Light Requirement for Seed Germination of Payson Sedge

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Abstract

Payson sedge (*Carex paysonis* Clokey) is a dominant component of many alpine floras in the western United States. This species appears to be a highly adapted colonizer (early invader) on disturbances such as acidic mine spoils at high elevations, and its rhizomatous growth habit offers promise for revegetation of these sites. The few natural seedlings observed in the field suggest that seed germination of Payson sedge is low compared with that of other alpine colonizers, and seeding trials with this species have met with poor success. Therefore, studies were designed to determine the germination requirements of this species. The effects of 2 levels each of light (visible vs. complete darkness), temperature (constant 25° C vs. variable 25/3° C day/night), and seed position in soil (surface vs. buried) on germination were investigated under controlled conditions in the laboratory. The highest germination percentage ($\bar{x}$ = 28.8%) was attained under conditions of complete darkness followed by exposure to light at variable temperatures. There were no significant differences ($p<0.05$) in germination levels under conditions of light coupled with variable temperature ($\bar{x}$ = 21.3%), and complete darkness followed by light at constant temperature ($\bar{x}$ = 22.8%). Germination levels were low ($\bar{x}$ = 10.0%) under light at constant temperature and seeds subjected to complete darkness alone germinated poorly ($\bar{x}\leq1.2\%$). We recorded low levels of germination ($\bar{x}\leq2.8\%$) from treatments of buried seeds exposed to both light conditions and both temperature levels. A requirement for light coupled with low germination levels of buried seeds suggests that standard revegetation techniques, where seeds are buried beneath the soil surface, may be inappropriate for Payson sedge. We recommend surface seeding in the fall so that extended periods of natural snow cover will promote germination the following spring.

Key Words: *Carex paysonis*, **plant establishment, alpine vegetation, seed germination, alpine revegetation**

Revegetating disturbed alpine rangelands is often complicated by the harsh climatic conditions and the limited pool of available adapted species in this life zone. Alpine areas are dominated by cryopedogenic processes and rigorous climatic conditions including short growing seasons, low soil and air temperatures, desiccating winds, and periodic drought during the growing season (Brown and Johnston 1979, 1980; Johnson and Billings 1962). Also, the alpine flora include few annuals (Billings 1974) and rarely are introduced species from more temperate climatic zones successful for revegetation (Brown et al. 1984, Eaman 1974).

Disturbances caused by mineral exploration and mining activities severely compound these limiting conditions for plant growth. Mine spoils in western alpine regions are often highly acidic due to the oxidation of iron pyrites, and they frequently contain toxic concentrations of metals such as aluminum, iron, and copper that become available for plant uptake. Mining also destroys the thin organic soil layer, thus reducing the water-holding capacity of the surface and accentuating the potential for water stress. These conditions further reduce the pool of adapted species available for revegetation.

Numerous promising revegetation techniques and plant species have been identified for alpine disturbances (Brown and Johnston 1979, 1980; Brown et al. 1984; Chambers et al. 1984). One species that shows particular promise for revegetation of acid mine spoils is Payson sedge (*Carex paysonis* Clokey). We have observed Payson sedge on acid spoils of numerous high elevation mine disturbances on the Beartooth Plateau in southwestern Montana. It is often the only vegetation present.

Typically, Payson sedge is strongly rhizomatous and forms conspicuous, low-growing, dense mats that are often isolated from other vegetation on disturbed sites (Fig. 1). The generally circular mats, up to 3 m in diameter (Fig. 2), are usually composed solely of Payson sedge, but in some instances they provide favorable habitats for the establishment of invading species that are not found on bare mine spoil. Howard (1978) reported that seedling mortality was lower within these communities and that mat interiors had higher levels of nitrogen and potassium and lower soil temperatures, windspeeds, and radiation flux densities than adjacent areas. Payson sedge appears to be a true pioneer species that ameliorates disturbed microhabitats by creating more suitable edaphic and microclimatic conditions for the colonization of new species. It is unlikely that these invading species would have become established on acid spoils if the Payson sedge mats were not available.

The apparent tolerance of Payson sedge to highly acidic (pH 2.1 to 2.5) mine spoil (Haggas, Brown, and Johnston, unpublished data) suggests that it has considerable promise for revegetation of such disturbances in alpine and subalpine ecoystems. Although we have seeded Payson sedge on several mine sites in the Beartooth Mountains since 1974 (Brown and Johnston 1976, 1979, 1980), seedling establishment has yet to be observed either within the plots or elsewhere on the disturbances.

The objective of the present study was to evaluate the influence of light, temperature, and seed position in the soil on germination of Payson sedge. By investigating the physiological requirements of this species, we hope to determine if standard revegetation techniques will provide a favorable environment for seed germination.

Methods

Seeds of Payson sedge were collected in August 1981 from a disturbed subalpine site on the McLaren Mine (elevation 2,950 m) about 8 km north of Cooke City, Mont., in the Beartooth Mountains. Seeds were later air dried in paper bags and stored in a refrigerated room at 3° C. Based on visual inspection under a dissecting microscope, about two-thirds of the seeds were either immature or had empty achenes, and were discarded. Only filled seeds from which the perigynium had been removed were used.

The effects of 2 levels each of light (light flux density of 183 or 224 μ mol s^{-1} m^{-2} vs. complete darkness), temperature (constant at 25° C vs. variable at 25/3° C day/night), and seed position in soil (surface vs. buried 0.5 cm below the surface) on germination were investigated under controlled conditions in two growth incubators in the laboratory. Treatments consisted of 3 replicates each of (1) exposure to light, (2) complete darkness followed by light, (3) seeds planted on the soil surface, and (4) seeds buried below the soil surface.

Plexiglas boxes (11.0 by 11.0 by 4.0 cm) with removable inset lids were used as germination containers. Each box contained 1.5 cm (160 ml, 200 g) of a sand/soil/peat mixture (ratio of 2:1:1, pH 6.8) and approximately 200 seeds. This mixture, although not typical of alpine mine spoil material, provided an optimum medium for seed germination and plant growth as determined in earlier greenhouse studies. The soil in all boxes was moistened with distilled water (90 ml), then dusted with about 0.5 g of a fungicide (5% N-[trichloromethyl)thio]-4 cyclohexane-1,2 dicarboximide) prior to

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Fig. 1. *Payson sedge mats on disturbed acidic spoil at the McLaren Mine near Cooke City, Montana.*

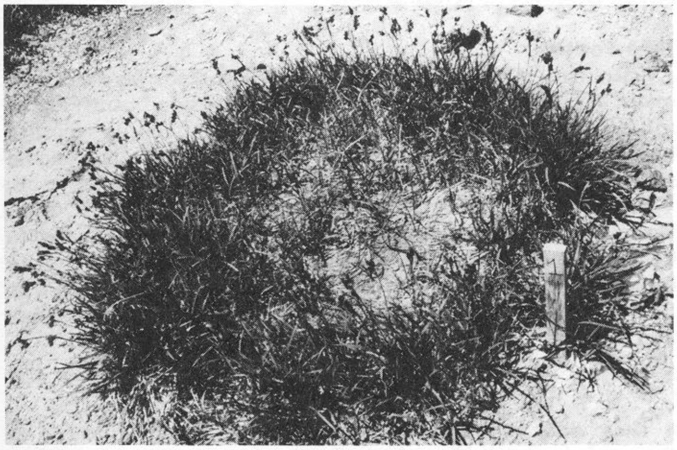

Fig. 2. *Payson sedge mat on disturbed acidic spoil at the McLaren Mine. Note the lack of regeneration in the mat interior.*

sealing to reduce fungal growth. Additional water was not required during the study.

One growth incubator was set at a constant temperature of 25±2° C, and the second provided variable temperatures of 25±2° C during the light period and 3±° 1 C during the dark period (about 3 h were required to achieve temperature stability during the transition periods in this incubator). A 13-h photoperiod was provided in both incubators with a photon flux density of about 224 μ mol s^{-1} m^{-2}, supplied by a single cool-white fluorescent tube (GE-F48T10) mounted vertically in each incubator door. All references to light in this paper refer to the 13-h photoperiod unless otherwise specified.

Treatments requiring darkness in both incubators were provided by sealing the appropriate Plexiglas boxes within 2 black plastic bags (20.5 by 33.0 cm, 0.0381 mm thickness). Darkness was verified by measurements with a quantum sensor (model LI-185). Treatments exposed to light were similarly enclosed in transparent plastic bags. Temperatures within all of the boxes enclosed in bags were within 1° C of the incubator temperature. Photon flux density measurements recorded inside and outside of the transparent bags were 183 and 224 μ mol s^{-1} m^{-2}, respectively.

A single replication of each of the 4 treatments was randomly positioned on each of 3 shelves in each incubator, and the boxes were positioned at the front edge of each shelf close to the light source. The experiment continued for 8 weeks, but was divided into 2 periods of 4 weeks during which different light conditions were maintained. During the first 4 weeks, germination was not assessed in the dark treatments, but was estimated once each week for the 4 treatments exposed to visible light. Conditions of complete darkness were terminated at the end of the first 4 weeks, and all 24 germination boxes were removed from the plastic bags and exposed to the 13-h photoperiod for the second 4 weeks. Germination counts were made weekly and recorded when the cotyledon or the radicle emerged for seeds on the surface, or when the cotyledon became visible above the soil in treatments with buried seeds. Since emergence may not reflect germination, an attempt was made to examine all seeds planted below the surface after the study was terminated to verify that the number of seeds emerged was the same as those which germinated.

Data were analyzed using factorial analysis of variance techniques (Cochran and Cox 1966). Multiple mean comparisons were made using Fisher's LSD (Cochran and Cox 1966); means were considered significant at the 5% level.

Results

Germination was significantly ($p<0.05$) influenced by the combined effects of light, temperature, and seed position in the soil (Table 1). Generally, the data show that exposure to light promotes seed germination in Payson sedge ($\bar{x}$ = 20.7%), whereas little or no germination occurred in darkness ($\bar{x}$ = 0.9%). Variable temperatures combined with light promoted higher germination than constant temperatures combined with light. Exposure of seeds to a period of darkness followed by light at either constant or variable

Table 1. Mean weekly germination (%) of Payson sedge under controlled conditions of temperature, light, and seed position in the soil.[1]

Week No.	25° C				25/3° C			
	Light		Dark/Light		Light		Dark/Light	
	above	below	above	below	above	below	above	below
	% germination							
1	2.3 ± 0.6a	0.2 ± 0.2a	——	——	0.0 ± 0.0a	0.0 ± 0.0a	——	——
2	8.3 ± 0.7b	0.2 ± 0.2a	——	——	4.3 ± 0.7b	0.2 ± 0.2a	——	——
3	8.8 ± 0.9b	0.2 ± 0.2a	——	——	6.8 ± 0.2b	0.2 ± 0.2a	——	——
4	9.3 ± 0.7b	0.3 ± 0.3a	1.2 ± 0.2a	0.0 ± 0.0a	8.2 ± 0.2b	0.2 ± 0.2a	0.5 ± 0.3a	0.3 ± 0.2a
5	9.3 ± 0.7b	0.3 ± 0.3a	18.7 ± 0.7c	0.2 ± 0.2a	16.7 ± 4.4c	0.2 ± 0.2a	16.2 ± 1.9c	0.7 ± 0.4a
6	9.7 ± 0.9b	0.3 ± 0.3a	22.0 ± 0.6d	0.2 ± 0.2a	19.3 ± 4.4d	0.2 ± 0.2a	28.0 ± 2.3e	2.5 ± 0.5a
7	10.0 ± 0.8b	0.3 ± 0.3a	22.7 ± 0.9d	0.2 ± 0.2a	20.3 ± 4.5d	0.2 ± 0.2a	28.2 ± 2.4e	2.7 ± 0.6a
8	10.0 ± 0.8b	0.3 ± 0.3a	22.8 ± 1.1d	0.2 ± 0.2a	21.3 ± 4.2d	0.2 ± 0.2a	28.8 ± 2.5e	2.8 ± 0.7a

[1] Numbers at far left refer to weeks of light exposure. Dashes indicate time periods where conditions of complete darkenss were maintained and germination was not recorded. Significant means (LSD = 2.67, $p<0.05$) followed by standard errors are indicated by different lower case letters along rows and down columns.

temperatures appears to enhance total germination and germination rate. Seed position above the soil coupled with light appears to be essential for germination.

Light

For seeds planted on the soil surface, after 4 weeks germination levels for treatments maintained under light were significantly greater ($p<0.05$) than corresponding treatments under darkness (Table 1). Few seeds germinated in the absence of light (1.2% or less). The most favorable conditions tested for germination of Payson sedge were those where imbibed seeds were, subjected to darkness followed by visible light and variable temperatures (Table 1). Germination levels recorded in this treatment at the conclusion of the experiment were significantly greater ($p<0.05$) than for any other treatment.

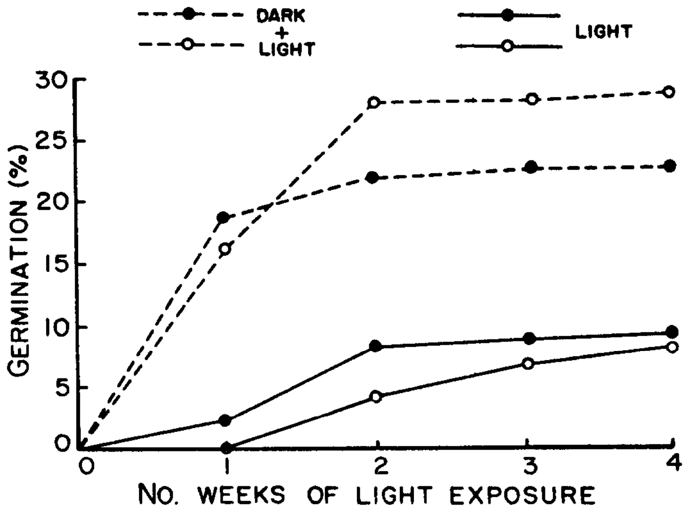

Fig. 3. *Relationship between light condition and germination rate of Payson sedge. Dark + light = 4 weeks complete darkness + 4 weeks 13-h photoperiod; light = 13-h photoperiod for 8 weeks. Germination data are from Table 1. Solid points = treatments at constant temperature (25° C); open points = treatments at variable temperatures (25/3° C).*

Although the combination of both conditions of darkness followed by light and variable temperature was most favorable for enhancing germination, the relative importance of each parameter can be demonstrated. Germination was significantly greater ($p<0.05$) under conditions of darkness followed by light than when exposed to light alone. Likewise, germination under variable temperature levels was significantly greater than that under constant temperature ($p<0.05$, Table 1).

Germination rates under treatments subjected to darkness followed by light at both constant and variable temperatures increased rapidly after 1 week of light exposure. More seeds germinated during each week of light exposure, and at a faster rate, in the treatments subjected to darkness followed by light than those that only received light ($p<0.05$, Fig. 3).

Temperature

Variable temperatures are apparently more favorable for Payson sedge germination than constant temperature. Weekly comparisons of germination indicate that seeds subjected to light (5–8 weeks, Table 1) or to darkness followed by light (6–8 weeks) were significantly greater ($p<0.05$) under variable temperatures than under constant temperature.

Seed Position

Germination levels of all treatments where seeds were scattered on the surface and exposed to visible light were significantly higher ($p<0.05$) than in treatments where seeds were buried. We recorded low levels of germination (2.8% or less) from treatments of buried seeds exposed to both light conditions and both temperature levels. These data were statistically similar throughout the experiment. Germination levels attained after the buried seeds were exposed to light for 4 weeks were statistically similar to data collected in both treatments at the conclusion of dark conditions (week 4, Table 1). Evidently, buried seeds did not receive sufficient light for germination under any of the light conditions tested.

Discussion

These data support the hypothesis that seed germination of Payson sedge is significantly ($p<0.05$) enhanced by light. Johnson et al. (1965) reported that 20 of 27 carices required light for germination. Other photoblastic sedges have also been documented by Amen (1966) and by Amen and Bonde (1964). Although a few seeds did germinate under conditions of darkness in several of our trials, we consider these levels too low for potential use in revegetation. Few members of the sedge family (Cyperaceae) germinate under conditions of darkness (Grime et al. 1981, Fulbright et al. 1982). Bliss (1958) reported that germination of arctic and alpine carices did not occur in the dark, and Johnson et al. (1965) stated that *Carex* germination was either lacking or substantially reduced under conditions of continuous darkness.

The most favorable conditions tested for seed germination occurred when we coupled the conditions of darkness followed by light with cold temperature in an attempt to simulate the light and temperature environment of Payson sedge following fall seeding at the McLaren Mine. The same promotive effect of darkness followed by light has been observed in ebony sedge *(C. ebenea)* (Amen and Bonde 1964) and in simple alpine sedge *(Kobresia simplicius-*

cula) (Arnold 1973).

Although the germination levels observed in this study may be lower than desirable for seeds used in revegetation, they are not particularly low compared with many other native plant species used in alpine revegetation. Brown and Johnston (1979, 1980) observed that seeding rates of many native species used in alpine revegetation must be increased over those used in more temperate regions because of low seed viability and germination. Also, levels of seed germination for a species at a given location are rarely constant from one year to the next. Local climatic variables substantially influence fruiting, ripening, seed production levels, and the degree of dormancy developed from year-to-year (Amen 1966). Hence, the levels of germination observed for Payson sedge in this study are probably not representative of what may occur for other collections of the species, and certainly are not as meaningful as the relative promotive effects of light and temperature on seed germination.

Mean germination levels of Payson sedge in our trials were similar to those of Tolmie sedge *(C. tolmiei)* (26%) reported by Johnson et al. (1965), and considered to be synonymous species by Hermann (1970). Although low germination levels of carices are well documented (Fulbright et al. 1982), there are few reports of their specific germination requirements. Johnson et al. (1965) reported that germination levels in 18 of 27 *Carex* species were 30% or less. Other *Carex* studies by Wiesner et al. (1967), Roche (1968), and Grime et al. (1981) also recorded germination levels less than 30%. Bliss (1958) observed that maximum germination in 2 arctic carices only reached 6.2%, whereas 3 alpine species, water sedge *(C. aquatilis)*, curly sedge *(C. drummondiana)*, and swamp carex *(C. scopulorum)*, failed to germinate. Wiesner et al. (1967) cited poor seed viability as being partly responsible for low germination levels in the carices, although this relationship is not clear.

Germination of *Carex* species has been increased by different treatments, but no single treatment appears to be universally effective. Some of the promotive germination treatments that have been studied include: physical scarification (Amen and Bonde 1964); scarification with an alpine soil leachate, tap water, or sand; a combination of sand scarification with an alpine soil leachate; gibberellic acid (McDonough 1969); and 5-year water storage (Comes et al. 1978). Some of these treatments occur naturally and can probably be relied upon following seeding for revegetation to promote germination. Although moist and cold stratification increased germination levels in several sedge species (Grime et al. 1981), including Tolmie sedge (Johnson et al. 1965), it did not substantially affect germination levels of Payson sedge (Haggas, Brown, and Johnston, unpublished data).

The results of the study have some important implications regarding revegetation of alpine disturbances when using Payson sedge in the seed mixture. In typical revegetation studies, seeds are usually planted below the soil surface to ensure contact between soil particles and the seed to facilitate the absorption of soil water and to avoid desiccation. However, these methods may be inappropriate for photoblastic species. Our data suggest Payson sedge should be seeded on the soil surface in order to meet the light requirement for germination. Planting Payson sedge beneath the surface virtually ensures the seed will not receive the required light for germination, except in those rare cases where erosion or other agents may expose them after imbibition occurs. Accordingly, it is recommended that Payson sedge not be included in seed mixtures, but rather be broadcast on the surface after the other species are planted. Wein and MacLean (1973) recommended surface seeding of sheathed cottonsedge *(Eriophorum vaginatum)* to satisfy the light requirement of this colonizing sedge for revegetation of disturbed arctic tundra.

Placement of seed on the soil surface during revegetation may result in higher seed losses and seedling mortality than occur with conventional techniques, despite light enhancement concerns for germination. Desiccation by wind and high solar radiation loads during germination is a particularly serious possibility, as are losses due to soil surface erosion, overland water flow, and biological predation. However, use of moderate amounts of straw mulch (Brown and Johnston 1979, 1980) or other materials on the soil surface after seeding that provide cover, yet permit light penetration, may provide sufficient stability and insulation against these agents to permit seed germination and seedling development. In any case, conventional levels of seedling density and establishment observed with other species following revegetation are not likely with Payson sedge because of potentially high levels of mortality.

The promotive effect of darkness followed by light suggests Payson sedge would best be seeded in the late fall prior to winter snow cover. Thus, the seeds would receive whatever beneficial effects may result from cold stratification, microorganism activity, and extended darkness during periods of deep snow accumulation in the winter. At the McLaren Mine snow depths often exceed 3 to 5 m during the winter, which may effectively eliminate light reception at the surface (Sellers 1969). However, as snow depths decrease to 1 m or less with the spring melt, light penetration levels may be sufficient to initiate effective photoblastic reactions in surface-planted seeds. During or after spring snowmelt, the imbibed seeds would be in prime condition for germination after exposure to light, and increased seedling survival during this normally critical period of plant establishment would be expected. Spring seeding is not recommended because: (1) the normally extended dark period provided by a deep snowpack prior to light exposure would not be available, and (2) unreliable precipitation events in the spring may allow seeds to lose critical levels of moisture before germination and radicle development are complete, which is of particular importance to surface-planted seeds.

Because the results of the present study are based on precleaned and filled seed, we cannot be certain that optimum germination will be achieved if the seeds are not cleaned prior to planting. However, we feel that Payson sedge has the physiological tolerances necessary to germinate and grow on acid mine spoil material based on other germination studies on both untreated McLaren Mine spoil and on limed spoil over a pH range of 4.6 to 9.1 in a greenhouse environment. We found that conditions of low pH do not inhibit germination, and that it may actually be higher on more acid spoils (Haggas, Brown, and Johnston, unpublished data).

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