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Quaking Aspen - Seed Germination and Early Seedling Growth

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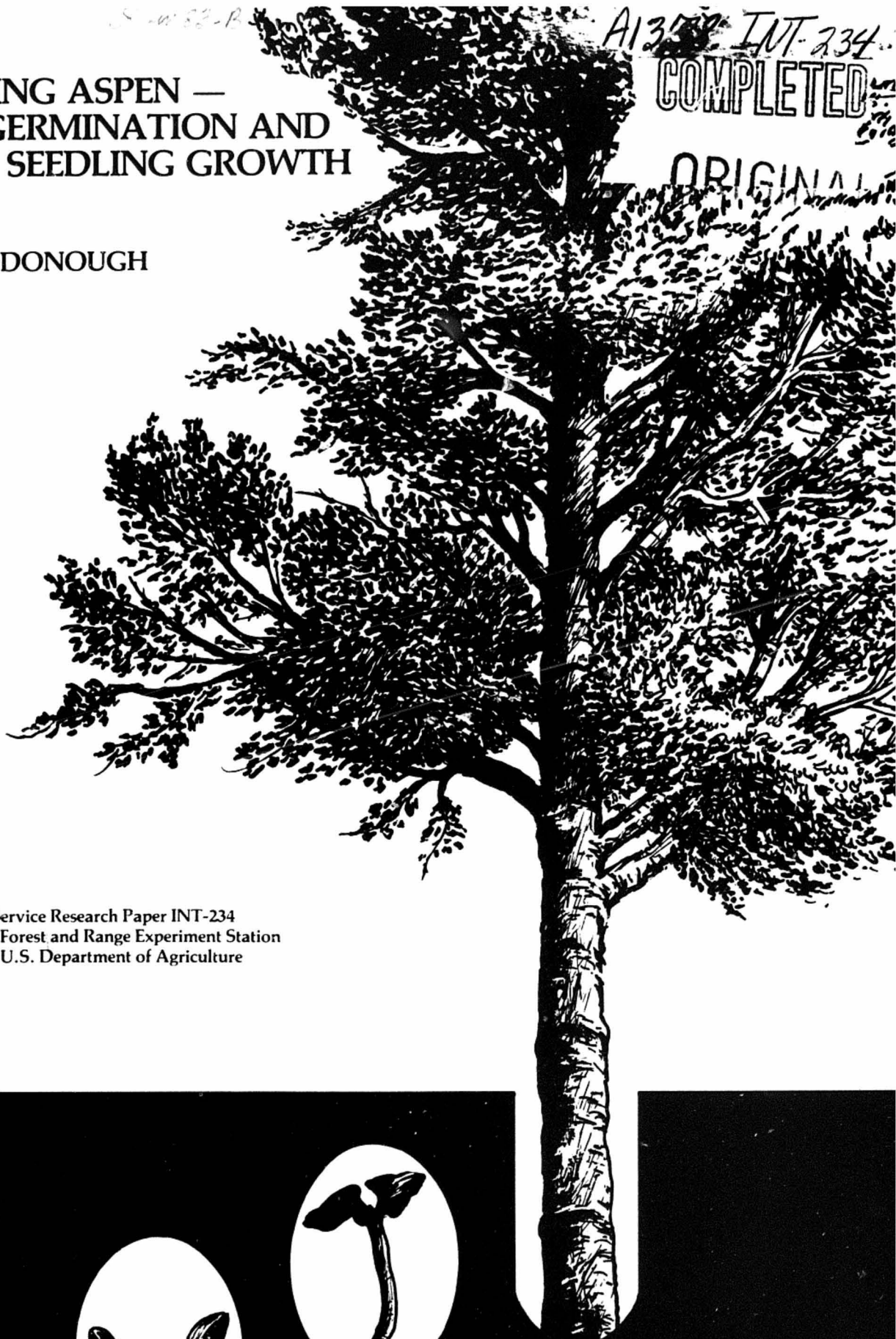


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QUAKING ASPEN — SEED GERMINATION AND EARLY SEEDLING GROWTH

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Intermountain Forest and Range Experiment Station
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RESEARCH SUMMARY

Although freshly dispersed aspen seeds germinate quickly and nearly completely over a broad range of temperatures, early growth of seedlings is highly sensitive to availability of water, temperature, and physical and chemical conditions of the seedbed.

QUAKING ASPEN — SEED GERMINATION AND EARLY SEEDLING GROWTH

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INTRODUCTION

The suckering of aspen (*Populus tremuloides* Michx.) as a highly effective means of vegetative propagation is well known and has been widely studied (Baker 1918; Day 1944; Maini 1967; Schier 1974). Less is known about seed propagation, sometimes viewed as having only minor importance because early research (Baker 1918) had indicated that rare seedling establishment was due to low or nonexistent germinability.

However, numerous seedlings have been found in nature (Faust 1936; Larson 1944; Barnes 1966). These findings, in conjunction with pot culture and laboratory studies (Faust 1936; Moss 1938), show that aspen produces abundant germinable seeds that have no dormancy, but have a critical requirement for adequate soil water through the period of germination and early seedling growth. There is also a somewhat less critical requirement for the onset of these conditions soon after dispersal, because exposure of dry seeds to higher temperatures and humidities leads to rapid loss of germinability.

Reproduction by seed probably has several important consequences relative to successful establishment and spread of the species. Genetic variability in a changing environment, widespread dissemination, and new colonization by wind-dispersal of the seed are assured. Yearly production of seed by a mature tree is estimated at 1.6 million (Maini 1968). Even if the probability of any one successful establishment is low, reproduction by seed in aggregate could be important. The probabilities warrant further investigation of the environmental conditions that promote or inhibit germination and early growth. Also of interest are possible differences in germinability and seedling growth from seeds of clones varying in vigor. Specific information is needed on responses by seeds and seedlings to important environmental variables. Then, with appropriate management practices at particular sites, the probability of reproduction and spread by seed may be increased.

MATERIALS AND METHODS

General Procedures

Capsules were collected in the spring of 1976 and 1977 in Logan Canyon (Wasatch National Forest in northern Utah) from four clones, two of which had been classified as vigorous and two as declining, by criteria described by Schier (1974). The physical and topographical characteristics of the sites occupied were similar. Seeds were cleaned in a separator, air-dried for 2 days at 68°F (20°C), and, unless noted otherwise, stored in vapor-tight bottles at 25°F (-5°C).

Normal germination was identified as perceptible geotropic curvature of the hypocotyl and root, and incipient germination as bulging of the root-hypocotyl junction without further growth. In aged seeds and seeds under conditions of stress, abnormal germination was observed--hypocotyl elongation without concomitant root growth.

Tests were run separately on seeds from each of the four clones for effects of temperature on germination and growth of seedlings. Otherwise, seeds from the three clones that produced highest germination were bulked for the determinations. The standard temperature for germination, emergence, and growth was 68°F (20°C) unless noted otherwise.

Germination and Seedling Growth

For germination and growth, respectively, 9 cm petri dishes and 0.29 gal (1.1 liter) plastic pots were used. There were 25 seeds from each clone per dish with four replications and five seedlings from each clone planted individually in 20 pots. Substrates were distilled water-saturated filter paper and sieved aspen topsoil held near field capacity. Early postgerminative growth was measured on 20 seedlings with an

ocular micrometer and binocular microscope. For periodic measurements of root growth, the main roots from additional sets of seedlings were excavated, washed, blotted, and laid out on blotting paper. The significance of differences was evaluated at the 5 percent level by variance analysis and multiple range tests (Goldstien 1964).

Seed germinators and environmental chambers were used for temperature and light control: 8 h photoperiods (102 lumens/ft² - 1100 lumens/m²) for germinations and 16 h photoperiods (1859 lumens/ft² - 2 x 10⁶ lumens/m²) for growth. Germination counts were made daily and terminated 3 days after the last observed germination. Since standardized germination tests specify light treatment for species of *Populus*, possible light effects were tested by wrapping additional sets of dishes in double thicknesses of aluminum foil. These dishes were uncovered for counts 3 days after maximum germination under illumination.

Substrate Water

Seeds were allowed to imbibe on double circles of filter paper in thermocouple psychrometer chambers. Microliter volumes of distilled water were added for a series of substrate water potentials of approximately zero to -7.9 atm (-8 bars). There were 10 chambers with 10 seeds per chamber for each level of water potential. Equipment and procedures have been described elsewhere (McDonough 1975a).

The effect of pronounced variations in soil water content near the surface on germination and early growth was evaluated by passing sets of seeds through diurnal cycles of wetting and drying. In each cycle, seeds were allowed to imbibe on 0.2 in (0.5 cm) layers of sieved aspen topsoil at field capacity in 3.5 in (9 cm) petri dishes for 4, 8, or 12 h. There were 25 seeds per dish with 10 replications. The dishes were then partially uncovered to permit slow drying during the remainder of the 24 h period. This process was repeated for five cycles before a final 72 h wet phase to allow for continued growth of still viable seedlings.

Seedbed Conditions

There were plantings at the periphery of aspen woodland during late spring and early summer in two blocks of four squares (1.6 ft; 0.5 m), 100 seeds per square. The soil surface was raked free of litter and stones before planting. After initial irrigation of all squares to promote germination, squares were irrigated daily as required or left unirrigated.

Twenty-five seeds were planted in each of 10 pots and covered with 0.08, 0.16, or 0.24 in (2, 4, or 6 mm) of lightly compacted soil or left uncovered. Emergence in relation to depth of planting was monitored over a 20-day period at controlled temperatures of 50°, 68°, and 86°F (10°, 20°, and 30°C).

Similarly, seeds were planted on the surface of potted sand, clay, or on aspen topsoil with the litter layer left intact or sieved to remove all debris. Soil with intact surface litter was collected in and around the aspen sites where selected associated species predominated--cheatgrass (*Bromus tectorum* L.), coneflower (*Rudbeckia occidentalis* Nutt.), groundsel (*Senecio jerra* Hook.), and tarweed (*Madiia glomerata* Hook.).

Possible effects of allelopathic substances in litter as inhibitors of seedling growth were tested with solutions of compounds chemically representative of natural inhibitors in plants and soil (Rice 1974)--catechin (Flavonoid), coumarin, gallic acid (tannin), and parahydroxybenzoic acid (phenol). Filter paper in petri dishes (25 seeds per dish in five replications) was saturated with solutions of 0.6 to 11.7 grains/gal (10 to 200 p/m), or to maximum solubility in water.

Seed Longevity

Air-dried seeds were stored in open containers under heated room conditions-- 68° to 77°F (20° to 25°C) and 20 to 40 percent RH, in cold storage, or in filter paper packets surrounded by air-dried soil in sheltered containers on an aspen site. Germinability following 4 to 8 weeks under these conditions was tested in petri dish germinators at six controlled temperatures-- 36°, 50°, 68°, 77°, 86°, and 95°F (2°, 10°, 20°, 25°, 30°, and 35°C). There were 25 seeds per dish in five replications.

RESULTS

Germination and Growth

Normal germination at various incubation temperatures in the 36° to 86°F (2° to 30°C) range was uniformly high (fig. 1), but declined precipitously at higher temperatures to 104°F (40°C). Abnormal germination as a percentage of the total became appreciable--24 percent at 95°F (35°C) and 100 percent at 104°F (40°C). Constant darkness did not inhibit germination. There was no evidence that seeds from declining clones (1 and 3 in fig. 1) had reduced germinability. The significantly lower germination of vigorous clone 4 was probably due to presence of a small percentage of defective seeds; microscopic examination of 100 showed 9 to be undersized or shriveled.

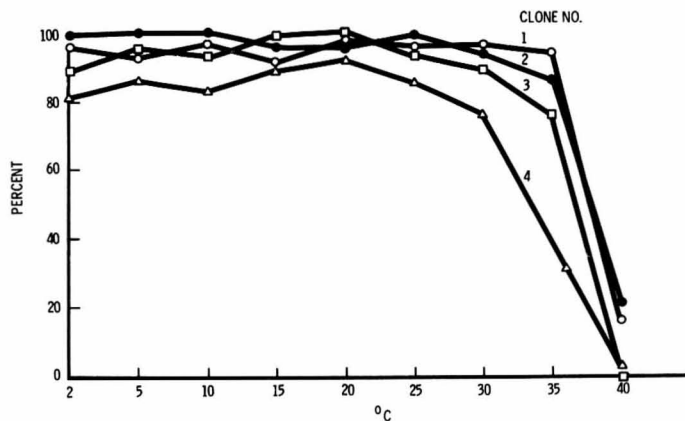


Figure 1.--Percentages of germination of seeds from vigorous (2, 4) and declining (1, 3) clones.

Onset of germination was rapid at all but the lowest temperatures (fig. 2). Rates of germination (days required to reach 10 percent of the total) increased from 36° to 68°F (2° to 20°C). The differences at yet higher temperatures were not significant.

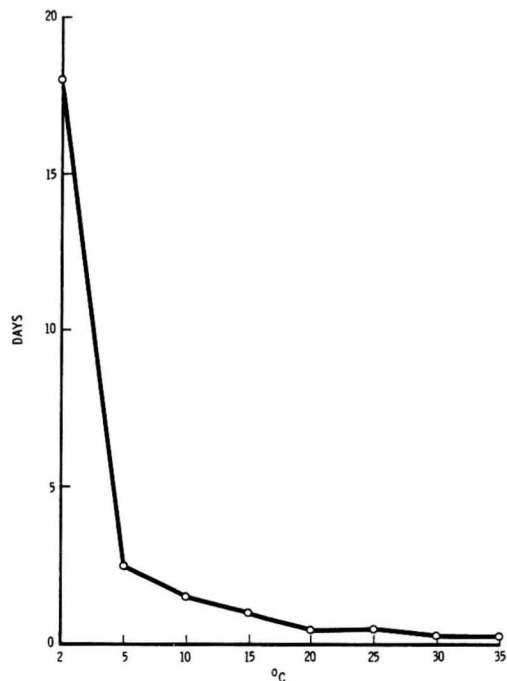


Figure 2.--Germination rates in days to 10 percent of total.

In postgerminative growth of seedling parts (fig. 3), incipient root protrusion, elongation and curvature of the hypocotyl, and greening of the cotyledons were earlier observed events. Development of a crown of root hairs at the root-hypocotyl junction, enlargement and unfolding of the cotyledons, and extension of the plumule followed. During this period, growth of hypocotyl and root hairs was rapid; the root hairs quickly attained final length. Root growth slowed perceptibly after an initial spurt. The plumule grew no more during the first week.

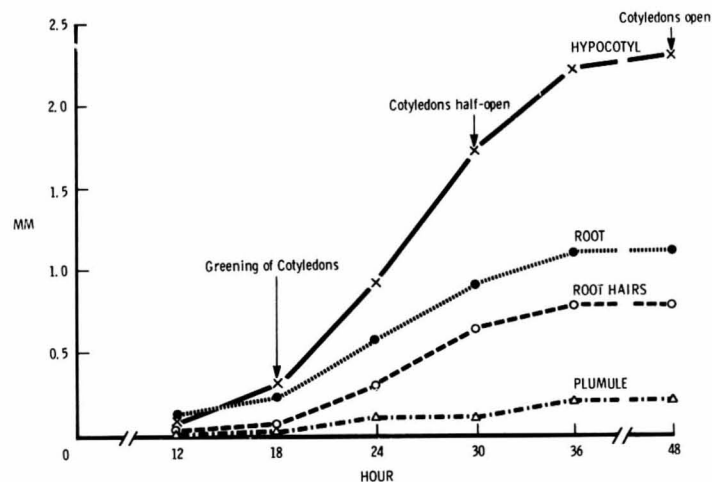


Figure 3.--Postgermination growth of seedling parts.

For seeds germinated at 68°F (20°C) and grown for a month at four temperatures (fig. 4), there was a trend toward best stem growth at 68°F (20°C), and root growth at 50° to 68°F (10° to 20°C). The data used in figure 4 are combined from the four source clones. Separately evaluated differences in growth of stems between seedlings derived from vigorous and declining clones were not significant. Axis elongation at 36°F (2°C) was very slow, although seedlings remained viable and showed accelerated growth when transferred to 68°F (20°C). Growth at 86°F (30°C) was rapid initially but fell off quickly. Root elongation, which amounted to approximately half that of the stem, began slowly and accelerated after the second week.

Substrate Water

Normal germination declined significantly at substrate water potentials of -2.3 atm (-2.3 bars) and was completely inhibited at -7.7 atm (-7.8 bars), as shown in table 1. As water potentials lowered, successively fewer seeds progressed beyond incipient germination.

Inhibition of germination and growth by wet-dry cycling depended upon the duration of phases and number of cycles (table 2). Because of the differing lengths of the drying phases, soil water potentials at the end of each drying cycle averaged -3.0, -10.9, and 17.8 atm (-3, -11, and -18 bars) for progressively longer drying phases. Longer wetting phases allowed more germination early in the cycling and more seedling development, but they impaired growth and survival. The extent of root tip necrosis and reduced hypocotyl length shows this (table 2). With 4 h wetting phases, germination

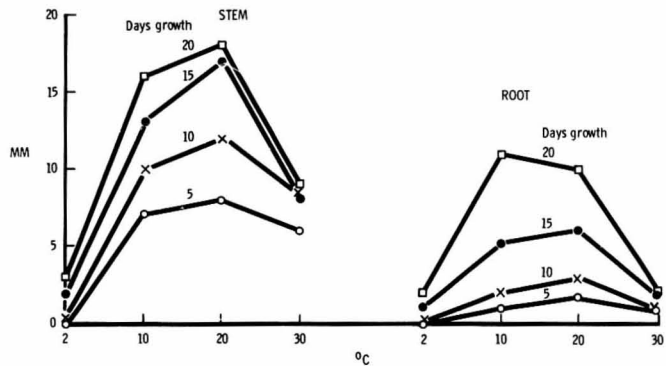


Figure 4.--Growth of alfalfa stems and main roots at 32° to 86°F (2° to 30°C) and during intervals of 5 to 20 days.

Table 1.--Seed germination in relation to substrate water potential

Water potentials atm (bars)	Germination		
	Incipient	Normal	Incipient/total
	Percent		
-0.6 (-0.6)	0	97	0
-2.3 (-2.3)	11	77	13
-4.4 (-4.5)	21	48	50
-7.7 (-7.8)	6	0	100

Table 2.--Germination percentages per cycle during five wet-dry cycles of 4 to 12 hours. Percentage survival and root tip necrosis, and hypocotyl length of germinated seeds after an additional 72 hours of wetting

Wet-dry hours	Cycle					Survival	Root necrosis	Hypocotyl length
	1	2	3	4	5			
4-20	0	7	12	5	3	76	11	4.7
8-16	31	23	17	8	1	43	44	3.4
12-12	62	22	3	0	0	29	74	2.5

was incipient or proceeded to barely detectable root growth during the cycling; with 8 and 12 h wetting, growth of hypocotyl and root ranged to 0.12 in (3 mm).

In late spring field plantings, when soil water levels are favorable for many species, irrigation was required for even modest survival (fig. 5). In squares irrigated as required by a drying soil surface, survival declined 24 percent in the 2 days following emergence, and 35 percent over the remaining 12 days to a final 4 percent. When irrigation was discontinued, none survived the following 2 weeks. Early survival in nonirrigated blocks, aided by rain on day 3, was comparable. However, even after an additional 2 days of scattered light showers, survival declined to zero by day 12. Under the drier conditions of early summer, plantings gave similar results for irrigated blocks, but further reductions for nonirrigated blocks--from 22 percent on day 2 to zero on day 8.

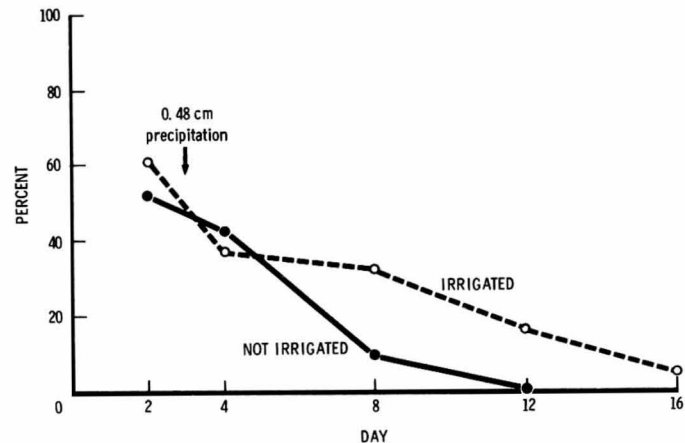


Figure 5.--Emergence and survival percentages of seedlings on an aspen site.

Soil Factors

Percentage of seedling emergence was influenced by depth of planting and temperature during emergence (fig. 6). In general, emergence declined as depths and temperatures increased. A depth of 0.08 in (2 mm) was inhibitory at 86°F (30°C). A 0.16 in (4 mm) depth significantly depressed emergence at the lower temperatures. At 0.24 in (6 mm), emergence was virtually eliminated at all temperatures.

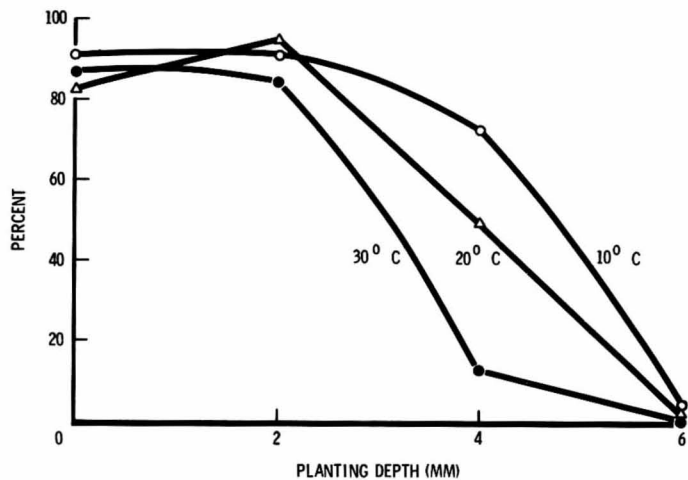


Figure 6.--Seedling emergence percentages at four planting depths and three temperatures.

When water is adequate, emergence occurs equally well on mineral substrates. Litter depressed emergence significantly, the amount depending upon the primary plant composition. Tests showed the following percentages of emergence:

Clay	96
Sieved aspen topsoil	92
Sand	89
Aspen seed hairs	85
Aspen leaves	84
Groundsel	81
Coneflower	79
Cheatgrass	63
Tarweed	59

Examination of the surfaces under magnification indicated that the effect was physical, at least in part; some seeds were stranded on pieces of litter (or seed hairs) that wetted with difficulty or dried out more rapidly than the mineral soil. This left the seeds not fully imbibed, or left the seedlings desiccated after growth had begun.

The four inhibitor compounds depressed root hair and root growth at concentrations of 0.6 to 2.9 grains/gal (10 to 50 p/m). Other seedling parts were less sensitive. Coumarin (fig. 7) was most effective and gallic acid least.

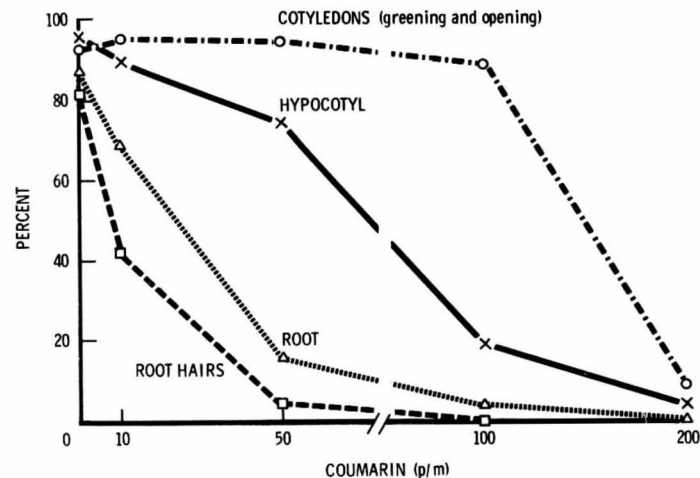


Figure 7.--Percentage of seedlings showing detectable growth of various parts in the presence of coumarin.

Seed Aging

Loss of germinability depended on age, conditions of storage, and temperature during germination (fig. 8). Field storage in containers protected from precipitation but not from fluctuating temperatures and humidities was more detrimental to longevity than storage under the narrower range of atmospheric conditions of room storage. Seeds refrigerated at 25°F (-5°C) retained 90 percent or more germinability through 48 weeks, the longest interval tested.

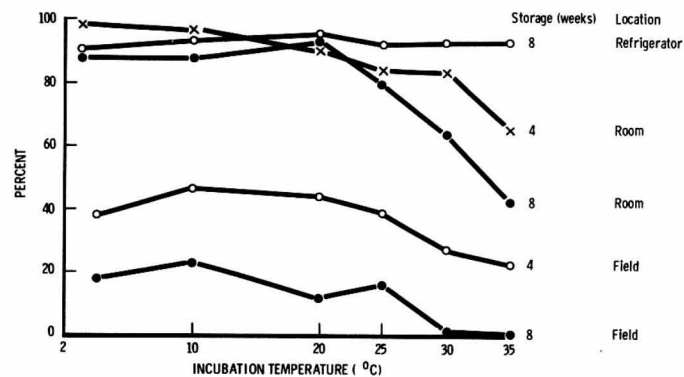


Figure 8.--Effect of storage conditions and incubation temperature on percentage seed germination.

Under unfavorable storage conditions, there was a trend toward reduced germinability at test temperatures higher than 68°F (20°C). Also, abnormal germination as a percentage of the total increased with temperature. For example, after 4 weeks of field storage, the percentages were 11, 28, and 41 at 50°, 68°, and 86°F (10°, 20°, and 30°C), respectively. No such seedlings survived when transplanted. These seeds were also more susceptible to osmotic inhibition. The germination percentages were 17 percent and 4 percent at -2.3 atm (-2.3 bars) and -4.4 atm (-4.5 bars), respectively, compared to 77 percent and 48 percent for refrigerated seeds.

DISCUSSION AND CONCLUSIONS

The wide range of temperature tolerance for germination (fig. 1) and rapid germination rates (fig. 2) potentially favor large numbers of seedling starts. However, progressively higher temperatures become increasingly detrimental (figs. 1, 4, 6, 8); lower temperatures near freezing are depressing (figs. 2, 4), but not permanently so after transfer to intermediate regimes. The initial rapid growth at 86°F (30°C) represents a short term optimum only, since growth falls off rapidly after the first week (fig. 4.), and mortality increases. The damaging effects of higher temperatures also are seen in the reduced germination of aged seeds (fig. 8). The trend in longer term temperature optima lies in the intermediate range and is 68°F (20°C) for the stem and 50° to 68°F (10° to 20°C) for the root (fig. 4). Stem growth significantly exceeds root growth at all tested temperatures (fig. 4).

Air temperatures of 86°F (30°C) or higher are rarely reached on mountain sites. However, direct solar insolation on a dark soil surface and other characteristics of a microsite may result in temperatures well above atmospheric and would represent a limitation to seedling establishment. Germination and slow growth near freezing (figs. 2, 4) suggest the possibility of seedling survival under the insulating snow cover which occurs during occasional years at the time of seed dispersal.

From the limited number investigated, there is no evidence that declining clones produce seeds having lower germinability or seedlings with inferior growth. Any physiological basis for a clone's decline appears unrelated to factors that control vigor of its seeds' germination and early growth. Declining clones may produce fewer seeds per unit of photosynthetic surface (not investigated) and a smaller total number of seeds. Otherwise, these results indicate that both types of clones probably have about equal potential for contributing to seedling establishment.

High and continuous availability of water is critical for initial and firm establishment of seedlings. Normal germination is substantially reduced at approximately -2.0 atm (-2 bars), and successively fewer seeds progress beyond the incipient germination stage with lowering soil water potentials (table 1). These values are higher than the -3.9 to -7.9 atm (-4 to -8 bar) range that inhibited germination in several crop plants (Kaufman 1969), and toward the higher end of seed and substrate water potentials of -2.0 to -19.7 atm (-2 to -20 bars) in several range and pasture plants (McDonough 1972, 1975a, 1975b). This sensitivity to even mild deficits of water ranks aspen among the least tolerant species.

The turgor required by the seedling axis to start elongation and penetrate the testa is predictably more sensitive to lowering water potentials than the initial swelling due to inhibition (table 1, incipient/normal germination). The capacity to start growth in opposition to lowering substrate water potentials is further reduced by seed aging. Thus, with lengthening intervals between dispersal and onset of conditions suitable for germination, the capacity to overcome obstacles to growth by turgor development is reduced more rapidly than germinability.

In wet-drying cycling (table 2), loss of water during the pregermination to incipient germination stages is less harmful to eventual seedling growth and survival than less water loss at later stages. This is seen in the progressive extent of reduced hypocotyl length and root tip necrosis with longer wetting phases (table 2). Seeds in the pregerminative and incipient germination stages attained under shorter wetting phases apparently retain sufficient water for continued metabolic activity. Germination peaks toward the middle of the cycle and extensive growth resumes during the final wetting phase (table 2). Rapid changes in soil water conditions at the surface on exposed sites are common and may be a factor in reducing emergence and survival.

The rate and pattern of early seedling growth (fig. 3) appears to favor quick starts on suitable sites. However, even when water supply is adequate through the first week or more, a continuing supply is required for the firmer establishment that results from enlargement of the photosynthetic surface and increased capacity for water and nutrient uptake by appreciable plumule and root growth. These limitations probably cause high mortality even under favorable field conditions (fig. 5, irrigated).

A mineral surface is favorable for emergence; physical and chemical heterogeneity of the surface and burial are unfavorable (tabulated results above and fig. 6). The more pronounced inhibition of emergence by litter parent compounds (fig. 7) suggests allelopathic effects in addition to the purely physical effects that surface heterogeneity has on availability of water. Inability to emerge from even relatively shallow plantings is a liability, in that lower temperatures and higher soil water levels of the deeper layers favor germination and growth. The inability of the seedling to penetrate shallow layers of soil may be attributed to weak turgor development and scant nutrient reserves in the minute seeds.

Lower temperatures favor retention of germinability during aging of air-dry seeds, and germination of aged seeds during incubation (fig. 8). Storage under highly fluctuating field temperatures and humidities is more detrimental than storage at room temperature or refrigeration. Since low temperatures and high water levels prevail under a snowpack, late season snowfall should favor initial seedling starts. In contrast, early and extended onset of milder and drier weather would result in loss of turgor potential and germinability before the other hazards of establishment are faced. The timing of seed dispersal in relation to seasonal weather fluctuations may result in potentially good or bad years for establishment. Since hazards increase as spring progresses, it would be mandatory that a large, early season crop of seedlings be available for even modest survival through the first growing season.

Given the exacting seedbed requirements of this species, there seems to be hardly any practical scheme of management that would promote seedling establishment significantly over the normally large and thinly seeded dispersal areas. Seed collections and controlled dispersal over restricted areas of prepared ground subject to irrigation would have small effect, be prohibitively expensive, and have doubtful lasting value. Under favorable weather and site conditions, natural seeding and establishment may well be sufficient to insure the benefits of reproduction by seed.

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