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Seed germination of willow species from a desert riparian ecosystem

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Abstract

The restoration of riverine riparian areas following mechanical, herbicidal, or biological control of the invasive species tamarisk (*Tamarix ramosissima* Ledeb.) is a major issue in the western United States. Recruitment of seedlings of native woody species is necessary in these restoration efforts. Species of willow (*Salix*) are often considered essential in these efforts. We studied the germination of seeds of tree willow (*Salix lutea* Nutt.) and coyote willow (*S. exigua* Nutt.) at a wide range of constant or alternating incubation temperatures. Seeds were collected from native stands in the delta of the Walker River in western Nevada over a 3 year period. Seed germination was very similar for both species. On 2 of the 3 years of testing the seeds had 100% germination at some incubation temperatures and some germination over almost all of the 55 temperature regimes used in the experiments. A late frost in May of 2000 markedly reduced total germination of both species, but did not greatly restrict the temperature regimes where some germination occurred. Optimum germination, defined as that not lower than the maximum observed minus one half the confidence interval at the 0.01 level of probability, occurred over a very wide range of temperatures, but for tree willow only the temperature regimes 15/25 (15° C for 12 hours and 25° C for 8 hours in each 24 hour period) and 15/30° C always supported optimum germination. No temperature regime always supported optimum germination of coyote willow seeds, but the most frequent optima tended to be at lower temperatures than for tree willow. Because of the similarity in germination responses and overlapping phenology, seeds of these 2 species probably compete for germination safesites.

Key Words: *Salix exigua, S. lutea,* coyote and tree willow, incubation temperatures, seedbed temperatures

Resumen

La restauración de áreas ribereñas después del control mecánico, químico o biológico de la especie invasora "Tamarisk" (*Tamarix ramosissima* Ledeb.) es un problema mayor en el oeste de Estados Unidos. El establecimiento de plántulas de especies leñosas nativas es necesario en estos esfuerzos de restauración. Especies de "Willow" (*Salix*) a menudo son consideradas esenciales en estas acciones de restauración. Estudiamos la germinación de semillas de "Tree willow" (*Salix lutea* Nutt.) y "Coyote willow" (*S. exigua* Nutt.) en un amplio rango de temperaturas de incubación constantes y alternantes. Las semillas se colectaron durante un periodo de 3 años en poblaciones nativas del delta del río Walker en el oeste de Nevada. La germinación de la semilla fue muy similar para ambas especies. En 2 de 3 años de prueba, las semillas tuvieron 100% de germinación en algunas de las temperaturas de incubación y algo de germinación en casi todos los 55 regímenes de temperatura evaluados en el experimento. Una helada tardía en Mayo de 2000 redujo marcadamente la germinación total de ambas especies, pero no restringió grandemente los regímenes de temperatura donde algo de germinación ocurrió. La germinación óptima, definida como no menos que el máximo observado menos una mitad del intervalo de confianza a un nivel de significancia de 0.01, ocurrió en un amplio rango de temperaturas, pero para "Tree willow"solo los regímenes de temperatura 15/25 (15° C por 12 horas y 25° C por 8 horas en cada periodo de 24 horas) y 15/30° C siempre produjeron la máxima germinación. No hubo un régimen de temperatura que mantuviera la germinación óptima para las semillas de "Coyote willow", pero la germinación optima tiende a ser a mas bajas temperaturas que para el "Tree willow". Debido a la similitud en la respuestas de germinación y la frenología que se traslapa, las semillas de en estas dos especies probablemente compitan por sitios seguros para germinación.

Willow species (*Salix* sp.) are important components of riparian communities throughout much of North America. They occur as both small to moderate sized trees and as shrubs. Many, but not all of the shrubby willows are browsed by wildlife or domestic livestock (Sampson 1924). Despite having flowers arranged in catkins, willow species are insect pollinated. When they flower, large numbers of insects are attracted to the catkins. Insectivorous birds follow their prey, making willow communities important habitats for birds. In the virtually treeless landscapes of the Great Basin, riverine willow communities often provide the only woody nesting cover for a variety of birds.

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In the central Great Basin and extending throughout the Southwest, the exotic shrub or small tree tamarisk (*Tamarix ramosissima* Ledeb.) has invaded vast reaches of riverine habitats. On any specific sites it is an open question if tamarisk replaced the native woody species or the woody species were destroyed and tamarisk invaded the ecological void. Currently, limited releases have been made in the Great Basin of a biological control agent for the suppression of tamarisk. A beetle (*Diorhabdo elongata*), imported from Asia, shows promise for suppressing tamarisk. Will this biological suppression lead to seedling recruitment of the native woody species?

The western Great Basin riverine riparian areas most impacted by the invasion of tamarisk are the sink of the Humboldt River, the north sink of the Carson River in the Stillwater marsh area, and the delta of the Walker River. The Humboldt River sink is naturally treeless. The north discharge arm of the Carson River has well developed gallery forest of Fremont cottonwood (*Populus fremontii* S. Watson), almond willow (*Salix amygduloides* Anderson), tree willow (*S. lutea* Nutt.), coyote willow (*S. exigua* Nutt.), buffalo berry (*Shepherdia argentea* Nutt.) and the exotic Russian olive (*Elaeagnus angustifolius* L.). In the Stillwater marsh itself, there are vast linear stands of tamarisk on water control structures and along road banks. The few Fremont cottonwoods present are probably adventive since tail water was delivered to the area as drainage from the Newlands Irrigation District.

The delta of the Walker River is the site of one of the most extensive stands of tamarisk. In 1909 the shore of Walker Lake was located just south of Schurz, Nevada. Up-stream diversion of water for agricultural, municipal, and wildlife habitat uses in both California and Nevada have resulted in a dramatic drop in lake level. The river currently periodically enters the lake about 25 km to the south and about 100 m lower in elevation than the 1909 shore level based on unpublished maps on file with the Walker River Paiute tribe. The vast lake plain exposed by this drying has been incised by the meandering Walker River as it attempts to erode to a new base level. Tamarisk, Fremont cottonwood, tree, and coyote willow invasion has followed the dropping lake level. Tamarisk has been the much more successful of these woody species. Coyote willow is the second most abundant species, probably because it forms extensive clonal stands. Tree willow and Fremont cottonwood are both heavily preyed upon by beavers (*Castor canadensis*). Fremont cottonwood has also been utilized as a source of fuel wood.

Fremont cottonwood and the willow species belong to the family Salocaceae. Tamarisk is a member of the completely un-related family Tamaricaceae. Despite having no phylogenetic relationship, Fremont cottonwood, tree, and coyote willow all produce relatively small seeds that are wind dispersed with the aide of seed borne hairs, and have very short periods of seed of viability. The seeds of all of these species require quite specific moist seedbeds for germination and seedling establishment. As a first step in understanding the seed and seedbed ecology of these species, our purpose in this study was to investigate the germination of seeds of tree and coyote willow at a wide range of constant and alternating temperature regimes.

Methods

Seeds of tree and coyote willow were harvested from native stands located in the Walker River delta (38° 53.539'N 118° 46.733°) Win 1999, 2000, and 2001. The seeds were collected at maturity in late May or early June each year. Seeds were collected from many different trees over an extensive area of the delta. The seeds were transported to the laboratory and the experiments established immediately, with as little time as possible between collection and the seeds being wet in the germination plates.

In all experiments 4 replications of 25 seeds each were used in a randomized block design. Seeds were placed on top of non-toxic commercial germination paper in closed Petri dishes and kept wet with tap water. Germination trials were conducted in the dark. Seeds were considered germinated when the radical emerged 5 mm. Germination counts were made after 1, 2, and 4 weeks incubation. Constant incubation temperatures were 0, 2, and 5° C and at 5 degree increments through 40° C. In addition, alternating regimes included 16 hours at each constant temperature, plus 8 hours at each possible higher temperature per 24 hours. For example, 35° C alternated with 40° C only, while 0° C alternated with 2, 5, 10, 15, 20, 25, 30, 35, and 40° C. This made a total of 55 constant and alternating temperature regimes (Young et al. 1991).

The germination response of seeds of the 2 species of willow was compared using the seedbed temperature definitions (Young and Evans 1982):

a. Very cold: 0/0 (constant 0° C), 0/2 (0° C for 16 hours and 2° C for 8 hours in each 24 hours), 0/5 and 2/2° C.
b. Cold: 0/10, 0/15, 2/5, 2/10, 2/15, 5/5, and 5/10° C.
c. Cold fluctuating: 0/20, through 0/40° C and 2/20 through 2/40° C.
d. Fluctuating: 5/30 through 5/40° C, 10/35, 10/40, 15/40° C.
e. Moderate: 5/15 through 5/25, 10/10 through 10/30° C, 15/15 through 15/35° C, 20/20 through 30/35° C, and 25/35° C.
f. Warm: 20/40, 25/35, and 25/40° C, 30/30 through 30/40° C, 35/35, 35/40, and 40/40° C.

The categories of seedbed temperatures reflect germination environments of field seedbeds based on several years of monitoring in the Great Basin (Evans et al. 1970, Evans and Young 1970, 1972).

Data from each base temperature and its alternating temperature regimes were used to generate a quadratic response surface with estimated means and confidence intervals at the 1% level of probability (Young et al. 1980, Evans et al. 1982). A number of germination parameters were calculated from the quadratic response surfaces (Table 1) (Young and Evans 1982). Profiles were compared using the multiple response surface comparison method described by Palmquist et al. 1987.

Results and Discussion

The seeds of willow species are small, fragile, light, and sufficiently aerodynamic to be dispersed by the wind. The aerodynamics is enhanced by relative dense covering of silky hairs. These hairs are many times longer than the diameter of the seed. The seeds of most species of willow only remain viable for short periods of time (Young and Young 1992).

It is immediately apparent when you examine the temperature-germination profiles for tree (Table 2) and coyote willow (Table 3) that the seeds of these species germinate over a wide range of constant or alternating incubation temperatures. Coyote willow seeds germinated at all 55 temperatures tested and tree willow seeds had some germination at all temperature regimes except a constant 40° C.

The second factor that is apparent when examining the profiles is the seeds of both species are highly viable with 100% germination occurring at least at 1 temperature regime (Tables 2 and 3). At least 90% germination occurred over a wide range of temperatures.

Germination responses were very similar for the seeds of both species for the 1999 and 2001 seed production years (Table 4). In 2000 a severe frost occurred on May 10th. This dropped average germination from an average of 67 to 74% for both species to 27 to 29%. Maximum germination dropped from 100% to 67 to 79%. Despite the severe late frost, some germination occurred at 93 and 96% of the temperature tested for tree and coyote willow respectively.

Table 1. Germination parameters calculated from quadratic response surfaces (Young and Evans 1982).

Calculated parameter	Derived parameter	Purpose
Calculated within profile		
Mean germination	Sum divided by 55	Gross comparison of profiles
Percentage of regimes with germination response	Number with germination divided by 55	Indication of breath of germination
Percentage of regimes with optimum	Number of regimes with germination no less than Maximum observed minus confidence interval divided 55	Indication of breath of temperatures that suppot optimum germination
Mean of optima	Sum of optima divided by number of optima	Provides measure of potential germination
mum germination	Highest observed germination	Indication of potential viability
Calculated among germination profiles		
Frequency of optima	Times temperature regime supports optima divided byotal number of profiles	Provides an estimate of optimum temper or germination with statistical precision

Table 2. Quadratic response surface with estimated percentage germination and confidence interval ($P \geq 0.01$) for seeds of tree willow incubated at 55 constant or alternating temperatures. Seed produced in the Walker River Delta in 1999.[1]

Cold period temperature C	Percentage germination Warm period temperature C									
	0	2	5	10	15	20	25	30	35	40
	(%)									
(C°)										
0	15 ± 11	24 ± 10	40 ± 9	76 ± 11	80 ± 13	92 ± 13	92 ± 13	90 ± 13	74 ± 14	20 ± 11
2		35 ± 14	42 ± 15	70 ± 10	92 ± 14*	94 ± 7*	91 ± 10	90 ± 11	86 ± 13	50 ± 12
5			585 ± 17	98 ± 8*	80 ± 8	88 ± 11	96 ± 6*	88 ± 11	86 ± 12	58 ± 9
10				70 ± 16	76 ± 6	86 ± 10	[100 ± 4*	100 ± 8]*	94 ± 10	80 ± 12
15					70 ± 8	88 ± 8	[100 ± 10]	*98 ± 8*	90 ± 8	90 ± 11
20						90 ± 13	80 ± 19	88 ± 14	94 ± 14*	96 ± 9*
25							78 ± 12	80 ± 9	98 ± 1	84 ± 14
30								90 ± 9	84 ± 10	80 ± 16
35									76 ± 16	60 ± 18
40										0 ± 20

[1]Number following mean is one half the confidence interval as determined from regression equations used to develop response surface (Palmquist et al. 1987). The maximum calculated germination is enclosed by brackets [ ]. Means not lower than the maximum and one half of its confidence interval, our definition of optimum germination, are marked with and asterisk *.

We define optimum germination by relating optima to the maximum germination minus one half of its confidence interval at the 0.01 level of probability. Note that in the 3 years of testing the mean of optima and percentage of regimes supporting optima did not significantly vary between tree and coyote willow (Table 4). Only in 2000 when the seed quality was lowered by frost damage was the mean of optima lower for both species. The percentage of temperature regimes supporting optimum germination differed significantly for both species for each year of seed production. Seed quality was exceptional for both species in 2001. To have 60 and 78% of the temperature regimes supporting optimum germination when the maxi-

Table 3. Quadratic response surface with estimated percentage germination and confidence interval ($P \geq 0.01$) for seeds of coyote willow incubated at 55 constant or alternating temperatures. Seed produced in the Walker River Delta in 1999.[1]

Cold period temperature C	Percentage germination Warm period temperature C									
	0	2	5	10	15	20	25	30	35	40
	(%)									
(C°)										
1	0 ± 9	15 ± 7	70 ± 8	80 ± 8	[100+10]*	90 ± 8*	90 ± 8	85 ± 11	80 ± 9	80 ± 11
2		15 ± 7	72 ± 6	90 ± 11*	95 ± 11*	90 ± 10*	90 ± 9*	90 ± 9*	89 ± 11	80 ± 9
5			80 ± 11	85 ± 9	90 ± 8*	92 ± 9*	90 ± 10*	84 ± 10	85 ± 10	80 ± 7
10				90 ± 11*	92 ± 9*	86 ± 9	84 ± 7	82 ± 6	80 ± 8	78 ± 11
15					70 ± 11	89 ± 9	90 ± 8*	85 ± 10	90 ± 11*	85 ± 8
20						85 ± 7	90 ± 9*	95 ± 4*	90 ± 10	80 ± 9
25							80 ± 11	96 ± 7*	95 ± 8*	90 ± 9*
30								98 ± 10*	86 ± 5	80 ± 12
35									95 ± 10*	70 ± 14
40										10 ± 14

[1]Number following mean is one half the confidence interval as determined from regression equations used to develop response surface (Palmquist et al. 1987). The maximum calculated germination is enclosed by brackets [ ]. Means not lower than the maximum and one half of its confidence interval, our definition of optimum germination, are marked with and asterisk *

Table 4. Comparison of temperature germination profiles for seeds of tree and coyote willow collected in the Walker River delta in 1999, 2000, and 2001.

Germination parameter	Year of seed production and species					
	1999		2000		2001	
	Tree willow	Coyote willow	Tree willow	Coyote willow	Tree willow	Coyote willow
	(%)					
-						
Mean germination	71a	74a	27b	29b	67a	70a
Temperature regimes with some germination	98	100	93	96	93	89
Mean of optima	96a	92a	63b	79b	100a	100a
Regimes with optimum germination	20b	40b	9c	4c	60a	78a
Maximum	100a	100a	67b	79b	100a	100a
Seedbed temperature categories						
Very cold	21a	19a	5b	17a	1b	8b
Cold	77b	86b	25c	37c	70b	100a
Cold fluctuating	78a	87a	35b	44b	82a	80a
Fluctuating	74a	83a	27c	22c	72b	60b
Warmer	87a	88a	27b	12c	77a	79a
Moderate	87a	81a	42b	39b	100a	99a

[1]Means within rows followed by the same letter are not significantly different at the 0.01 of probability based on overlap of the confidence intervals (Palmquist et al. 1987).

mum observed is 100% exceeds the species potential of any of the some 800 temperature-germination profiles that have been completed in our laboratory.

In terms of categories of seedbed temperatures, the seeds of both species of willow had exceptional germination at every category except very cold temperatures (Table 4). Very cold temperatures are characteristic of seedbeds that freeze at night and barely thaw during the day. Even in 2000 when the seed quality was damaged by frost, there was some germination at very cold seedbed temperatures. Surprisingly, in 2001 when overall germination responses were the highest, the germination of both species was the lowest at very cold temperatures, but the highest at the cold category of seedbed temperatures (Table 4).

The frequency that a given temperature supports optimum germination provides an excellent indication of the true optimum temperature for germination of seeds of a given species. For tree willow seeds, only 15/25° C (16 hours at 15° C and 8 hours at 25° C in each 24 hours period) and 15/30° C always supported optimum germination (Table 5). For coyote willow seeds, no single temperature regime always supported optimum germination (Table 6). Optima were spread over a vast range of temperatures from a constant 2° C to 30° C and included 10/40, 15/40, and 20/40° C. Two thirds of the time 29% of the temperature regimes supported optimum germination. These temperatures were generally colder than the 100% constancy regimes for tree willow. Some of the 66% frequency temperature regimes for optimum germination extended into regimes with 0° C cold period temperatures.

Despite their world-wide distribution and ecological importance, very little research has been conducted on the seed and seedbed ecology of the willow species. The seeds have a very transitory period of viability making them available for research purposes for only a very short period annually. The hair covered seeds are difficult to collect, process, and count. In forestry and horticulture most species of willow can readily be propagated by cuttings. Junttila (1976) determined that for 4 species of willows from Norway, optimum temperatures for germination ranged from 26 to 32° C. The optima for tree and coyote willow seed extend broader than this range, but certainly cover these incubation temperatures. In one of the few other germination studies for willow seeds and incubation temperatures, Gorobets (1978) found that seeds of 2 species of Russian willows could germinate at a wide range of temperatures.

Tree willow and coyote willow grow in the Walker River Delta sympatricly. There growth forms are radically different. As the name implies, tree willow tends to form a single dominant trunk and becomes a small tree. Coyote willow occurs in dense clumps with multiple stems more or less the same size. Coyote willow clumps are much more abundant than the tree willows, but beavers prefer tree willows and generally shun coyote willow stems. In the Walker River delta, cattle prefer the tree willow browse and there seldom is evidence of browsing on coyote willow.

Comparing the germination of these 2 species of willow, it is obvious that in terms of germination requirements for incubation temperature they are very similar. They both produce super abundant, highly viable, widely distributed seeds. Conventional observations and nursery

Table 5. Frequency that a given temperature regime supported optimum germination of seeds of tree willow collected in the Walker River delta from 1999 through 2001.

Cold period temperature C	Frequency of optima Warm period temperature C									
	0	2	5	10	15	20	25	30	35	40
	(%)									
(C°)										
0							33	33		
2					66	66	33	33		
5				33	33	33	66	33	33	
10				3	33	33	66	66	33	
15					33	66	100	100	33	
20						33	66	33	66	3
25							33	33	33	33
30								33	33	
35									33	
4										

Table 6. Frequency that a given temperature regime supported optimum germination of seeds of coyote willow collected in the Walker River delta from 1999 through 2001.

Cold period temperature C	Frequency of optima Warm period temperature C									
	0	2	5	10	15	20	25	30	35	40
	(%)									
(C°)										
0				33	66	66	66	33	66	
2			33	66	66	66	66	66	66	
5				33	66	66	66	33	33	
10				66	66	33	33	33	33	
15					33	66	33	33	33	33
20						33	33	33	33	33
25							33	33	33	33
30								33		
35									33	
40										

practices (Young and Young 1992), suggest that willow seeds must disperse to damp sandy to silt seedbeds soon after maturity to have a chance for seedling establishment. In the Walker River delta, tree and coyote willow seeds probably compete for the same safe sites for germination and establishment. Their phenology of flowering and seed dispersal is quite close, but tree willow usually disperses seeds before coyote willow.

The management of riverine willow populations to enhance seedling recruitment is obviously a very complex under taking. This study provides a first step toward understanding the seed and seedbed ecology of these species.

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