SEXUAL REPRODUCTION, SEEDS, AND SEEDLINGS

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Natural genetic interchange and extensive colonization of aspen by seed strongly depends upon favorable climatic and microclimatic conditions and upon human intervention. At times, in regions with the right combination of environmental conditions, there is significant reproduction by seed; elsewhere such establishment is rare. Seed production generally is profuse; but this potential for regeneration is considerably reduced by the exacting survival requirements of aspen seedlings. Under the marginal conditions that prevail in some regions, aspen can consistently reproduce only vegetatively (Cottam 1954, Graham et al. 1963). (See the VEGETATIVE REGENERATION chapter.) Despite this, studies of the mechanism of sexual reproduction in aspen are valuable for increasing knowledge of the species' reactions to stable and changing environments. Where reproduction of aspen by seed is desirable in areas that are naturally inhospitable, the existing environmental conditions may be modified, or by selective plant breeding, the seedling reaction to existing conditions may be changed so as to increase the probability of successful reproduction.

Sexual Reproduction

Aspen flowers have either pistils or stamens, but generally not both as is common among other flowering plants. As a result of extensive vegetative reproduction and constancy of genetic composition, all trees within a clone generally are either staminate or pistillate. However, perfect flowers possessing both parts occasionally have been observed (Lester 1963, Pauley and Mennel 1957, Strain 1964). Estimates of the number of trees in clones that have some perfect flowers range from 5% to 20% (Santamour 1956, Schreiner 1974).

Although the staminate-pistillate ratio among clones in a given locality is generally 1:1, the ratio may vary considerably and may be as high as 3:1 or more (Pauley and Mennel 1957). Also, instances have been reported of clones within localities that produce only staminate flowers (Strain 1964), and clones which alternate between staminate and pistillate in different years (Graham et al. 1963), or show various combinations of perfect, staminate, or pistillate flowers within or between inflorescences on the same tree (Einspahr and Winton 1976). Apparently, determination of reproductive structures is unstable in clones with certain genetic combinations. Otherwise, it occasionally is influenced by local environmental conditions, or results from competition among reproductive branches on individual trees for water and nutrients.

Aspen reach reproductive maturity and begin flowering by 10 to 20 years of age, with a peak in seed production at 50 years and with 3- to 5-year cyclic variations in light to heavy seed crops (Fechner and Barrows 1976, Maini 1968, Moss 1938, Schreiner 1965). Individual reproductive shoots produce 2-10 inflorescences (catkins) each with 50-100 flowers, and 2-10 seeds per flower (Einspahr and Winton 1976, Henry and Barnes 1977). The seeds (1-2 million/kg) are provided with a tuft of dispersal hairs at the basal end, and have an air-dry water content of 6%. The plumose seeds are thereby adapted for wind dispersal to distances of 1,600 feet (500 m), or several miles under high wind conditions (Stoeckler 1960). The seeds are not damaged by water transport and will germinate while floating or submerged (Faust 1936). Water dispersal is important for deposition on suitable wet sites.

In common with all other seed plants, sexual reproduction in aspen involves two distinct entities—sporophytes and gametophytes (Lester 1963). The asexual sporophyte (the aspen tree) which reproduces directly by root sprouting is interposed between successive generations of the sexually reproducing gametophyte. Within certain parts of the flower, the sporophyte produces two kinds of spores by meiosis, a process that involves a halving of the number of chromosomes per cell during nuclear and cell division. The spores can be distinguished, using a microscope, as large and small—megaspores within the ovaries of pistillate flowers and microspores within the anthers of staminate flowers, respectively. Still in place, the spore nuclei undergo several nonreductional chromosomal divisions to form megagametophytes (female) and microgametophytes (male).

Gametophytes are multinucleate microscopic plants, rendered nearly vestigial by evolutionary reduction in size and complexity. Among the nuclei are the egg and sperm that are later randomly joined by nuclear fusion (fertilization) to initiate a sporophyte embryo. This restores the original number of chromosomes found in the sporophyte. As a result of these twin processes of halving and doubling of the number of chromosomes, the constituent genes are recombined in ways that differ from those of the previous sporophyte generation. Because genes largely control morphology and physiology of the individual clones, such recombinations insure sufficient variety among progeny to adapt to long-term climatic changes and to a wider range of potential habitats (see the GENETICS AND VARIATION chapter).

During one growing season, the various parts of the flower and spore-producing tissues are progressively differentiated. Buds located on short shoots below a vegetative (leaf) bud begin differentiation into floral and spore-producing tissues that will become visible as

staminate and pistillate flowers during the following spring (Beetle 1974, Fechner and Barrows 1976). Within staminate flower buds, the four-lobed stamens are first differentiated in early summer, followed by spore-producing tissue within each lobe. Formation of microspores is delayed until the buds are subject to several weeks of freezing temperatures in winter. A similar differentiation occurs within the pistillate flower buds during late summer, except that the megaspore nucleus divides once to initiate megagametophyte development before undergoing the winter dormant period.

Gametophytes complete development, floral parts enlarge, and flowers open during April-May of the following spring. First, pollen is wind-dispersed from the anthers of the staminate flowers. At least one of the vast numbers of pollen generally comes into contact with a receptive portion of the style of a pistillate flower. A tube-like growth of the pollen then proceeds to the vicinity of the ovary with its enclosed female gametophyte. Shortly after contact, a mobile sperm nucleus fuses with an egg nucleus. By repeated cell divisions, the fusion nucleus develops into the embryo of the seed—the sporophyte of the next generation.

These events are completed during a 4- to 6-week interval. The strings of capsules (catkins) developed from the ovaries of pistillate flowers open along two slits. The tufted seeds are exposed to wind for dispersal over a wide area (fig. 1). Meanwhile, other reproductive buds begin, repeating the annual process of spore and gametophyte formation and sexual reproduction.

Figure 1.—Maturing pistillate catkins. Aspen woodland in mid-June at 7,200 feet (2,200 m) elevation on the Wasatch National Forest of northern Utah.

Seed Germination

Seeds can tolerate a broad range of temperatures during germination. In various collections, high germination percentages have been reported between 0° and 39° C (Faust 1936), 5° and 37° C (Strain 1964), 5° and 25° C (Zasada and Viereck 1975), and 2° and 30° C, with limited germination to 40° C (McDonough 1979). However, temperature extremes are detrimental. At 2° to 5° C, germination rates are sharply lowered; and at temperatures above 25° C, total germination is reduced progressively to near zero. High temperatures inhibit germination, decrease emergence through a covering soil layer, and retard seedling growth. The percentage of abnormal germination—failure of any root growth or expansion of the cotyledons (seed leaves)—is increased also. Dark soil seedbeds, when exposed to sunlight, may reach temperatures that significantly inhibit germination and growth.

Standardized seed testing rules (International Seed Testing Association 1966) specify germination temperatures between 20° and 30° C, light, and first counts after 3 days. Somewhat in contrast, the aspen seed examined from northern Utah had optimum temperatures for both rate and total germination between 15° and 25° C, with no light requirement, and with earliest germination between 12 and 20 hours (McDonough 1979).

Early Growth

Several studies (Faust 1936, McDonough 1979, Moss 1938, Strain 1964) provide detailed information on germination and early seedling growth in aspen. Swelling of the root tip and the junction between root and hypocotyl (basal stem segment) without rupture of the seedcoat (incipient germination) are the earliest observed events (fig. 2). Further progress is either delayed or prevented by incubation at temperatures below 10° C, by placement in osmotic media, by cyclic wetting and drying the seeds, or by the presence of inhibitor compounds.

Normal germination over a 30- to 48-hour period progresses by rupture of the seed coat, root protrusion, formation of root crown hairs, growth and geotropic curvature of the root, and, lagging slightly, growth of the hypocotyl (fig. 2). Growth of the crown is terminated by adhesion to the surface with the completion of root curvature. Root growth slows perceptibly after the initial thrust. Hypocotyl growth tends to proceed uniformly at a rate and extent that strongly depends on light levels. Chlorophyll synthesis in the cotyledons is completed as root and hypocotyl growth proceed (fig. 2). The seed coat then is cast off, and the cotyledons unfold (fig. 2). The plumule, the cluster of developing leaves and stem segments above the cotyledons, is apparent at this time. However, there is a 6- to 10-day delay before growth is perceptible.

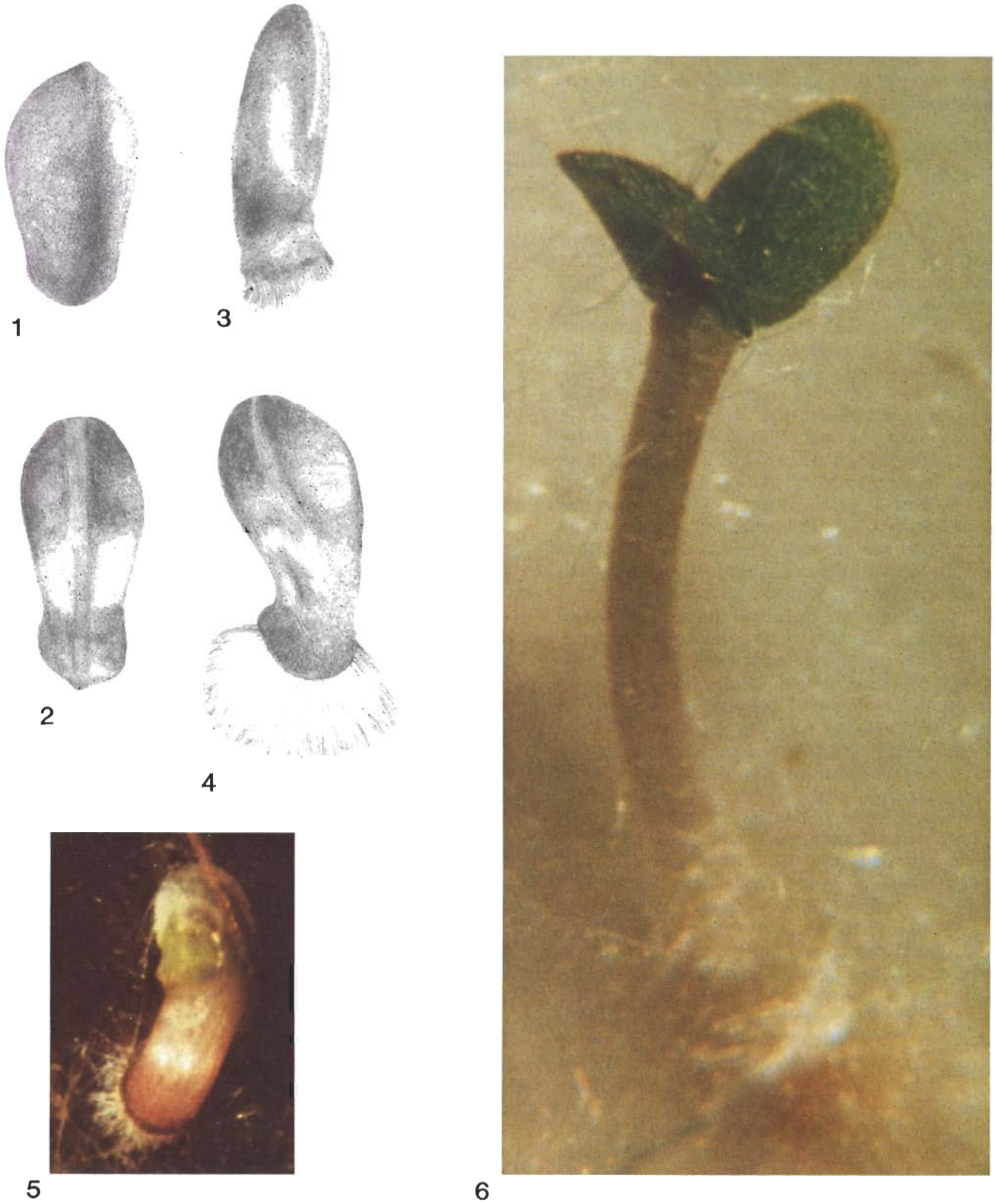

Figure 2.—Germination of an aspen seed: (1) incipient germination, (2) initial root protrusion, (3) initiation of root hairs, (4) elongation and curvature of the root-hypocotyl axis, (5) an "S"-shaped axis and development of chlorophyll in the cotyledons, and (6) unfolding of the cotyledons and extensive growth of the hypocotyl.

Abnormalities in germination are common and are conditioned by high temperature, presence of inhibitors, and wet-dry cycling of the seeds. These conditions damage or kill the active growth area of the root and result in extension of the hypocotyl only. Abnormal germination always kills the seedling.

Limitations on Seedling Growth

Established seedlings are found in the field (Barnes 1966, Faust 1936, Larson 1944), but this is believed to be uncommon (Einspahr and Winton 1976, Maini 1968). Only in regions where climatic and site conditions are particularly favorable does reproduction from seed contribute significantly to maintenance and spread of the species (Andrejak and Barnes 1969, Maini 1974). Therefore, Baker's (1918b) suggestion that sexual reproduction is defective because of failure of seed set or low germinability of seeds was widely accepted for many years. However, studies with seed collections from various regions of North America (Einspahr and Winton 1976, Maini 1968, Moss 1938) demonstrated that the paucity of established seedlings in nature results from rapid loss of seed germinability and from exacting requirements for seedling growth and survival, rather than from low or defective seed production.

Optimum conditions for germination and survival include an alluvial seedbed with adequate drainage, moderate temperature, and freedom from plant competition. Maini (1968) listed several factors involved in the failure of aspen seedlings to become established: (1) rapid loss of germinability with age; (2) presence of inhibitors in the seed hairs, soil, or litter; (3) rapid drying of the soil at and near the surface; and (4) unfavorably high surface temperatures.

Seeds deteriorate rapidly, except under optimum storage conditions of low temperature and humidity (Faust 1936, Zasada and Densmore 1977). In western Canada, seeds remained viable for 2-4 weeks after maturation (Moss 1938), a duration that is probably representative of longevity in the field. Seeds stored in air-dried soil, from mid-spring through early summer, on a mountain site in northern Utah, protected from precipitation but not from fluctuating temperature and humidity, declined 40% to 60% in germination after 4 weeks, and 75% to 100% after 8 weeks (McDonough 1979). The extent of loss also depends upon incubation temperature during germination, deterioration increasing with increasing temperature.

Inhibitors do not occur in the seed hairs, as suggested by Maini (1968). If the hairs were wetted and the seeds were fully imbibed, seeds germinated equally well whether they were embedded in masses of hairs or were isolated (McDonough 1979).

Lack of optimum seedbed conditions (i.e. a flat, well-watered, mineral soil surface) decreases germination and emergence. A heterogenous seedbed strands some seeds on rapidly drying surfaces, such as particles of litter or soil prominences. There, either seeds do not germinate, or else root hair growth is insufficient to make firm contact with the water-supplying substrate.

Germination and emergence also are reduced when the remains of particular understory species predominate in the litter. Naturally occurring inhibitors in litter (e.g. coumarin) severely inhibit root growth at concentrations of 10 ppm (McDonough 1979).

In addition to physical and chemical seedbed effects, emergence is decreased by relatively shallow burial. Emergence is reduced 20% to 80% from a 4-mm depth at optimum temperatures; there are greater reductions at higher temperatures (McDonough 1979). Such sensitivity is a disadvantage, because even minor disturbance loosens surface-germinated seeds. Also, the likelihood of desiccation by extreme temperatures and fluctuating soil water content is greater at the surface.

Germination and early seedling growth are highly sensitive to small soil water deficits. Pot culture and field plantings require regular and carefully controlled irrigation to prevent wilting and desiccation (Einspahr and Winton 1976, Moss 1938). On osmotic media, normal germination is reduced 20% at -2 to -3 bars and 50% at -4 to -5 bars. This range of water potentials had much less effect on germination of many other range and pasture plants (McDonough 1971, 1975). Osmotic inhibition is even more pronounced on aspen seeds previously stored under suboptimal conditions (McDonough 1979). This high water requirement is necessary to pass from incipient to normal germination, and for the hypocotyl and root to penetrate the substrate. Maximum growth is reduced by soil solutes, by high incubation temperature, and by aging of the seeds.

The exacting seedbed requirements for successful germination and early seedling growth illustrate several problems of seedling development. One involves failure of the root hairs to penetrate the soil surface. These hairs perform the critical water-absorbing function until significant root growth occurs (Day 1944, Moss 1938); but they are subject to rapid drying. Other disadvantages include weak anchorage to the surface, slow growth of the root and plumule, and etiolation (spindly growth) of the hypocotyl under reduced light. Despite these limitations, however, aspen seedlings effectively colonize regions other than western United States where environmental and land use conditions meet the species' requirements.