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EFFECTS OF WATER AND TEMPERATURE

John R. Jones, Merrill R. Kaufmann, and E. Arlo Richardson

Distribution

Aspen's geographic and elevational ranges indicate a species that tolerates severe cold but does not tolerate sustained high temperatures, or semiarid or even dry, subhumid conditions. Much can be inferred from observation of the sites on which quaking aspen grows in the West. Aspen's distribution is related to its regeneration characteristics, its pathology, and its relations with other plants. Water and temperature, to some degree, affects each of these relationships.

Where the northern grasslands approach the foothill and boreal forests, groves of aspen grow in depressions and on north-facing slopes (Brown 1935, Lynch 1955, Moss 1932), where concentration of soil moisture or reduction of evapotranspiration compensates somewhat for inadequate or marginal precipitation. In the central and southern Rockies, aspen reaches its lowest elevations along stream bottoms in the ponderosa pine, mountain brush, sagebrush or even pinyon-juniper climax zones (Baker 1925, Russo 1964, Vestal 1917). This implies a minimum moisture requirement for aspen that is greater than that of prairie, ponderosa pine forest, mountain brush species, or sagebrush.

Despite available or even abundant groundwater, however, aspen is not found along streams in relatively hot deserts. This indicates intolerance of high temperature effects—either direct effects or indirect effects such as sustained high atmospheric moisture stress.

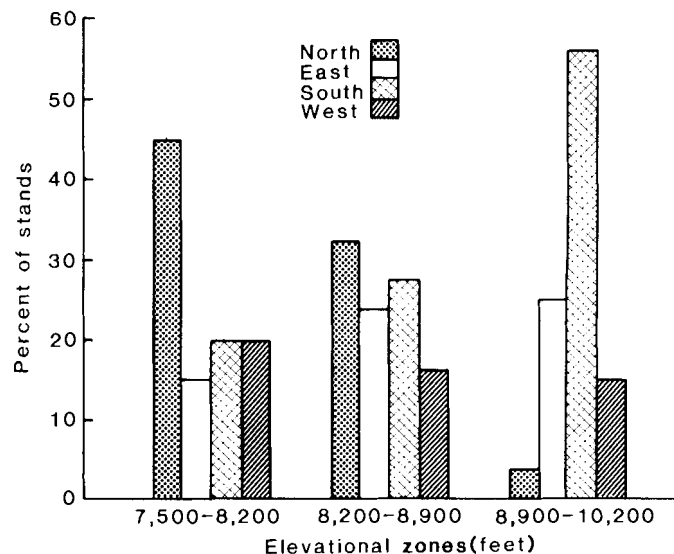


Figure 1.—Percentage of aspen stands on different slope directions, at different elevations, in the Wind River Range, Wyoming (Reed 1971).

In the Interior West, even within the elevational zone where it is prominent, aspen favors certain slope aspects (Baker 1925, Choate 1965, Dixon 1935, Langenheim 1962, Marr 1961, Reed 1952, Reed 1971), as diagrammed in figure 1 for the Wind River Range in Wyoming. In the lower part of that elevational zone, it is most abundant on north-facing slopes (fig. 2), and in the upper part on south-facing slopes. At lower elevations, which are drier and warmer, aspen survives best on the cooler, wetter, north-facing slopes. At higher elevations, because of the shorter growing season and colder temperatures, aspen survives best on south-facing slopes. At intermediate elevations, it shows less definite preferences (Langenheim 1962, Reed 1971).

On the Kamas Ranger District (Wasatch National Forest, Utah), Richardson¹ found the elevation of greatest prevalence of aspen between 8,500 and 9,000 feet (2,600 m and 2,750 m), but some clones were found near the 7,000-foot (2,150-m) level and others to near 10,000 feet (3,050 m). At the lower elevations, most of the aspen were found on north-facing slopes. As elevation increased, the dominant area of aspen dropped into the canyon bottoms and level plateaus. At higher elevations, the south-facing slopes became the most important aspen habitat.

Aspen forest is not prominent in the Black Hills of South Dakota (Green and Setzer 1974), which are mostly within the ponderosa pine climax zone. Severson and Thilenius (1976) found the aspen stands there almost exclusively on north-facing slopes—the slightly wetter and cooler sites. In interior Alaska, in contrast, aspen grows mainly on south-facing slopes (Zasada and Schier 1973)—the slightly warmer sites. In the cool, wet climate of Newfoundland, aspen is virtually absent from the wettest districts and areas with the coldest summers (Page 1972).

The scarcity of aspen in the upper subalpine zone in the West probably is not caused by cold summers or late-lying snow, because it is found even higher, frequently at timberline (Cox 1933, Jones and Markstrom 1973, Marr 1961), where summers are quite cold, and snow collects and persists late in patches of scrub. Instead, aspen scarcity in the upper subalpine probably reflects the relative infrequency of fires and competition from heavy invasion of Engelmann spruce and subalpine fir or corkbark fir (fig. 3).

¹Information compiled by E. Arlo Richardson, Utah State University, Logan.

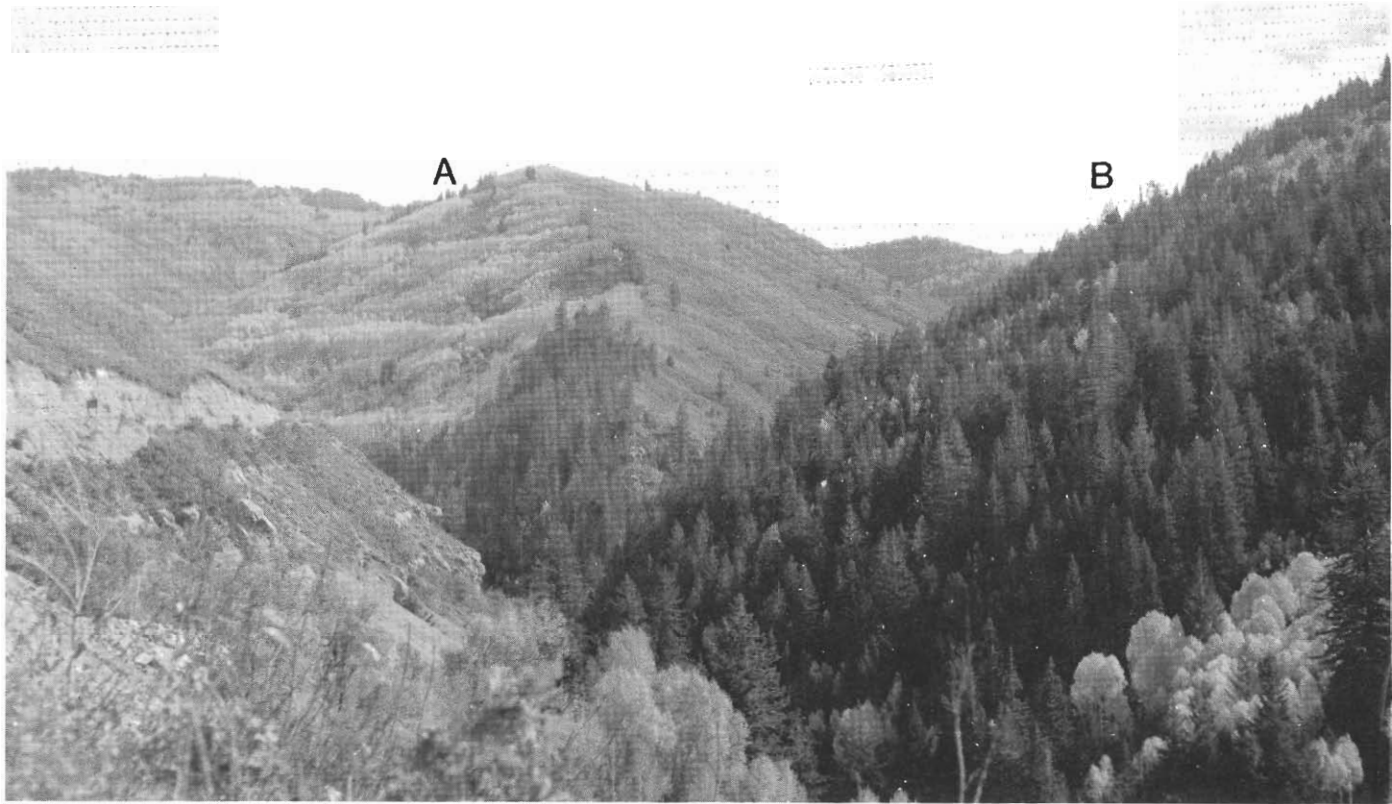


Figure 2.—Effects of slope direction on vegetation type in Utah. The photo, taken facing east, shows (A) aspen forest and (B) Douglas-fir forest on northerly slopes, and mountain brush on south-facing slopes. Manti-Lasal National Forest (Choate 1965).

Drought Resistance and Avoidance

Kaufmann (1982b) found that leaf conductance of quaking aspen decreased by more than 50% when xylem pressure potential decreased from -16 bars to -23 bars. In contrast, needle conductance was unaffected by xylem pressure potentials as low as -22 bars in Engelmann spruce (*Picea engelmannii*), -19 bars in subalpine fir (*Abies lasiocarpa*), and -18 bars in lodgepole pine (*Pinus contorta*). Somewhat in contrast, Tobiessen and Kana (1974) found that quaking aspen in New York continued to transpire rapidly when leaf water potential was as low as -60 bars. In comparison, they noted water loss from associated bigtooth aspen and white ash decreased sharply at -30 and -20 bars of leaf water potential, respectively. This suggests that the stomata of quaking aspen leaves in the eastern United States do not close effectively under water stress.

Recent unpublished work by Kaufmann indicates that the annual transpiration of aspen trees is less than that of Engelmann spruce, subalpine fir, and lodgepole pine, although the understory evapotranspiration may be greater beneath aspen. This work suggests that aspen sites often are wetter than conifer sites simply because the aspen trees extract less soil water. Lower annual

transpiration by aspen results from low leaf area index, evaporative cooling of leaves, and shorter growing season, factors which offset the higher foliage conductances of aspen than those of conifers (Kaufmann 1982a, Kaufmann et al. 1982).

Differences in environmental conditions can result in differences in aspen stomatal responses in the West versus the East. Full aspen canopies in the West are more open than eastern hardwood canopies, resulting in more air mixing and more uniform temperature and humidity profiles. In West Virginia, Lee and Sypolt (1974) found deciduous forest canopy temperatures on a 20% south-facing slope were about 9°F (5°C) warmer at midday than on a 20% north-facing slope. Therefore, in those forests, vapor pressure gradients would be much greater on the south slope, and water loss would either be greater or stomata would close earlier in the day. For aspen forests in the West, this might be true for small aspen trees near the ground but probably not for full aspen canopies. Small aspen trees in the West may experience more temperature difference between north and south slopes because of irradiance effects in these canopies, which have poorly mixed air. For large trees, however, canopy temperatures of subalpine forests generally are not influenced by irradiance differences associated with slope and aspect (Kaufmann 1984). In fact, unpublished data collected by Kaufmann indicates

that aspen leaf temperature is as much as 9°F (5°C) cooler than air temperature in full sunlight, not warmer. This probably is the result of evaporative cooling associated with high transpiration rates.

The wood of living aspen has a rather high water content—the weight of water in a block of green aspen wood is about equal to the weight of the oven-dried wood itself. Water stored in boles and branches may provide a small reserve from which transpiring leaves can draw during the day—a reserve replaced to some degree during the night by translocation from the roots. Aspen trunks shrink notably in diameter during droughts (Kozlowski and Winget 1962a), and contain consistently and substantially more water during dormancy than when the leaves are on (Bendtsen and Rees 1962, Lothner et al. 1974).

Perhaps most important, aspen regeneration from existing mature root systems, and the fast initial growth that results, is a superb system for avoiding drought during the seedling stage. It is a mechanism that gives aspen strong competitive advantage over other western forest

species, and a mechanism which largely defines its role in the western landscape.

Seedlings

Explicit information on the moisture and temperature needs for germination and seedling establishment has been presented by Barth (1942), Benson and Dubey (1972), Borset (1954), Faust (1936), McDonough (1979), Moss (1938), and Strain (1964). Seedlings can germinate over a wide range of temperatures, from as low as 32°F (0°C) to at least as high as 98°F (37°C); however, temperature extremes are detrimental. Seedling establishment requires continually favorable moisture. Once wetted, the seed germinates within a few hours or at most a few days, even if submerged. Once the seed has germinated, the seedling will be killed by even superficial soil drying during at least the first week and apparently the first 2 weeks or longer; the period probably depends to some degree on temperatures. (See the SEXUAL REPRODUCTION, SEEDS, AND SEEDLINGS chapter.)

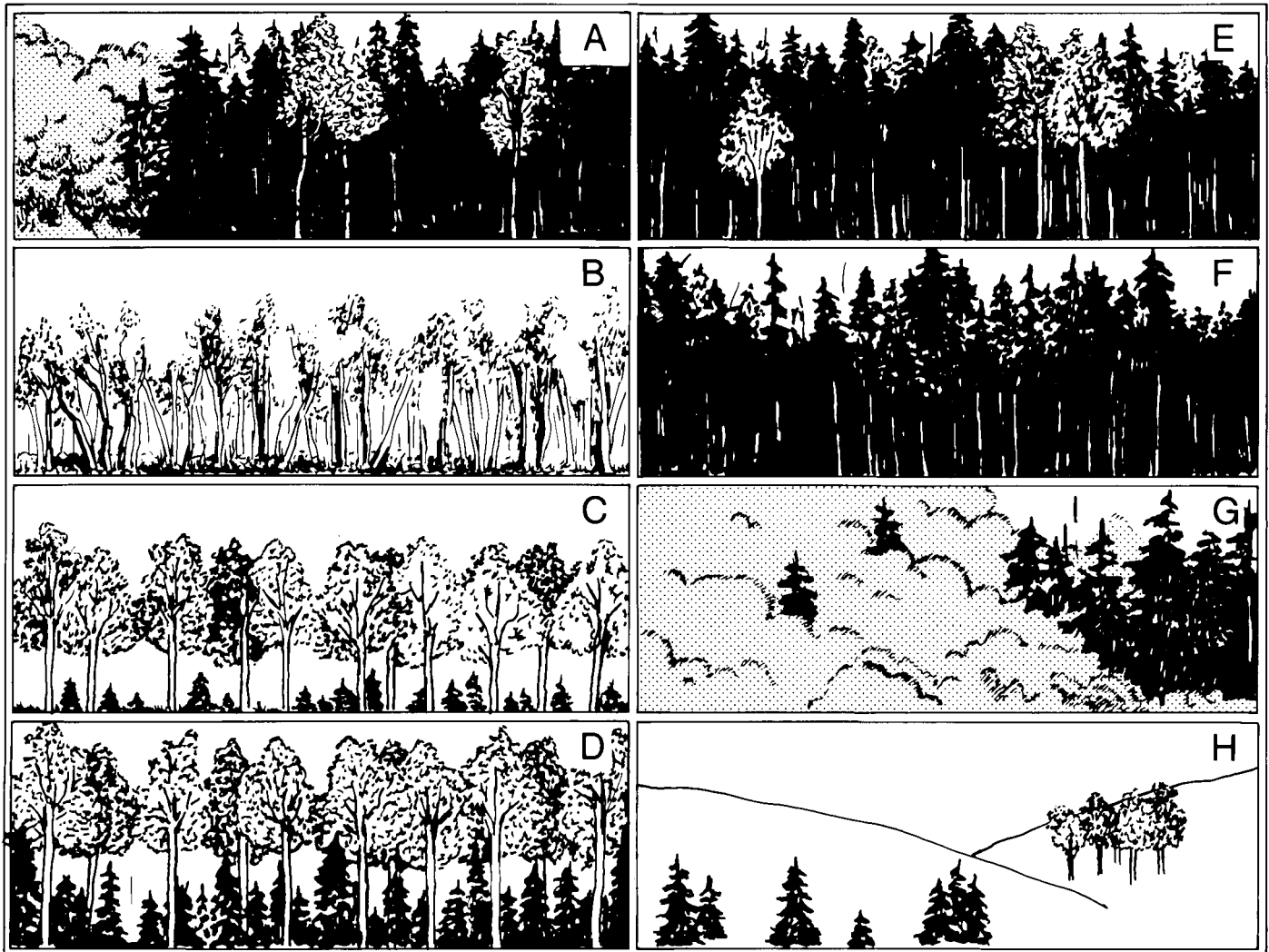


Figure 3.—Hypothetical sequence of events on a 10,600-foot Colorado site, with cold, wet summers, late-lying spring snow, and early autumn snow cover. The climate favors rapid invasion of aspen stands by conifers and long intervals between fires. (A) Fire destroys a 180-year-old mixed forest; (B) 5 years later aspen are 6

feet tall; (C) 30 years later; (D) 80 years later aspen are 60 feet tall with Engelmann spruce and subalpine fir understory; (E) 200 years later; (F) 300 years later aspen are gone; (G) after 350 years extreme drought and fire coincide; (H) after 400 years site is subalpine meadow.

Dixon (1935) reported aspen seedlings on spring banks in south-central Utah. Faust (1936) and Larson (1944) described a stand of aspen established from seed on the drawdown shore of Strawberry Reservoir in Utah, on what had been sagebrush land before the dam was built. In both cases, the moisture regimes were exceptionally favorable.

However, aspen stands, which must have originated with a seedling at some time, can be found in rather dry habitats as well as on sites where moisture is relatively abundant. The explanation seems to lie in the variability of weather and microsites, combined with vegetative regeneration. One or a few protected microsites in a habitat, temporarily free of competition, and having at least a few good seeds, need only have coincided with one suitable summer 1,000, or even 5,000 years before. One such summer could establish many aspen seedlings in a region, scattered about on a variety of habitats, expanding and perpetuating themselves by root suckers. Over centuries or millenia, events would then reduce the number and types of sites occupied, until another extraordinary summer renewed the cycle.

Suckers

Successful suckering requires less ideal moisture conditions than does seedling establishment. The shallow sections of roots from which the suckers arise are supplied with water from greater depths. Gifford (1964) concluded that enough water to support growth of sprouts was translocated through the parent root from moist soil to regions of high moisture stress.

The promptness of suckering, as well as the number and initial growth of suckers on root cuttings, varies with temperature but is satisfactory over a considerable range (Maini 1968, Maini and Horton 1966b, Zasada and Schier 1973). However, there were fewer suckers, and sucker growth was slower, at the cool day/night temperature regime of 68°F/50°F (20°C/10°C) than at warmer regimes (Zasada and Schier 1973); these cooler temperatures are similar to the day/night midsummer air temperatures in the shade of subalpine forests in the Rocky Mountains.

Unusually low temperatures can be disastrous. In the late spring and summer, when sucker and shoot growth are active and succulent, frost can cause serious injury (Baker 1925, Sampson 1919).

Growth

Recent unpublished studies by E. Arlo Richardson indicated that aspen clones in the mountains above Logan, Utah have the following cardinal temperatures for growth and development: base temperature, below which no appreciable growth will occur, is 39°F (4°C); optimum temperature, at which the maximum rate of growth will occur, is 77°F (22°C); critical temperature, above which little or no growth will occur, is about 97°F (36°C). These cardinal temperatures are preliminary, because they are based on very limited information.

There probably are differences among clones, especially those that grow in markedly different climatic regimes.

Richardson's studies also indicate that aspen requires a limited amount of winter chilling before growth can begin in the spring. By applying the chill unit model for fruit trees developed by Richardson et al. (1974), he found that aspen required about 300 chill units to complete their winter dormancy. (A chill unit is 1 hour at 43°F or its equivalent.) The required energy accumulation between the end of rest and bud swell was a little more than 1,600 growing degree hours (°F) using the asymmetric model developed by Richardson and Leonard (1981). Accumulations for other phenological stages have not been determined. The rate of growth of aspens may be estimated from how the actual temperature regime relates to the cardinal temperatures for this species.

Height Growth

The start of aspen height growth in spring is related to temperature. Allowing for considerable variation in the temperature responses of different genotypes, growth starts earliest at the lower elevations. Although aspen photosynthesis seems to be affected relatively little by high leaf moisture stress during the day, overall height growth is influenced quite strongly by the moisture regime—the balance of moisture supply and evapotranspiration.

Bate and Canvin (1971) found that well-established second-year Ontario seedlings grew better at day/night temperatures of 59°F/50°F (15°C/10°C) and 59°F/59°F (15°C/15°C) than at warmer temperatures. This agrees with observations in the West which indicate that aspen height growth is best in the upper montane and lower subalpine zones—roughly from about the elevation where Engelmann spruce first enters the forest, up to a point perhaps 1,200 feet (350 m) higher. However, in the upper 500–1,000 feet (150–300 m) of the spruce-fir zone, aspen normally is more or less stunted (fig. 4).

The zone of best aspen height growth seems to be defined by the temperature regime. Available moisture determines where, within that optimum temperature zone, the best growth takes place. For example, where aspen occurs on exceptionally moist sites within the ponderosa pine climax zone, its height growth is not especially good, and is usually poorer than in the cooler temperatures found 1,000–2,000 feet (300–600 m) higher.

The amount of available water is directly reflected in height and volume growth. Stoeckeler (1960) pointed out that aspen grows 15–25 feet (5–8 m) taller in north central Minnesota than on comparable soils in the Turtle Mountains of North Dakota, where the temperatures are quite similar but precipitation is less. On a sandy loam soil in Wisconsin, regular irrigation of sapling plots produced volume growth 63% greater than that on unwatered plots, mostly by its effect on height growth (Einspahr et al. 1972).

The available water held in the soil (conventionally that held between 1/3 and 15 bars tension) moves downhill in significant quantities at slow, sustained rates (Hewlett 1961, Hewlett and Hibbert 1963). As a result, it responds to topographic features—more soil water is available in deeper soils in and below concavities, and less soil water is available in shallower soil in and below convexities. Usually, the heights of aspen on those sites directly reflect these differences.

In the Lake States, soil characteristics which contribute to more than ordinary supplies of available water normally are associated with superior aspen height growth; and those with less have poor growth (Kittredge 1938; Stoeckeler 1947, 1960; Voigt et al. 1957). That same basic relationship presumably is true in the West. In the West, topographic and climatic variations are larger and more complex within small geographic areas. Therefore, the relationship of aspen height growth to the soil's capacity to provide water is obscured.

Jones (1971a) tried to integrate monthly precipitation and temperature values, topographic variables, and soil variables into a model that would simulate the moisture regime in its effect on aspen height growth. Other data were separately integrated to simulate the growing season temperature regime. Height growth was significantly related to both the moisture regime and the temperature regime; but only about 30% of the site index variance was accounted for. That probably was a result of the shortcomings of the model and the genetic variability among aspen clones.



Figure 4.—The dominants in this even-aged aspen stand are nearly 100 feet (30 m) tall at the lower end and scrubby saplings near the crest, 1,000 feet (300 m) higher. Temperature effects are probably confounded by soil and terrain differences. Fishlake National Forest, Utah (Choate 1965).

Diameter Growth

Except in dendrochronology, diameter growth has been used much less than height as a barometer of environmental effects. Diameter is more influenced by stand density than is height; therefore, site relations are confounded. Much less has been published about moisture and temperature effects on diameter growth than on height growth.

Because the beginning of diameter growth in spring is keyed to temperature, diameter growth begins earlier at lower elevations (Covington 1975, Strain 1964). With ideal conditions for producing photosynthate (adequate water and nutrients, moderate temperatures, and little insect or disease damage to the foliage), the longer growing season at lower elevations should permit diameter growth to continue later there, too. Such conditions seldom occur.

Duncan and Hodson (1958), in an extensive Minnesota survey, found that aspen diameter growth increased, at a declining rate, with increased April–June precipitation. On a sandy loam in Wisconsin, irrigation alone did not increase diameter growth appreciably in a sapling stand; fertilization without watering caused a modest increase; irrigation and fertilization together caused a large increase in diameter growth (Einspahr et al. 1972).

Frost Damage, Insects, and Diseases

Freezing damage to aspen occurs mainly when warm spring days are followed by a severe freeze. That sequence is most likely in nocturnal cold-air sinks at relatively low elevations. Perhaps mature leaves are less susceptible to freeze damage than new or immature leaves. Strain (1964) reported that immature aspen leaves in California were severely damaged by a 26°F (−3°C) temperature on June 3. Marr (1947) reported similar damage by an early June freeze in Colorado.

Aspen shoots are believed to become susceptible to frost damage when the cambial cells become filled with sap in the spring. This begins just below the leaf buds when they begin to swell. Egeberg (1963) reported twigs killed by 6 days of severe freezing in April, in Colorado. Cayford et al. (1959) reported similar frost damage in Canada following 7 days of unseasonably warm April weather which had caused leaf buds to swell. The most severe freeze damage reported was in Utah in 1919 (Korstian 1921). After an exceptionally warm spring, many aspen had fully expanded leaves. On May 30 and 31 temperatures dropped to 15°F (−9°C). All the leaves and much of the previous year's shoot growth was killed. For several weeks, the aspen looked entirely dead. Strain (1966) found that mature aspen with June frost damage grew much less in diameter that summer than adjacent, undamaged aspen.

There is limited evidence that aspen may suffer fewer severe insect and disease attacks on its cold uppermost fringe sites than at lower elevations where it is relative-

ly common and grows much faster. At least it appears to live longer near timberline (Greene 1971, Strain 1964). Observation suggests that at its warm lower fringe, aspen is particularly prone to attacks by insects and disease.

Hofer (1920) reported that, in the Pikes Peak region of Colorado, the poplar borer was prevalent in aspen only below 8,000 feet (2,450 m) and was not found at all above 9,000 feet (2,750 m). It was most frequent on dry sites. However, another damaging borer, *Xylotrechus oblitteratus*, replaced the poplar borer at higher elevations. This suggests that the temperature or moisture effects of elevation may have been mainly on the insect rather than on host susceptibility.

After severe drought in Canada's aspen grovelands, aspen lost vigor; and while in a state of severe decline, they were heavily attacked by the poplar borer and by a

fungus, *Cytospora chrysoperma* (Riley and Hildahl 1963).

In Utah, epidemics of aspen leaf blight, caused by *Marssonina populi*, seem to coincide with wet summers (Harniss and Nelson 1984, Mielke 1957). Spores of *Venturia tremulae* (*Polaccia radiosum*), which causes shepherd's crook in young sucker stands, are released only on rainy days (Dance 1961). In Canada, decay in aspen is more common on very wet or very dry sites than sites in between those extremes (Basham 1958, Thomas et al. 1960).

The incidence of insect and disease damage in aspen is largely controlled by the climatic variables that control insect or pathogen populations. The impact of this damage to the well-being of the western aspen stands appears to be greatest on the dry marginal sites.