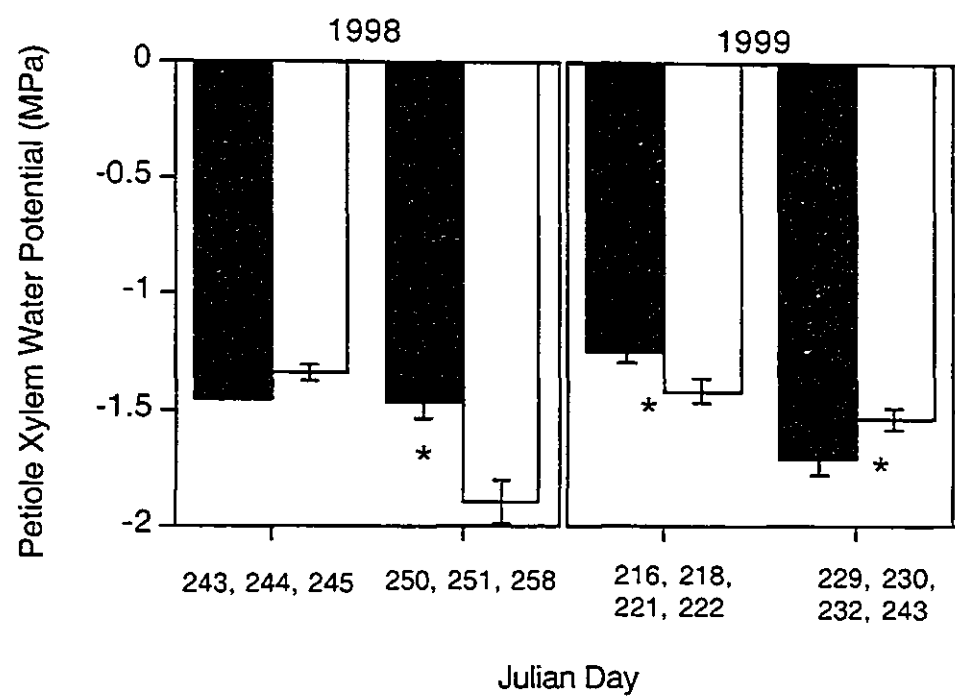**Figure 4-3:** Mean ($\pm$ 1 s.e.) petiole xylem water potential (Ψ_{xp}) of drought-affected

($\square$) and nonaffected (■) cottonwoods, *Populus balsamifera* and *P. angustifolia*,

along Willow Creek, Alberta at the Pine Coulee Project (n=35 to 77). The drought-

affected cottonwoods experienced a water table decline from 1996 to 1998 and the

water table recovered in 1999. * $p<0.05$.

Rd is an inverse measure of transpiration and it was expected that the drought-affected grove would have greater Rd (lower transpiration) while the water table was lowered. Grove (df=1, F=15.5, p<0.0001), measurement date (df=3, F=7.1, p=0.0001) and the interaction of grove and date (df=3, F=5.1, p=0.002) all significantly affected Rd. In 1998, the drought-affected grove displayed greater Rd than the nonaffected grove (Figure 4-4). In 1999, after the water table had recovered, there was no significant difference in Rd between the two groves.

Transpirational demand is very high in *Populus* trees (Zelawski 1973) and increasing Rd through stomatal closure is one way that *Populus* reduce their transpiration. Consistent with this, the Rd was much greater in the drought-affected grove in 1998. With the depressed water table, the drought-affected grove would not have had a sufficient and reliable water supply to meet the transpirational demands. With the recovery of the water table in fall 1998, the drought-affected grove would have an increased water supply and transpiration was restored to the level of the nonaffected grove in 1999.

As both Ψ_{xp} and Rd are related to the water status of cottonwoods, these two parameters are often correlated. With more negative Ψ_{xp}, indicating that the water is under greater stress in the xylem vessels, there is often increased Rd. However, these two measures were only minimally correlated in the present study. With data shown in Figure 4-5, there was a slight correlation between Rd and Ψ_{xp}, but the negative correlation was produced because the few leaves with very low Ψ_{xp} had low Rd. Coefficients of determination (r^2) were only 0.027 and 0.034 for the collective 1998 and 1999 data, respectively.
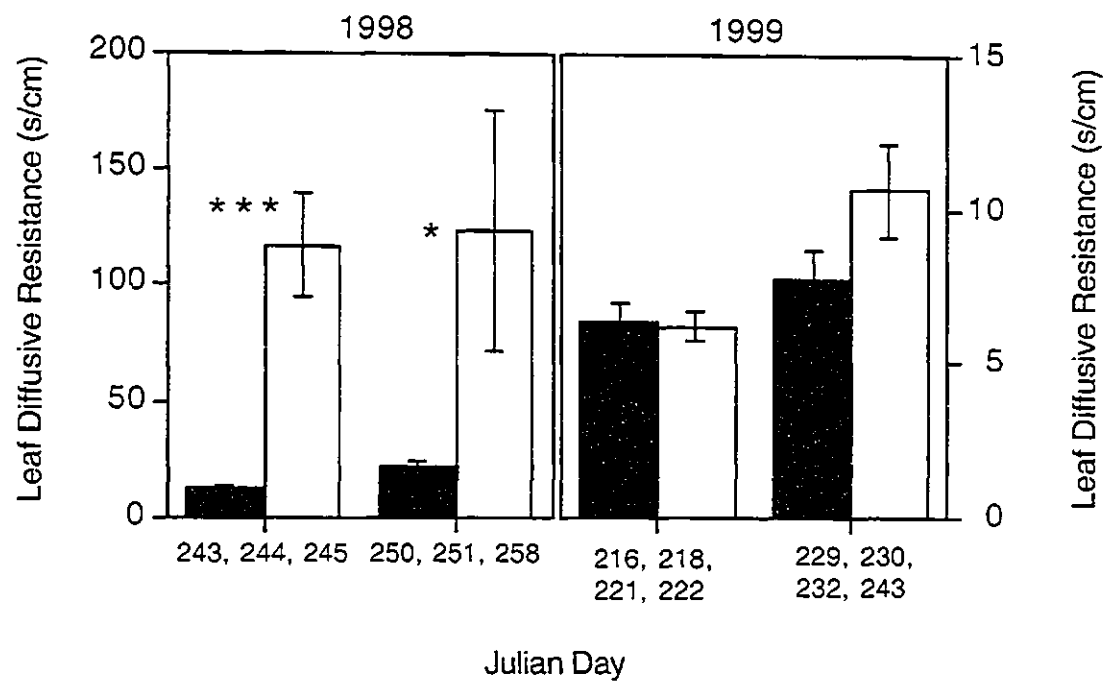
Figure 4-4: Mean leaf diffusive resistance (Rd) (± 1 s.e.) of drought-affected (□)

and nonaffected (■) cottonwoods, *Populus balsamifera* and *Populus angustifolia*,

along Willow Creek, Alberta at the Pine Coulee Project (n=70 to 150). The drought-

affected cottonwoods experienced a water table decline from 1996 to 1998 and the

water table recovered in 1999. Note the different y-axis scales. *** $p < 0.0001$,

* $p < 0.05$.
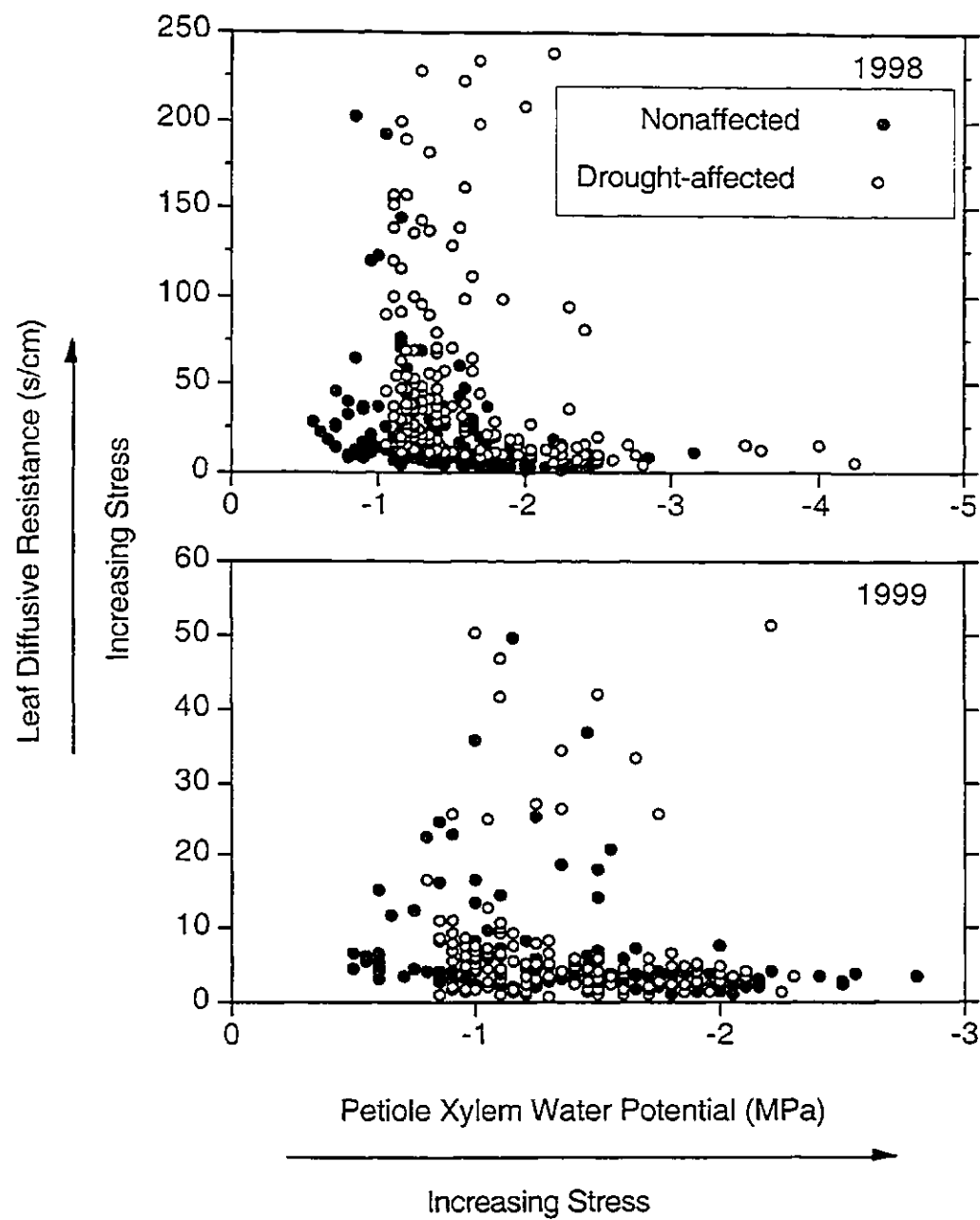
Figure 4-5: Individual measurements of petiole xylem water potential (Ψ_{xp}) and leaf diffusive resistance (Rd) of cottonwoods, *Populus balsamifera* and *P. angustifolia*, along Willow Creek, Alberta at the Pine Coulee Project in drought-affected and nonaffected groves in 1998 (n=338) and 1999 (n=296). The drought-affected cottonwoods experienced a water table decline from 1996 to 1998 and the water table recovered in 1999. Note the different x- and y-axes.

Measurements of Ψ_{xp} and Rd of two trees throughout a day were made in the drought-affected grove on September 3, 1998 and the nonaffected grove on September 4, 1998. Again, there was little correlation between Ψ_{xp} with Rd (Figure 4-6). The trees in the drought-affected grove showed differences in Ψ_{xp} as great as 0.5 MPa the course of the day, while the Rd measurements were similar. In the nonaffected grove, the tree with the more negative Ψ_{xp} throughout the day also had the lower Rd.

Overall, there was little correlation of Ψ_{xp} and Rd in the cottonwoods studied. This lack of correlation between Ψ_{xp} and Rd for *Populus* stomata has been demonstrated in previous studies. Schulte et al. (1987) found that some *Populus trichocarpa* stomata behave contrarily to common stomatal patterns (Kozlowski and Pallardy 1997), by decreasing Rd with more negative Ψ_{xp}.

In southern Alberta, leaf senescence and abscission normally occur in late September and through October. In 1998, the drought-affected grove showed precocious leaf senescence and abscission as the majority of the leaves had senesced or abscised by September 5 (Figure 4-7). The nonaffected grove on the same date showed how cottonwoods typically look in early September with little senescence or abscission. By September 15, 1998, the drought-affected grove had abscised 26.1 ± 5.4% total leaf area compared to the nonaffected grove that had abscised 0.3 ± 0.3% leaf area. Of the leaves remaining on the trees, the drought-affected grove had nearly four times the senescent leaf area compared to the nonaffected grove (46.5 ± 5.6% vs. 11.7 ± 2.7%). In August and September 1999 and 2000, the two groves senesced and abscised at similar times and later in the season than the drought-affected grove in 1998.
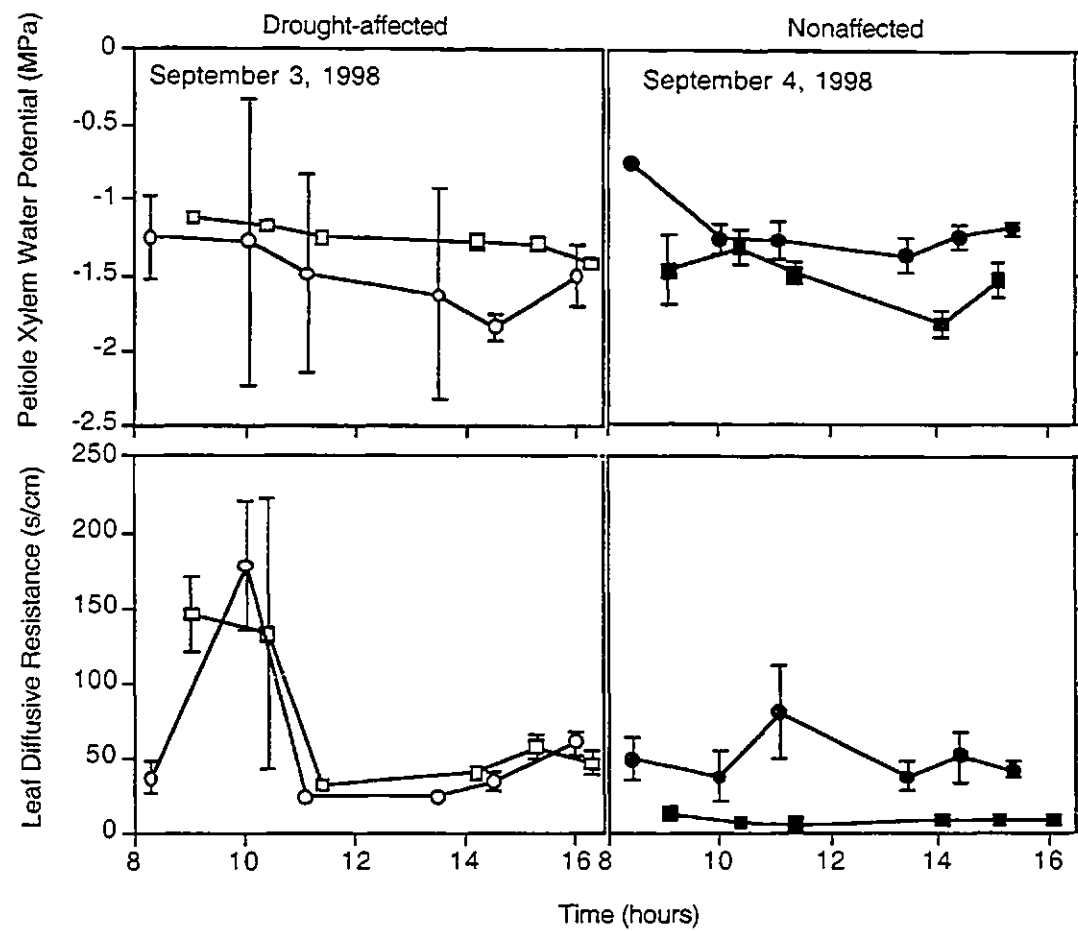
Figure 4-6: Mean (± 1 s.e.) petiole xylem water potential (Ψ_{xp}, n=5) and leaf diffusive resistance (Rd, n=10) of four *Populus balsamifera* cottonwoods along Willow Creek, Alberta at the Pine Coulee Project in 1998. Two drought-affected cottonwoods, measured September 3, experienced a water table decline from 1996 to 1998. The nonaffected trees were measured on September 4.
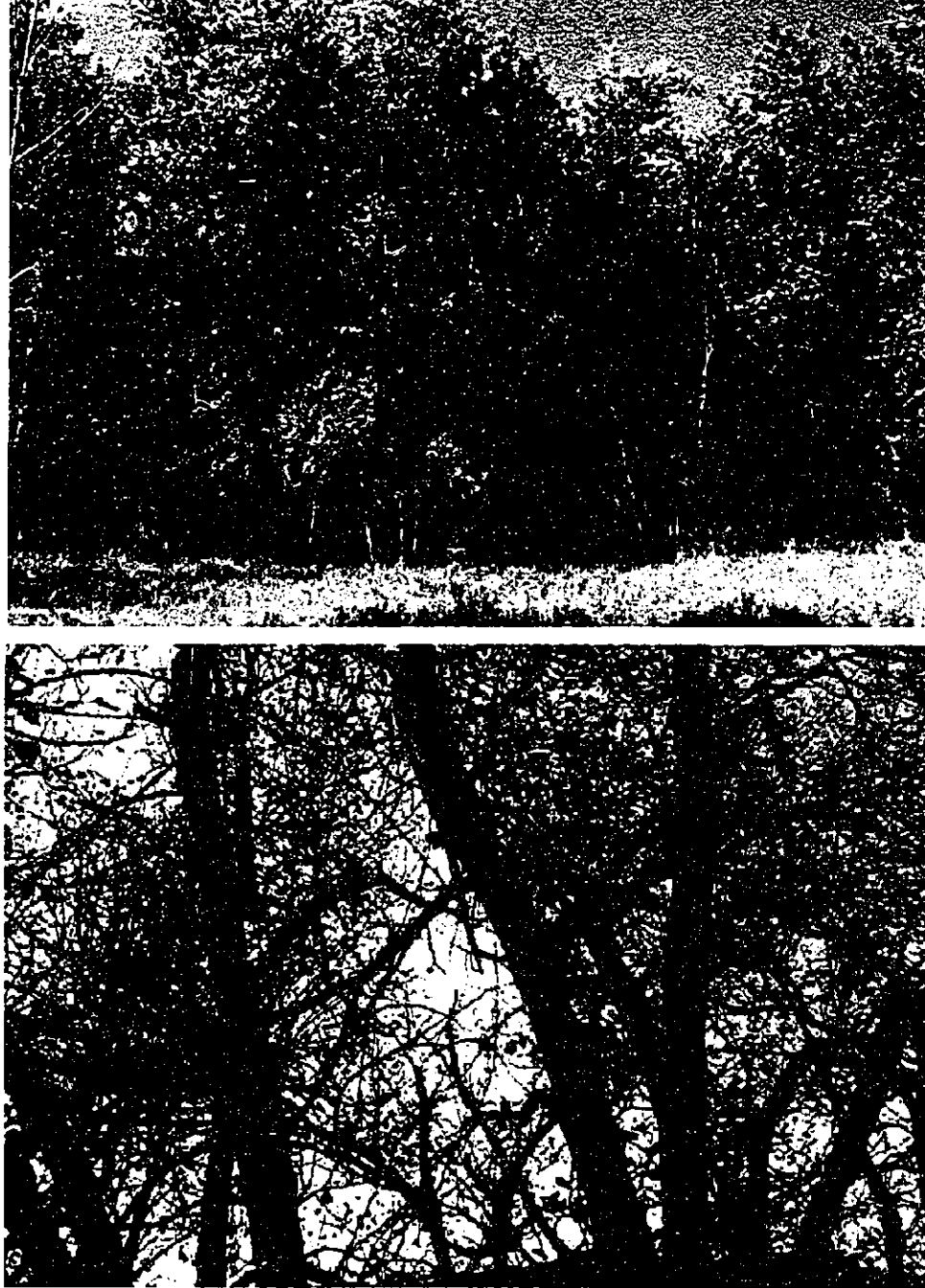
Figure 4-7: Riparian cottonwoods along Willow Creek, Alberta at the Pine Coulee Project on September 5, 1998. The nonaffected grove (top) is just commencing autumnal senescence. The drought-affected grove (bottom) experienced a water table decline from 1996 to 1998 and leaves have precociously senesced and abscised

Reductions in leaf area by leaf senescence and abscission are mechanisms used by *Populus* trees to reduce the transpirational demand and mediate water stress (Braatne et al. 1992, Busch and Smith 1995). In previous studies, drought stress has accelerated cottonwood leaf senescence and increased abscission (Schulte et al. 1987). These provide an early visible sign of water stress accompanying water table declines (Scott et al. 1999). The obvious precocious leaf senescence and abscission in the drought-affected grove in 1998 demonstrate the drought stress resulting from the water table decline. The lack of precocious senescence and abscission in 1999 and 2000 suggests the removal of drought stress with water table recovery.

Since cottonwood branch growth is limited by water availability (Willms et al. 1998, Scott et al. 1999), it was expected that the drought-affected grove would have shorter annual branch increments for the years when the water table was depressed. However, no significant differences in annual branch growth increments were detected between the drought-affected and nonaffected grove between 1994 and 1999 (Figure 4-8). There were differences across years for trees from both the drought-affected and nonaffected groves. This suggests that the lack of treatment affect was not due to random variation or insufficient experimental design.

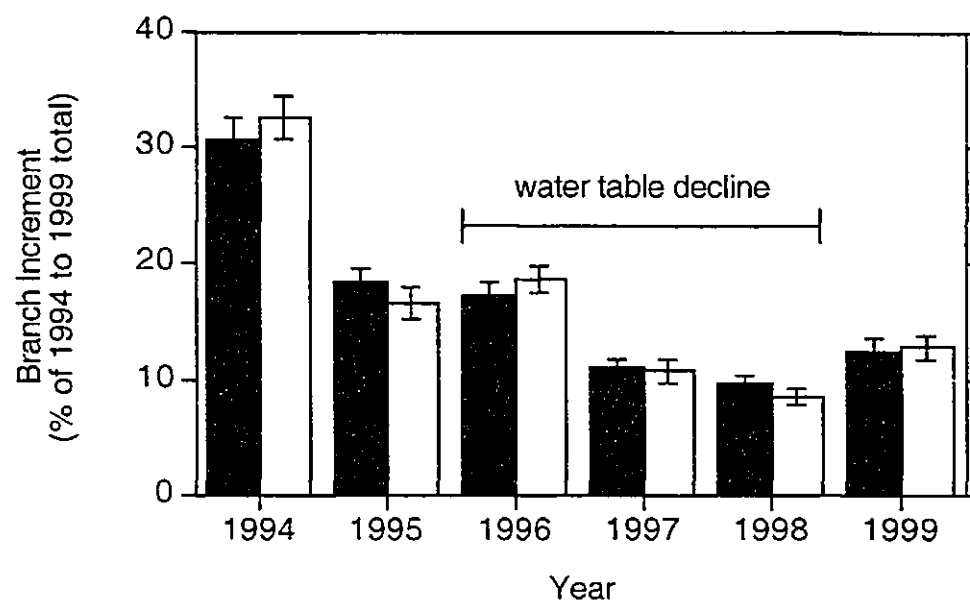**Figure 4-8:** Mean (± 1 s.e.) percentage contribution of annual branch growth increments to total branch elongation from 1994 to 1999 of drought-affected (□) and nonaffected (■) cottonwoods, *Populus balsamifera* and *P. angustifolia*, at the Pine Coulee Project along Willow Creek, Alberta. The drought-affected cottonwoods experienced a water table decline from 1996 to 1998 and the water table recovered in 1999 (n=50).

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Branch growth increments integrate the environmental conditions over the early growing season, probably reflecting water table status, rainfall and temperature. The other physiological parameters measured in this study, Ψ_{xp} and Rd, were instantaneous, indicating whether the cottonwoods were experiencing drought stress at the specific time of sampling rather than across the entire growing season. Branch elongation has shown varying responses to drought stress in previous studies (Scott et al. 1999, Willms et al. 1998). Drought treatments that increase diffusive resistance are generally thought to also reduce shoot growth (Kelliher et al. 1980, Kranjcec et al. 1998, Mahoney and Rood 1992). Scott et al (1999) found that with water table decline less than 0.5 m branch growth was reduced, but with water table depletion greater than 1 m changes in branch growth were more complex.

CONCLUSIONS

The decreased Ψ_{xp}, increased Rd, and precocious leaf senescence and abscission of the trees in the drought-affected grove in 1998 indicated that the water table decline caused drought stress in these poplars. The recovery of these physiological conditions to levels comparable to the nearby nonaffected grove in 1999 following water table recovery supports this interpretation. Thus, these cottonwoods were reliant on the water table as a principal water source and were vulnerable to water stress when the water table was lowered.

This study indicates the importance of considering phreatophytic riparian vegetation during floodplain mining for gravel extraction. In this study the cottonwoods were able to recover from the depressed water table that resulted from the gravel mining. In larger or longer projects, cottonwood mortality could occur (Scoot et al. 1999), resulting in a loss of these trees and a corresponding loss of the environmental and aesthetic values associated with riparian vegetation.

Chapter 5

Conclusions

It was hypothesized that since willows are located closer to the stream and at lower elevations than cottonwoods, the willows would be more flood tolerant and less drought tolerant, and that these differences would contribute to the spatial separation between the genera. The results of this thesis support the hypothesis that willows are less drought tolerant than cottonwoods but differences in flood tolerance were less clear.

Previous studies have indicated that flooding or inundation tolerance is the principal determining factor in floodplain species distribution; with those species that are more flood tolerant closer to the stream (Noble 1979, Dionigi et al. 1985, Malanson 1993, Cordes et al. 1997, Naiman and Decamps 1997, Everson and Boucher 1998, Denneler et al. 1999). The present thesis indicates that in cottonwood-willow riparian forests in semi-arid regions, flood stress may not be as great a determining factor for the establishment and location of willows versus cottonwoods as drought stress. Drought occurs more frequently and with greater duration than flooding in these dry landscapes where water is often limiting. Other studies have also found that differences in drought tolerance influence the establishment and spatial locations of willows versus cottonwoods. Along the Rhine River, in the Netherlands, Van Splunder et al. (1996) determined that the distribution of *Populus* and *Salix* species was linked to drought resistance rather than flood tolerance. Stromberg et al. (1991) also found that the distribution of *Populus fremontii* and *Salix gooddingii* along the Hassayampa River system was at least

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partially determined by drought tolerance and not based on increased flood tolerance of willows.

In the three studies of the present thesis, willows (*Salix* sp.) and cottonwoods (*Populus* sp.) responded very similarly to the drought and flood stresses experienced. However, willow seedlings were more vulnerable to water table decline than cottonwood seedlings, suggesting reduced drought tolerance. Saplings of one willow species displayed increased transpiration rates with increased flooding depths implying slightly increased flood tolerance. Drought stress was also experienced by mature cottonwoods during water table decline and the cottonwoods' water status recovered following water table recovery, further confirming their vulnerability to drought stress.

In contrast to more humid regions where flood tolerance may control tree distributions, across semi-arid regions of North America factors such as reduced drought tolerance, increased use of clonal processes for reproduction and increased tolerance of the physical stresses of flooding or ice scour of willows may allow willows to persist at lower elevations and closer to the stream in riparian zones than cottonwoods. The present studies also confirm that ensuring willow and cottonwood roots have access to the water table or capillary zone throughout the growing season, regardless of streamflow management or floodplain development, will favor the continued survival of these genera.

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Appendix A

Table A-1: Factorial ANOVAs for shoot height, shoot area and shoot dry weight of

Populus deltoides, P. balsamifera, P. angustifolia, Salix discolor, S. exigua and *S.*

lutea saplings grown for 115 days under water table depths of 0, 2.5, 5 and 7.5 cm

below substrate surface.

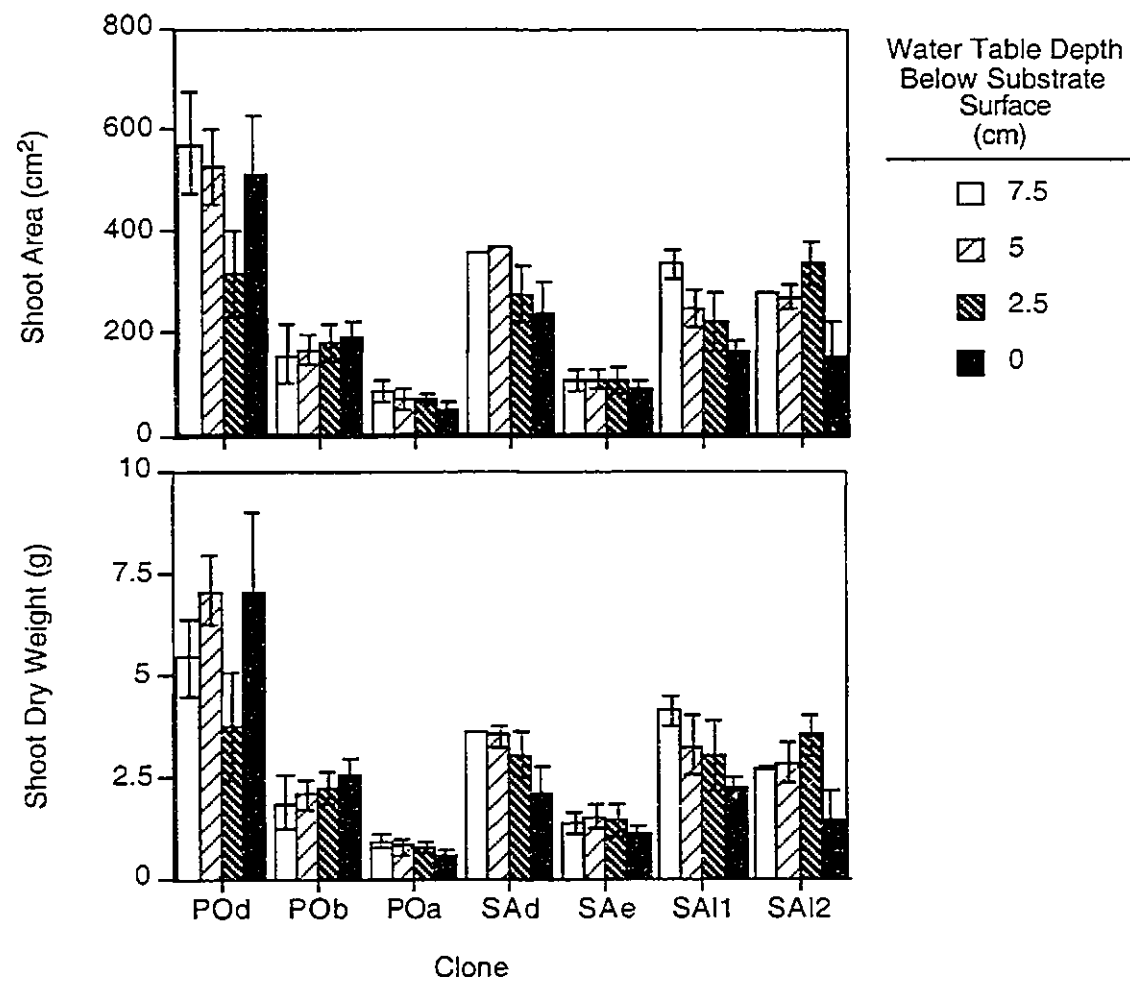| Parameter Source of Variation	d.f.	F-value	p-value
Shoot Height			
Depth of water table (D)	3	0.9	0.48
Clone (C)	6	16.3	***
D x C	18	1.0	0.43
Shoot Area			
Elevation of water table (E)	3	3.3	*
Clone (C)	6	49.4	***
E x C	18	1.8	*
Shoot Dry Weight			
Depth of water table (D)	3	1.4	0.25
Clone (C)	6	37.8	***
D x C	18	1.8	*

* p<0.05, ** p<0.01, *** p<0.0001.

Figure A-1: Mean (± 1 s.e.) shoot area and shoot dry weight of *Populus deltoides*
(POd), *P. balsamifera* (POb), *P angustifolia* (POa), *Salix discolor* (SAd), *S. exigua*
(SAe) and *S. lutea* (SAl1 and SAl2) saplings grown for 115 days under four water
table depths (n=1 to 12).