Water Relations of the Aspens

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LIST OF ABBREVIATIONS AND SYMBOLS

BTA	Bigtooth aspen (*Populus grandidentata*)
EA	European aspen (*P. tremula*)
ET	Evapotranspiration
LAI	Leaf area index
LSC	Leaf specific conductivity
MPa =	10^6 Pascals = 10 bars
PET	Potential evapotranspiration
RH	Relative humidity
RWC	Relative water content
SI	Site index
SPAC	Soil-Plant-Atmosphere Continuum
TA	Trembling aspen (*P. tremuloides*)
VPG	Vapor pressure gradient
r_a	Boundary layer resistance of leaf surface
r_d	Diffusive resistance of leaf surface
Ψ	Water potential
Ψ_m	Matric potential
Ψ_p	Turgor potential
Ψ_s	Solute or osmotic potential

I. INTRODUCTION

This review synthesizes the English-language literature on the water relations of three aspens, Populus tremuloides (trembling aspen, hereafter abbreviated TA), P. grandidentata (bigtooth aspen, BTA), and P. tremula (European aspen, EA). The synthesis is structured according to plant water relations as studied by physiologists, ecologists, and hydrologists. Because parallel information was not borrowed from other species when data about aspen were lacking, the review contains discontinuities. It is hoped that these will identify needs for further research. This review assumes that the reader is familiar with the ecology of aspens and with the principles of plant water relations (Kozlowski 1981; Lange et al. 1976; Levitt 1980; Slatyer 1967).

II. TRANSPIRATION AND SOIL-PLANT-ATMOSPHERE CONTINUUM

The pathway and movement of water from the soil through the plant to the atmosphere is examined with the SPAC concept (soil-plant-atmosphere continuum). While SPAC analysis of agronomic crops is quite sophisticated, research on aspen has not yet produced a general model. The first section examines reports of total evapotranspiration (ET) and the effects of individual factors on ET, while subsequent sections review components of the SPAC: water uptake, water in the xylem, and water loss from leaves.

A. Transpiration

1. Amount of Evapotranspiration (ET) in Aspen Stands

Table 1 lists ET from aspen stands with all vegetation included. The totals are usually underestimates because roots absorbed water from depths lower than those measured in the studies (Johnston 1970; Mital 1980). Several studies have measured (Table 1, Figure 1) or calculated (Rauner 1976) the seasonal pattern of ET. Winter transpiration from leafless twigs is very low (Keller and Beda-puta 1973). Bylinska (1975) measured winter transpiration of 0.025 g water/g of 1-year shoot/day which may be compared with 35 g water/cm^2 of leaf/day in the summer (Eidman 1943).

Table 1. Evapotranspiration (ET) of aspen stands (usually determined by adding precipitation and soil moisture depletion).

Species	Location	Age	Soil Depth[b]	Growing Season ET	Seasonal Pattern Reported	Source
		(yr)	(m)	(cm)		
Trembling Aspen	Utah		1.8	40 to 50	Yes	Croft & Monniger, 1953
	Utah	@30	2.7	47 to 61	No	Johnston, 1970
	Utah	Mature (3.3)[a]	1.8	27 to 33	Yes	Johnston, 1969; Bartos & Johnston, 1978
	Utah	2 to 4	1.8	18 to 26	Yes	Johnston, 1969
	Utah	Mature	1.8	25 to 42	No	Tew, 1967
	Utah	1 to 3	1.8	17 to 41	No	Tew, 1967
	Colorado	Mature	2.4	39 to 58	No	Brown & Thompson, 1965
	Minnesota	Mature	2.4	22 to 33[c]	Yes	Mital, 1980
	Utah		1.8	41		Marston, 1966
European Aspen	Voronezh	8 (3)	2	20		Smirnov & O'dinokova, 1954
	Voronezh	25 (4)	2	23		Smirnov & O'dinokova, 1954
	Voronezh	37	2	20		Smirnov & O'dinokova, 1954
	Voronezh	63 (3)	2	18.5		Smirnov & O'dinokova, 1954
	USSR	12	--[d]	40	Yes	Silina, 1955

[a] Number in parenthesis is leaf weight in tons/ha.

[b] Thickness of soil used to determine soil moisture depletion.

[c] Early and late growing season not included.

[d] Seasonal transpiration estimated from transpiration of excised leaves.

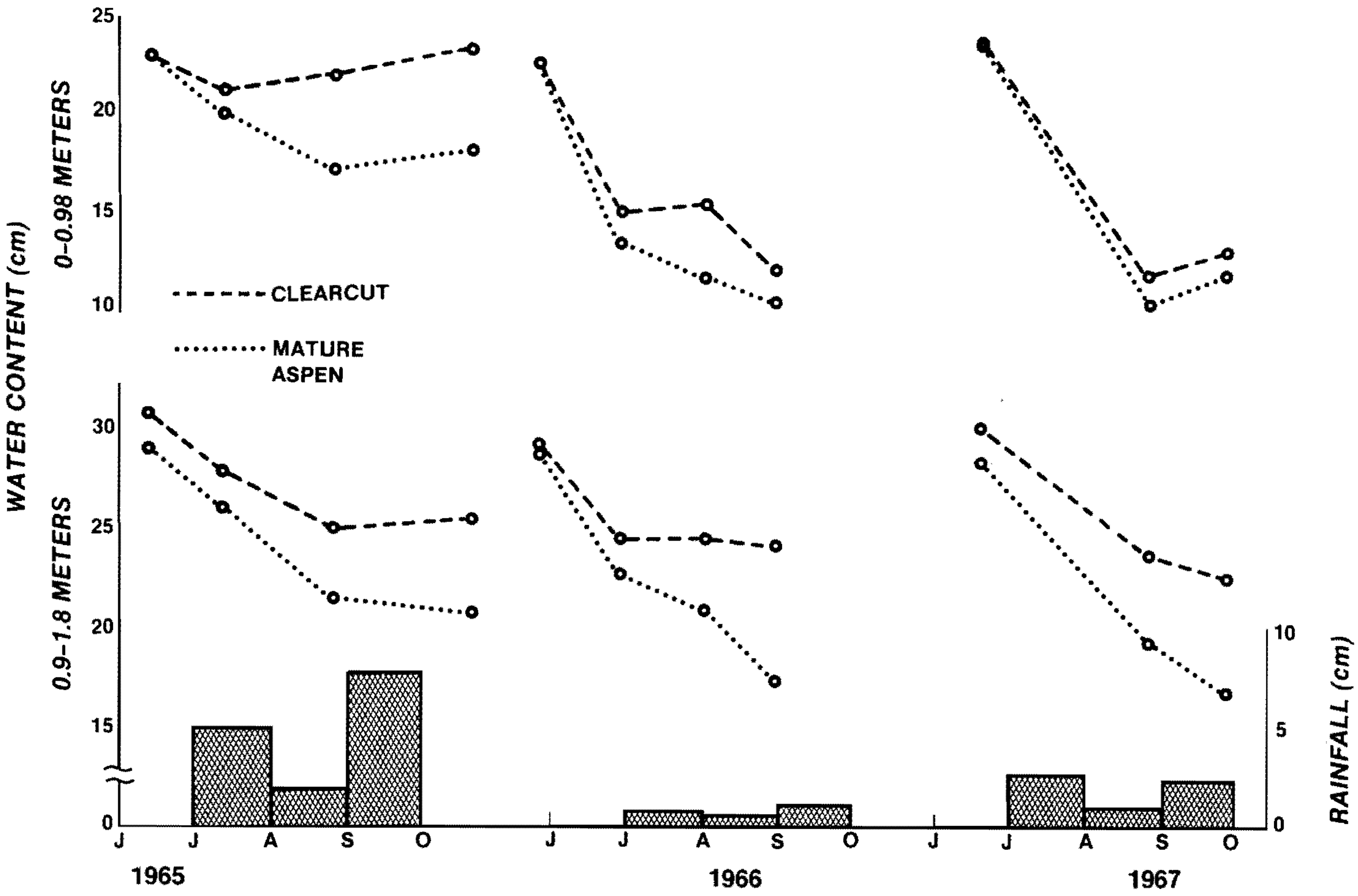

Figure 1. Seasonal moisture content beneath matching mature stands and sucker stands of Populus tremuloides in Utah. The sucker stand resulted from a 1964 clearcutting (from Johnston, 1969) (Courtesy of USDA Forest Service).

2. Meteorological Factors and Transpiration

Several authors have described the microclimate in aspen stands (Alekseev 1969; Drew 1973; Miller 1967, 1969; Rauner 1958, 1976, 1977), but only Rauner has determined a heat balance by season and canopy layers (Sec. IIA4). In a mixed EA-birch (Betula verrucosa) forest, 15 to 17 m tall and 40 to 50 years old, Bowen ratios approximated 1.17 before foliation, 0.49 during foliation, 0.34 during full leaf, 0.57 during senescence, and 1.67 after leaf fall. During full leaf, latent heat flux was equivalent to 5 mm/day.

Other studies, while showing that atmospheric factors control transpiration as would be predicted from SPAC theory, did not provide parameters for integrative models. In EA, ET increased with net radiation, solar radiation, air temperature, leaf temperature, and wind velocity (Akhormeiko and Zhuravleva 1957; Balek and Pavlik 1977; Gulidova 1958). Net and solar radiation were the most influential variables.

Tew (1967) studied ET of TA stands on Utah sites which simultaneously varied in aspect, elevation, and soil moisture-holding capacity. In sprout stands, ET was highest on south-facing and lowest on north-facing slopes. In mature stands, transpiration was influenced by both aspect and soil depth. Elevation had no consistent effect.

The ratio of measured to potential evapotranspiration, ET/PET, has been determined, or modeled (Sec. IIE) but often when factors in addition to evaporative potential were limiting ET. ET was calculated by adding precipitation to changes in soil moisture. For a mature TA stand in Utah, ET/PET (Thornthwaite) was 0.99 from May through September (Johnston and Doty 1972). The ratio would have been higher if soil moisture depletion below 1.8 m had been included as at least 8 cm can be absorbed from 1.8 to 2.7 m in a dry summer (Johnston 1970). In Minnesota, ET/PET (Thornthwaite) during a wet June and July was 1.23 on a loamy soil and 1.08 and 1.16 on two sandy sites (raw data provided by E. Verry, USDA Forest Service, Grand Rapids, Minnesota). On two sandy soils in Minnesota the author found mid-summer ET/PET ratios of 0.79 to 0.90 for Penman PET and 1.02 to 1.15 for Thornthwaite PET. Smirnov and Odinokova (1954) simultaneously measured soil moisture, precipitation, and pan evaporation. Studies of EA cited by Rauner (1977) may include some which determined ET/PET ratios.

3. Moisture Supply to Roots and Transpiration

Aspens transpire less when soil moisture is low. The most complete data relating transpiration to soil moisture are from growth chamber studies with EA involving the four soil moisture regimes described in Table 2 (Jarvis and Jarvis 1963a, b). In the drier treatments (C and D), transpiration decreased when soil Ψ dropped below -0.15 MPa and stomates shut at -0.9 MPa; transpiration did not immediately recover after rewatering. At substrate Ψ of -0.45 MPa, transpiration was at least halved both in this experiment and in a hydroponic study involving sudden addition of mannitol (Jarvis and Jarvis 1963c). Because these relationships were obtained with high root densities and homogeneous media, they can only be incorporated into transpiration models which partition uptake by soil layer and root density (Sec. IIE). The relationships may still not apply because frictional resistances and pre-conditioning regimes are different between forest trees and these seedlings and because juvenile leaves on young seedlings behave differently than leaves on mature forest trees (Jarvis and Jarvis 1963d). In the only measurements in forest conditions, Federer (1977) reported that TA stomates closed when soil Ψ reach an unknown value below -0.08 MPa.

Table 2. Relative rates of transpiration and net assimilation (NA) for European aspen grown at four soil moisture regimes. In each regime, soil water was cycled between approximately -0.01 MPa and the stated lowest potentials (Modified from Jarvis and Jarvis 1963a, b, d).

Treatment Designation	Description of Soil Water Potentials: Lowest Potentials Between Rewatering Ψ_m[a]	Ψ_{m+s}[a]	Average Potentials Ψ_m	Ψ_{m+s}	Rates Relative to Treatment A (percent): Transpiration	NA
	(MPa)	(MPa)	(MPa)	(MPa)		
A	-.05	-.18	-.01	-.11	100	100
B	-.10	-.25	-.01	-.13	89	101
C	-.21	-.42	-.04	-.19	71	94
D	-.40	-.64	-.08	-.24	52	82

[a] Ψ_m = soil matric potential; Ψ_{m+s} = soil matric plus osmotic potentials.

EA also transpired less when its root system was completely flooded; anaerobiosis was the presumed cause (Koshcheev 1955; Veretennikov 1964). If instead of complete flooding, the excess water remained 15 to 25 cm from the surface, transpiration was 40% higher than when the water table was deeper.

4. Stand Characteristics and Transpiration

Most aspen stands regenerate from suckering after disturbance. Because these suckers use the pre-existing root system, their ET rates quickly approach those of mature stands. According to Paul and Verry (1980), equality is achieved within 10 to 16 years and during that interval the difference between sprout and mature stands decreases exponentially. Based on 8 years of measurements of streamflow from an 80-acre clearcut in Minnesota, they derived the formula:

$$\Delta Q = 3.73 + 0.252\ P - 3.85\ \ln T$$

where ΔQ is surplus streamflow above control in cm, P is precipitation in cm, and T is years since cutting. In Utah, also, the transpiration of sprout stands rapidly approached mature stands (Figure 2) (Johnston 1969; Tew 1967). By the third and fourth year after clearcutting, sprout stands and residual mature stands depleted the upper 0.9 m equally, while inequality persisted between 0.9 and 1.8 m. The differences in ET between mature and sprout stands were generally larger at high elevations, on northern aspects, and on less stony soil. The lower ET of sprout stands can be attributed to fewer leaves, a shallower canopy, a smaller root system, and lower interception of precipitation.

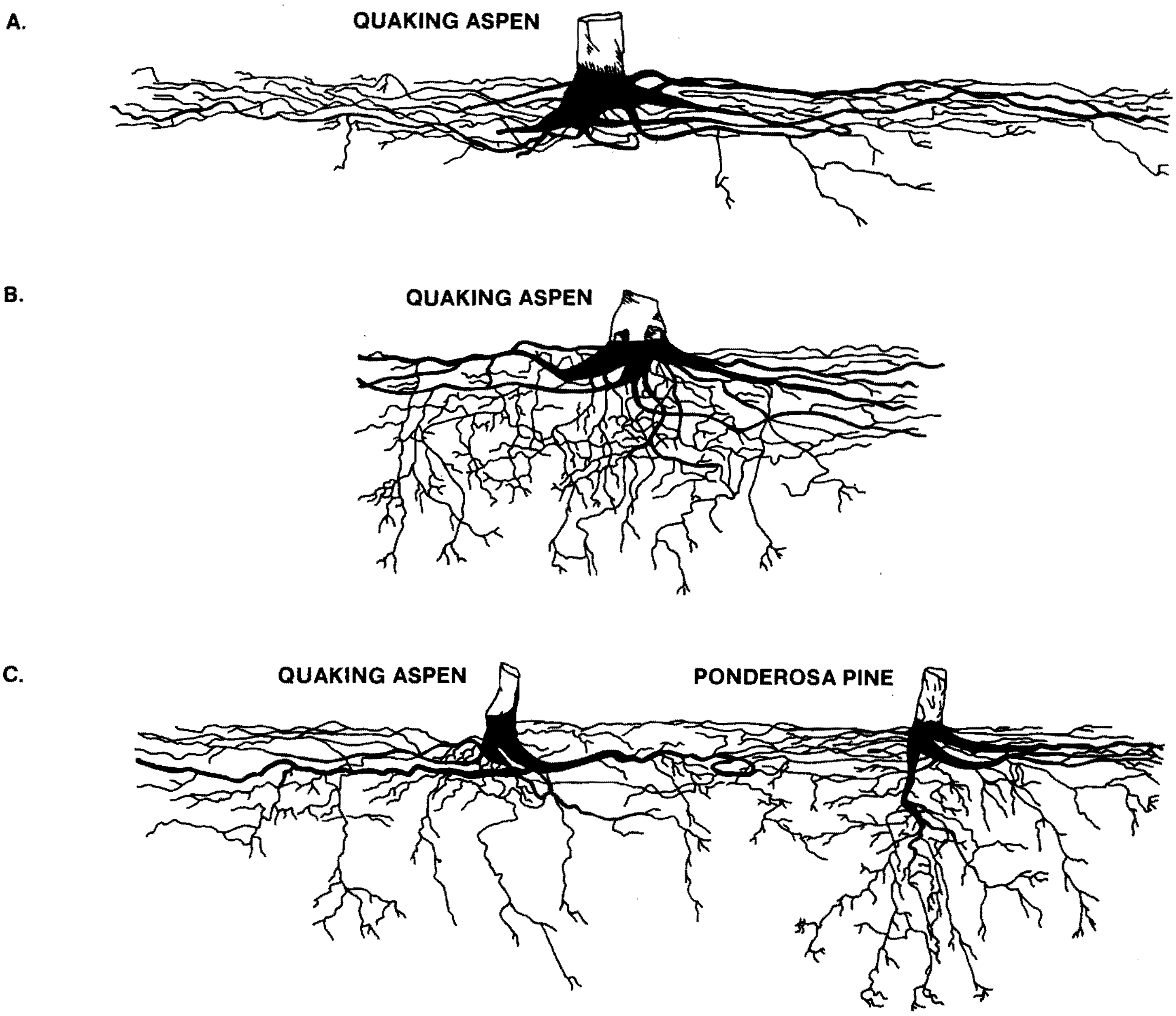

Figure 2. Development of the roots of trembling aspen on three distinctly different soils. A. Skeletal sandstone; this root system is from a tree 110 years old and 6.6 m high and 18 cm dbh. Maximum penetration was 0.7 m and maximum lateral spread 6 m. B. Chubbs stony loam. The tree is 97 years old, 11.4 m high, and 22 cm dbh. Maximum penetration was 1.2 m and maximum lateral spread 14.4 m. C. Edloe gravelly sandy loam. The aspen is 70 years old, 7.8 m high, and 11 cm dbh. Maximum rooting penetration was 1.5 m and maximum spread 9 m. The 85-year-old, 5.7-m-tall pine had roots of similar depth but only 3 m lateral spread. The pine was included to emphasize the very competitive root systems of aspen (Modified from Berndt and Gibbons 1958) (Courtesy of USDA Forest Service).

The distribution and density of leaves and roots are probably the most important stand characteristics influencing ET. Rauner's (1976, 1977) analysis of potential latent heat flux from different canopy layers quantified the importance of leaf area index (LAI) in transpiration. He examined a 20-year-old EA stand with a total LAI of 7, of which three units were in understory plants of other species. The potential latent heat fluxes beneath LAIs of 1 through 7, were respectively 88, 78, 64, 38, 15, 11, and 8% of the flux above the canopy. In the one study relating LAI to ET, a 25-year-old stand of EA, with 33% more leaf mass than neighboring 8- and 63-year-old stands transpired 20% more than the older and younger stands (Smirnov and Odinokova 1954).

In regions with little summer rainfall, rooting depth is probably the most important characteristic governing transpiration (Johnston, personal communication). For example, the persistent difference in transpiration between sprout and mature stands at the soil depth of 0.9 to 1.8 m (cited above) is most easily explained by assuming the sprouts had fewer roots at these depths.

5. Transpiration Inhibitors

TA stands sprayed with the transpiration inhibitor, phenylmecuric acetate (PMA) transpired less in early summer when canopy resistance was the limiting factor. Total seasonal water use, however, was the same, probably because soil water became limiting (Hart *et al*. 1969; Zan 1968). In a greenhouse study lasting 53 days, transpiration of TA was reduced 40% by a spray of 0.001M PMA (Johnston 1981, personal communication).

6. Transpiration of Aspen Compared to Other Species

The transpiration rate of individual EA has been compared with other species in controlled conditions (Eidmann 1943; Jarvis and Jarvis 1963b, c, d) and in the forest (Antipov 1971; Kaufman and Troendle 1981). Jarvis and Jarvis (1963b, c) found transpiration (mg/cm^2) at high soil moisture was similar for EA and birch, both of which transpired more than pine (*Pinus sylvestris*) or spruce (*Picea abies*). As soils dried, transpiration decreased most in pine with pine > birch $\geq$ aspen > spruce. While rankings varied among studies, EA transpiration was always relatively high per unit of leaf but since EA carry less leaves per ha than many species, aspen stands may not transpire more. Comparative stand data are lacking. ET by TA stands in Utah was about the same as that of a mountain brush community (Marston 1966) but generally much higher than that of herbs and grass, these last differences attributable to depth of rooting (Johnston *et al*. 1969).

7. Summary

ET of TA stands has been measured in Utah, Colorado, and Minnesota; EA has been studied chiefly in the Soviet Union. Young sprout stands evapotranspire less than healthy, mature stands for up to 10 to 16 years. Higher ET occurs in stands with more leaf area; undergrowth species may account for 10 to 15% of total ET.

Transpiration of aspens responds to environmental factors as might be expected from SPAC information gathered on other mesophytes; e.g., it increases with radiation, decreases with soil moisture deficits, and gives reasonable results when studied with a detailed energy budget.

B. Water Uptake

The usual variables in a SPAC analysis of water uptake include spatial distribution and density of roots, and resistance of roots to water absorption. As little is known about resistance, most of this section examines the density and distribution of roots.

1. Spatial Distribution and Density of Roots

The root system of aspens have a consistent pattern which changes with age and is modified by soil properties (Figure 2). TA will be discussed first. The root systems of TA seedlings develop rapidly (Shirley 1941; Day 1944), and young root suckers use a large portion of the parent root system (Sec. IIA4). The root systems of mature TA are characterized by two forms of large roots: (1) wide spreading laterals (Baker 1925; Brown 1935) which remain near the surface, and (2) vertical sinker roots arising from the laterals (Barnes 1966; Gifford 1966; Miles 1979). Miles (1979) also described a 1 to 2 m deep heart root with many branched anchor roots. The fine roots of aspen are very narrow (less than 0.5 mm) and can be mychorrizal (Trappe 1962; Vozzo 1974).

According to Maini (1968), the lateral root system has four or five well-developed laterals which branch within 2 feet of the tree base. Some of these branches become cordlike and extend considerable distance with little taper or branching. Reported maximum lateral spread includes 13.3 m for a 19-year-old TA (Day 1944); and 31 m for a TA in the prairie-forest border of Minnesota (Buell and Buell 1959). Most of the aspen roots were found within 40 or 90 cm of the soil surface (Figure 2) (Baker 1925; Miles 1979; Sandberg 1951) except in a soil with a dense clay B horizon, where almost all roots were limited to the surface 30 cm (Gifford 1966).

Although most of the roots are superficial, some laterals or sinkers arising from laterals penetrate deeply (Sandberg 1951; Brown and Thompson 1965; Berndt and Gibbons 1958; Gifford 1966), usually following old root channels (Day 1944). Sinker roots were found at a depth of 2.9 m in sandy loam, and 1.3 m in clay (Gifford 1966). Sinker roots had little branching or taper (Gifford 1966), but at their extremity spread into "dense fanshaped mats" (Day 1944, personal observation). Root counts in aspen stands (Table 3) support these qualitative judgements.

Table 3. Density of roots in stands of trembling aspen over shrubs and herbs (Omega) or northern hardwoods, shrubs and herbs (Warba). Roots of all species are counted (Mital 1980).

	Number of roots per 30 cm^2 of vertical soil surface			
	October Sample		July Sample	
Soil Depth (cm)	Omega Loamy Sand	Warba Very Fine Sandy Loam	Omega Loamy Sand	Warba Very Fine Sandy Loam
0-30	.92 (.35)[a]	1.04 (.41)	3.59 (.82)	2.25 (.65)
30-60	.32 (.13)	.36 (.15)	.79 (.19)	.32 (.11)
60-90	.05 (.03)	.21 (.07)		
90-120	.03 (.01)	.11 (.04)		
120-150	.01 (.01)	.07 (.03)		
150-180	.16 (.03)			
180-210	.04 (.01)			

[a] The first number represents all visible roots. The number in parentheses is for roots 0.6 mm or larger in diameter.

Although no firm generalizations can be made, almost every study suggests that soil properties influence the distribution and/or quantity of roots. For one example, small roots were nearly absent in a clay soil (Gifford 1966). For another example, Miles (1979) found the ratio of root biomass to stem diameter was higher on more gravelly soils.

The root systems of BTA and TA are similar, but under comparable ecological conditions, the roots of BTA were deeper (Maini 1968; Farmer 1962) and less branched (Maini 1968). The root system of EA as described in detail by Kostler <u>et al.</u> (1968) seems similar to that of TA. Sokolov (1967) reported that in the A-1 horizon roots finer than 0.4 mm comprised 27% of the root volume. Il'in (1973) noted that male trees had more horizontal roots than female trees.

2. Water Uptake and Root Distribution for TA

In four stands of TA, water was absorbed fastest from the soil layers containing the most roots (Mital and Sucoff, in press). The relation, however, was imperfect and generally a unit of root in the upper 1 m of soil absorbed less water than a unit of root in the soil below 1 m. In a very dry summer, they observed almost total depletion to 2.3 m although only occasional sinker roots proliferate at this depth.

3. Intraclonal Water Movement

Hayden (1968) found competition for water within a clone of BTA. When he exposed one ramet to wind and radiation, stem Ψ decreased in a second member of the clone. Perhaps water moved from the stem which was transpiring less into the stem which was transpiring more, or the common roots may have sent more water to the exposed stem at the expense of the untreated one.

4. Summary

The three species of aspen have similar root systems. Most of the system derives from lateral roots and is concentrated in the upper 20 to 100 cm of soil. Vertical sinker roots which may descend to at least 3 m are located along the lateral roots. Water uptake is greatest where roots are more abundant except that deep soils provide more water, and shallow soils less than would be predicted from root density. Root resistance to uptake or transport of water has not been studied.

C. Water Transport in the Xylem

This section examines the pathway of water movement through the xylem, the resistance to that movement, and the amount and significance of water storage in the main stem.

1. Water Movement In the Xylem

Water-soluble dye introduced from a single root moved to the top of TA and BTA by the pattern called interlocked ascent (Kozlowski and Winget 1963). Near the ground, ascent was vertical through several outermost annual rings. With greater height, a progressively increasing cross-section of sapwood became involved. Heartwood never transported water.

The leaf specific conductivity (LSC) of xylem to the passage of water was examined in BTA (Zimmerman 1978). LSC was defined as microliters of water passing through a stem or petiole segment per hour per gm of fresh leaves above the segment. The LSC of the bole (245 to 363) did not change with height and was much greater than that of branches, especially current-year shoots and petioles (LSC = 5 to 10). Junctions had much lower LSC than either of the joining branches and the LSC was only 1 to 3 at the junction of a petiole and branch. Total LSC from root to leaf was less for leaves on lower lateral branches than for leaves at the top of the tree. Functionally, these results mean that at the equivalent rates of transpiration, lower leaves must have more negative leaf Ψ's than leaves in the top of the tree. The results also mean that LSC decreases with branch order which might partially explain why aspens have few orders. These features may also contribute to earlier abscission of lower leaves. Most of the differences in LSC were attributed to vessel diameter. In a related study, Kaufmann and Troendle (1981) found for TA that the sapwood area in a cross-section of tree bole is directly proportional to the leaf area or leaf weight above it.

The rate at which water ascends aspen has been studied with dyes (Gibbs 1958), heat transport (Hart et al. 1969; Balek and Pavlik 1977), and magnetohydrodynamics (Roa and Pickard 1975). Peak velocities were 7 to 11 cm/min.

2. Water Content of Stems

Because water content influences the purchase, transport, and processing of pulpwood, it has been heavily studied relative to its importance in the SPAC. The water content of TA (Gibbs 1930, 1935, 1958; Jensen and Davis 1953) and EA (Il'in 1970) xylem changed seasonally. Xylem was wettest in winter, dried after leaf-out, and fluctuated during the summer. Winter moisture content (ODW) averaged 113%; summer, 80% (Bendtsen and Rees 1962). In contrast to wood, bark moisture was higher in summer than winter (Bendtsen and Rees 1962). On one site during winter, bark at 66% water content was adjacent to xylem at 131%, an observation of possible interest to explanations of frost cracking.

Water was unevenly distributed within stems (Isaeva 1966; Edgar 1970; Bendtsen and Rees 1962). In summer, the outer five rings were always wetter than the next five rings inward. Moisture decreased with height, especially in the outer rings (Bendtsen and Rees 1962; Danilin 1975). In winter, the inner rings were always wettest and there was less vertical gradient (Bendtsen and Rees 1962). Water content varied with other variables including gender, but each sex has advocates. Rangelov (1969) and Il'in (1970) found more water in female EA while Danilin (1975) found more in males. The higher water content in females may relate to a change in sex ratio with site (Il'in 1973b). In a transect upward from a river, females predominated in the flood plain while males predominated on the drier sites, ridges, and plateaus. Others have related the moisture content of EA to site (Il'in 1970; Akhromeiko and Zhuravleva 1957). Pathology also was influential. Over the year pathologic wetwood had more water (142% ODW) than heartwood (106%) or sapwood (88%) (Knutson 1968); and Phellinus tremulae reduced the water content of sapwood (Federov 1969).

3. Stored Xylem Water and Transpiration

Water stored during the night may be important in supporting the next day's transpiration. No direct data exist, but Hart et al. (1969) observed continued water movement in stems during the dark period. Water storage in aspen stems, however, probably has little effect beyond one day. A 30% change in stem moisture by weight (average winter - average summer moisture) in a stand with 315 m^3/ha of xylem amounts to only 3 to 4 mm of water, or about one day's transpiration.

4. Summary

Water moves through xylem by the interlocked ascent pattern. The conductivity of the xylem of BTA decreased with branch order and was lowest at the junctions of branch to branch, or branch to petiole. Water contents of xylem and bark vary with vertical and horizontal position in the stem and with season. Although stored stem water is important in the daily pattern of transpiration, it is not a buffer against prolonged drought.

D. Water Loss From Leaves

The leaf surface is at once the site of evaporation, the major resistance to water flux through the SPAC, and the site where the plant regulates its water loss through stomatal closure. Research with aspens has quantified this resistance (r_d) to the diffusion of vapor from inside to outside the leaf and examined which factors influence the resistance.

Water loss occurs through both leaf surfaces; cuticular water loss from the upper surface accounted for 9% of daytime transpiration in mature leaves of EA (the author's interpretation of Antipov 1971) and 6% in mature leaves of TA growing on moist soils (Mital *et al.* 1978). This last figure is based on measured r_d's of 50 and 3 sec/cm for upper and lower leaf surfaces. Cuticular transpiration was higher (13%) early in the season (Antipov 1971). While these data suggest that water loss from the upper surface may be important in times of drought, the remaining literature and the remainder of this section examine r_d only for the leaf surfaces with stomates.

1. Distribution and Size of Stomates

Stomates occur only on the lower leaf surfaces (hypostomatic) of TA and BTA. EA from forest stands is also hypostomatic (Antipov 1971), but young plants may be amphistomatic (Holmgren *et al.* 1965). The size of stomates varied little within a species when plants were grown under similar conditions (Larsen 1956) (Table 4), but in EA size differed between diploids and autotriploids (Smilga and Jervekilga 1978). Density of stomates in TA varied considerably among reports (Table 4).

Table 4. Dimensions and density of stomates on abaxial leaf surface of aspens.

	Populus tremuloides	Populus tremula	Populus grandidentata	Author
Guard cell length (microns)	31.2 ± 3.5[a]	25.3 ± 1.9	20.8 ± 2.2	Larsen (1956)
	32	--	24	Tobiessen & Kana (1974)
Stomate length (microns)	17.9 ± 4.7[b]	--	--	Hart *et al.* (1969)
	8 to 36	--	--	R. S. Johnston (per. comm.)
Stomate width (microns)	4 and >4[b]	--	--	Hart *et al.* (1969)
	8≤	--	--	R. S. Johnston (per. comm.)
Number of stomates/mm^2 Primary, secondary leaves	12,17	--	--	Stephens *et al.* (1972)
Unspecified	168	--	222	Tobiessen & Kana (1974)
Mature leaves	90 ± 6	--	--	Rushin & Anderson (1981)
Mature leaves	106	--	--	Personal observation
Unspecified	--	133	--	Larsen (1956)

[a] ± standard deviation.

[b] The dimensions may refer to the pore size after fixation in formalin-acetic acid-ethanol.

2. Diurnal Pattern of r_d

The diurnal pattern of r_d in aspens is typical of mesophytes. The major events are a decrease in r_d at dawn and an increase with darkness (Kimmerer and Kozlowski 1981; Fluckiger *et al.* 1977). Values of r_d near midday were generally 2 to 4 sec/cm when the soil was moist (Table 5). The boundary layer resistance as determined from plate models was 0.59 for EA (Holmgren *et al.* 1965) and 0.47 for TA (Kimmerer and Kozlowski 1981).

Table 5. Diffusive resistance (r_d) of mature aspen leaves in daylight. Soil was probably moist unless otherwise specified.

Species	Conditions	Date	Time	Method	r_d (sec/cm)	Source
P. tremuloides	4 weeks without rain, upland mesic wet	July	late a.m.	Energy budget	2.5 to 3.1	Miller & Gates, 1967
	4 weeks without rain, upland mesic dry				4.0 to 5.0	
P. tremuloides	At 6 m in 8 m tree	May-Sept.	All day	Permanent cuvette[c]	2.6 to 14.0[c]	Kaufmann, 1982b
P. tremuloides	Warm, sunny	6 dates	midday	Porometer	3.0	Small, 1972
P. tremuloides	Primary leaves Secondary leaves	late July		Porometer	3.1 2.4	Stephens *et al.*, 1972
P. tremuloides	Sun, exposed leaves	June		Porometer	3.5[a]	Federer, 1976
P. tremuloides		6/13-7/12	midday	Porometer	3.5 ± (.16)[b]	Federer, 1977
P. tremuloides	Suckers, 2 to 4 m	8/11	0800-1700	Porometer	3 to 4	Mital *et al.*, 1978
P. tremuloides	Growth chamber, leaf plastochron index of 10		midday	Porometer	0.8 to 1.4	Kimmerer & Kozlowski, 1981
P. tremuloides	Field grown, full sun	July-Aug.	a.m.	Porometer	3.7	Rushin & Anderson, 1981
P. grandidentata	4 weeks without rain, upland dry	July	late a.m.	Energy budget	3 to 10	Miller & Gates, 1967
P. grandidentata		6/13-7/12	midday	Porometer	3.0[a]	Federer, 1977
P. tremula	Growth chamber, leaf just mature			Transpiration calcution	2.3	Holmgren *et al.*, 1965
P. tremula	Growth chamber, leaf just mature			Porometer	2.0	Fluckiger *et al.*, 1978a
	Growth chamber, leaf mature 75 days				5.0	
P. tremula	Growth chamber			Porometer	4.0	Fluckiger *et al.*, 1978b

[a] r_d normalized to 15 mbar vapor pressure gradient.

[b] ± 1 standard error.

[c] Highest values may be from dry soils

3. Sampling and Clonal Variation in r_d of TA

When soils were moist, the variation in r_d among and within TA was surprisingly low. In one experiment, when four to six leaves were sampled from each of six neighboring saplings, the author found coefficients of variation in r_d among TA saplings were less than 5% at each sampling time from early morning to dusk. The only position effect was that leaves on heavily shaded short shoots low in the crown had consistently higher r_d's. Coefficients of variation would have been higher had more clones been used. Clonal variation in diurnal pattern and daily extremes of r_d were documented in the growth chamber (Kimmerer and Kozlowski 1981).

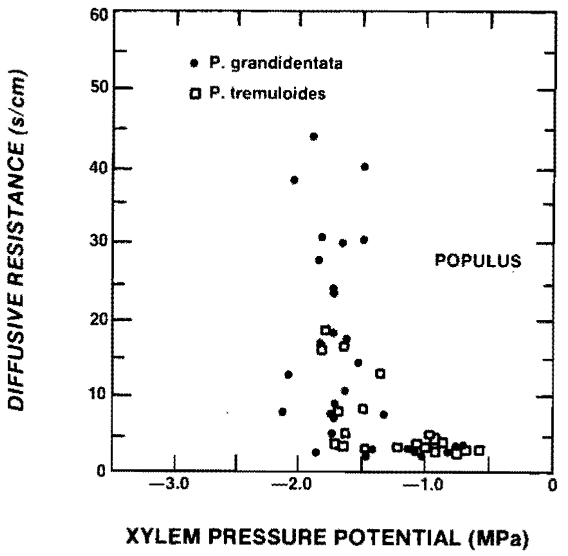

Figure 3. Diffusive resistance (normalized for vapor pressure gradient) and xylem water potential of trembling aspen and bigtooth aspen leaves, forest conditions (from Federer, 1977). (Courtesy of Society of American Foresters).

Federer (1977), sampling the upper crowns of BTA and TA under more varied conditions, found that the coefficients of variation within trees (four leaves/tree) were less than 20%. Coefficients were 5 to 15% for leaves within 2 m of the ground earlier in the year (Federer 1976). When the soils were dry, however, r_d was much more variable (Federer 1977; Tobiessen and Kana 1974; personal observations).

4. Changes in r_d With Leaf Age, Position, and Form

The r_d decreases during leaf development on forest trees of TA. The r_d was 5 to 7 sec/cm on leaves 3 cm long, 3.5 to 4 sec/cm near full elongation, and still lower several weeks later (Federer 1976; Federer and Gee 1974). Growth chamber seedlings behaved similarly and in addition showed high resistances in older leaves (Kimmerer and Kozlowski 1981; Fluckiger et al. 1977). Kaufmann (1982a, b, c), however, found r_d of TA was the same from leaf emergence to initial yellowing once the effects of photon flux and humidity had been removed.

In leaves on forest saplings, r_d varied less with position on a branch than with branch type. Toward the end of the simulated dry-down described in Section IID5, Mital et al. (1978) found that the leaves on short shoots (secondary branches with almost no internode between leaves) had three to four times higher r_d's than leaves on long shoots (primary or secondary branches with at least 1 cm between leaves).

Tree	Type of Shoot	Leaf Ψ (MPa)	r_d (sec/cm)	Leaves on Shoot
1	long	-3.9	13.5	wilting
	short	-3.0	38.0	unwilted
2	long	-3.6	11.5	wilting
	short	-3.5	47.7	unwilted

The higher r_d of the short shoots, if typical, suggests that trees with larger proportions of short shoots would be more drought resistant but might grow more slowly as the higher r_d also would limit CO_2 uptake. In fact, many genotypes of TA as they reach large size acquire larger proportions of short shoots.

Still other branch and leaf characteristics effect r_d. Leaves of TA which emerged after a defoliation had more stomates and lower r_d's than the leaves which escaped the defoliation (Stephens 1972). Leaves on young suckers or seedlings of EA may have different r_d's than leaves on mature plants (Jarvis and Jarvis 1963d). Kaufmann (1982) recently found that branches which will abscise in the autumn display unusual leaf r_d during July and August.

5. Effect of Environment on r_d

Light, soil moisture, vapor gradients, temperature, and wind influence the r_d of aspens.

Light and r_d. The stomates of aspens close rapidly in darkness and open rapidly on illumination; opening began within 7 to 15 minutes and was complete within 30 minutes for EA in a growth chamber (Jarvis and Jarvis 1963b). Stomates also close rapidly in darkness and the highest r_d in TA occurred soon after chamber lights were turned off; subsequently, throughout the dark period r_d gradually lessened to about half this maximum (Kimmerer and Kozlowski 1981). Most observers found relatively low r_d's during the dark period, suggesting either partially closed stomates and/or a permeable cuticle; e.g., r_d of EA was 11 sec/cm (Fluckiger 1978b), and r_d of TA was 8.2 sec/cm (personal observation in forest), and 3 to 10 sec/cm in a growth chamber, depending on clone (Kimmerer and Kozlowski 1981).

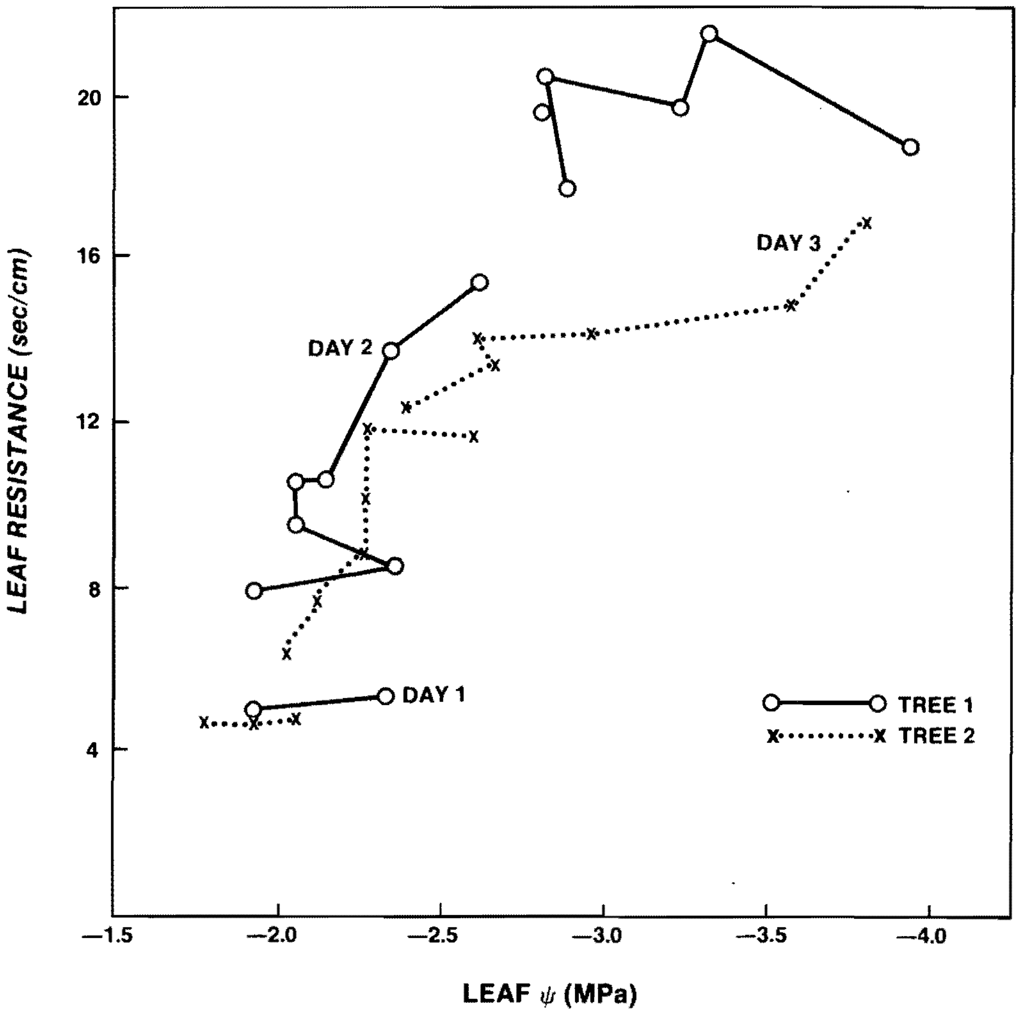

Figure 4. Course of r_d (on same leaves) and Ψ (on matching leaves) during the three days after a Populus tremuloides sapling was felled. About 85% of the leaves were removed immediately after felling.

Stomates of naturally growing TA and BTA followed an endogenous rhythm when kept in continuous darkness (Tobiessen 1982). In TA the opening and closing persisted at least into the third day. Kaufmann (1982a, b, c) was able to use photosynthetic flux as one of the two environmental variables which described r_d in TA. The equation is:

$$r_d^{-1} = b_1\,(\mathrm{PPFD})^{\frac{1}{2}}\,(\mathrm{DAH})^{-\frac{1}{2}} + b_2\,(\mathrm{PPFD})^{\frac{1}{2}}\,(\mathrm{DAH})^{-1} + b_3\,(\mathrm{PPFD})\,(\mathrm{DAH})^{-2}$$

where PPFD is the photosynthetic photon flux density and DAH is the absolute difference in humidity from leaf to air. The equation is based on hourly readings of one branch from late May into September, excluding the days following a freeze and hours with widely fluctuating PPFD.

Vapor Gradients

Federer (1977) like Kaufmann used vapor gradients between leaf and air to predict r_d in TA and also BTA. The equation for TA was:

$$r_d = 3.6 + 1.39\,(\mathrm{VPG} - 15) + 0.05\,(T - 25) \quad r^2 = 0.67$$

where VPG is the vapor pressure gradient between leaf and air in mb, and T is the air temperature in °C. Kaufmann (1982c) found no relation between r_d and temperature between 5 and 25C.

Leaves of EA were sensitive to relative humidity (RH) even after the stomates were "closed," and over a range of RH, EA leaves lost water more rapidly than did birch, spruce, or pine (Jarvis and Jarvis 1963d).

Wind, leaf quaking, r_d and r_a. Wind should increase transpiration by reducing the boundary layer resistance (r_a), and Hayden (1968) reports increased transpiration in BTA beginning at wind velocities of less than 0.02 m/sec. Stronger winds (5 to 6 m/sec) decreased r_d of EA, but only if sustained for at least 30 minutes (Fluckiger et al. 1978). Intermittent gusts of 1 second on EA or velocities sustained for 10 to 25 minutes on TA had no effect on r_d (Fluckiger et al. 1978; Rushin and Anderson 1981).

Related to wind is the quaking habit of aspen leaves. Enhancement of gas transfer is one proposed function of quaking, but theoretical and experimental evidence with other species suggests that quaking does not influence r_a in moderate winds (e.g., Grace 1978; Parlange et al. 1971). Consistent with this conclusion, Rushin and Anderson (1981) found r_d was the same with or without quaking at a wind of 5m/sec. However, the preliminary results of Hayden (1968) suggest that the effects of quaking on r_a at very low wind velocities still need investigation.

Soil moisture and r_d. As expected, r_d is higher when soils are dry. For example, in Figure 4 the low r_d's to the right are with soil Ψ's higher than -0.08MPa, while the high r_d's to the left occurred with soil Ψ's below 0.08MPa, perhaps -0.5 to -1.0 MPa (Federer 1977). Even nighttime transpiration was less when soils were drier (Jarvis and Jarvis 1963b).

6. Leaf Water Balance and r_d.

The relation of r_d to leaf Ψ or leaf RWC is of physiological interest and is needed for process models of ET (Sec. IIE). For TA, response curves between r_d and leaf Ψ were developed under natural drought (Federer 1977) and induced drought (Tobiessen and Kana 1974; Mital et al. 1978). Mital et al. (1978) felled two 4-m saplings at ground-line, removed 85% of the living branches, and immediately placed the trees in uniform shade at 8% of full sunlight. The r_d and leaf Ψ were monitored for three warm cloudless days.

According to Federer (1977), the stomates of TA remained open until leaf Ψ reached -1.3 to -1.8 MPa, at which values they abruptly closed (Figure 3). Mital et al. (1978) found rapid closure as leaf Ψ increased from -1.8 to -2.2 MPa and a slower but continued increase in r_d to leaf Ψ of -3 MPa (Figure 4). Tobiessen and Kana (1974) found instead of closure at a critical leaf Ψ, a continual increase in r_d as leaf Ψ decreased to -6 MPa (Figure 5). Kaufmann (1982a) observed higher r_d at a leaf Ψ at -2.2 MPa than at -1.5 to -1.7 MPa. If stomates close near zero turgor, the results of Eubanks (1969) and Rakhi (1978) are consistent with the values at closure suggested by Federer (1977) and Mital et al. (1978). The critical leaf Ψ were -1.6 to -2.3 MPa in TA (Table 6) and -1.9 MPa in EA. The gradual increase in r_d with increases in Ψ found by Tobiessen and Kana (1974) could have occurred because of the artificially rapid drying and resultant supression of abscissic acid production, increased hydropassive stomatal opening, cavitation of stem water and/or dying of intercostal mesophyll. When Tobiessen and Kana's data are fitted with a boundary curve (Figure 7) stomatal closure occurs abruptly at leaf Ψ of -3 MPa.

BTA stomates closed abruptly at a leaf Ψ of -1.3 to -1.8 MPa according to Federer (1977). Tobiessen and Kana (1974) also found that stomates of BTA closed fairly abruptly, at leaf Ψ's of -2.8 to -3.2 MPa, using mean values or -2 MPa with a boundary curve. The lower values may reflect a lag between water loss and stomatal closure in these rapidly drying leaves. Both studies agree that in severe deficits BTA developed higher r_d's than TA, 30 to 45 sec/cm for BTA but only 20 sec/cm for TA.

In EA the relation between RWC, leaf Ψ, and r_d varied with growth media and leaf form (Jarvis and Jarvis 1963d). Stomates of leaves (round petioled) on seedlings closed sharply at an RWC of 90%; the r_d on adult trees gradually and continually increased as the leaf dried.

7. Summary

Stomates occur only on the lower surface of TA and BTA. EA can be either hypostomous or amphistomous. Most transpiration is stomatal although the upper leaf surface can account for 6 to 9% of total daytime transpiration. Midday r_d's are about 2 to 4 sec/cm on moist soils and much higher on dry soils. Midday r_d can also be increased by a high VPG and sustained wind. Stomates open and shut rapidly in response to light and dark. However, the r_d of EA and TA remains moderate at night or during water stress reflecting high cuticular permeability or incomplete stomatal closure. Stomates on individually bagged branches may continue to follow a circadian rhythm in complete darkness. Stomates probably close abruptly at a critical leaf water deficit, although some experiments suggest gradual and continual closure.

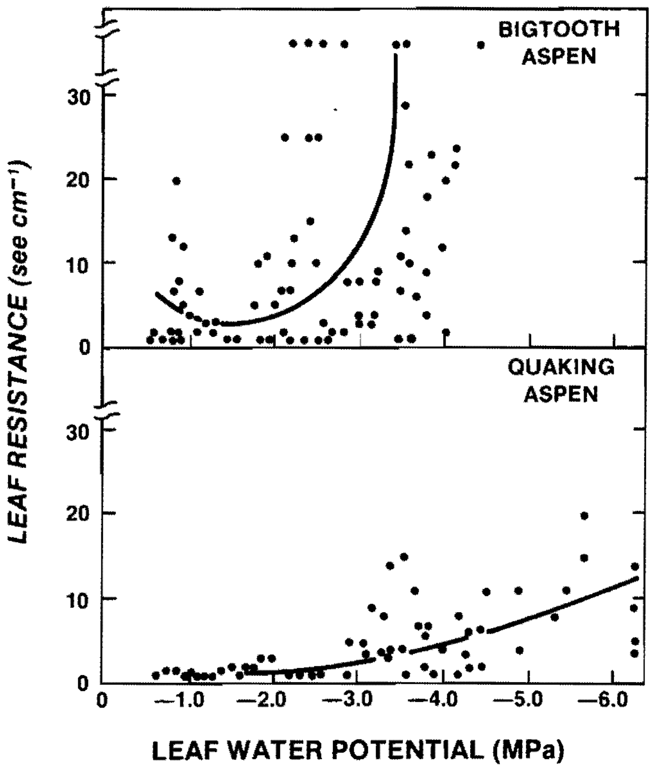

Figure 5. Diffusive leaf resistance and leaf water potential in bigtooth and trembling aspen. Data from leaves on cut branches in potometers (from Tobiessen and Kana 1974). (Courtesy of Ecological Society of America.)

Table 6. Leaf water status and size of P. tremuloides as related to concentration of polyethylene glycol in hydroponic media (after Eubanks 1969).

Approximate Ψ_s of Media	3600 foot candles			Plant Dry Weight[a]
	Leaf Ψ^b	Leaf Ψ_s^b	Leaf Ψ_p^b	
(MPa)	(MPa)	(MPa)	(MPa)	(g)
-0.5	-1.14	-1.74	-.60	4.4
-2.8	-1.34	-1.98	-.64	4.0
-5.1	-1.65	-1.98	-.33	4.0
-7.4	-1.89	-2.05	-.16	3.8
-9	-2.09	-2.13	-.04	3.0
-14.7	-2.28	-2.12	-.16	2.6

[a] Includes unspecified weight at start of experiment.

[b] Approximate values because of limits in methodology.

E. Modeling Evapotranspiration

The ET or transpiration of TA has been modeled by Leaf and Brink (1973, 1975) using EVTRAN; by Jaynes (1978) using APSCON; by Troendle and Leaf (1980) using PROSPER (Goldstein et al. 1974); and by Mital and Sucoff (in press) using the simple water budget, the Zahner model (Zahner 1967), SOGGY (Grigal and Hubbard 1971), and THIRSTY (original). Of these models, only PROSPER employs process-derived measures of plant and canopy resistance. The closeness of the predictions was documented only by Mital and Sucoff (in press) although Troendle and Leaf (1980) report that the PROSPER calibration of the annual balance was "fairly good" for a Minnesota watershed containing TA. A major difficulty in all these models was the selection and verification of an empirical or theoretical measure of plant and canopy resistance to water transfer.

F. Hydrologic Cycle

The SPAC system provides the transpiration term in the hydrologic cycle, and when modeling SPAC for forests, other parts of the water budget must also be considered. This review, however, did not intentionally search for all literature on the hydrology of aspen stands. Selected hydrology literature is listed in Table 7 categorized by forest type, location, and components of the hydrologic cycle. Additional references are available in Leaf and Brink (1973, 1975), Leaf and Troendle (1980), Rauner (1976, 1977) and Jaynes (1978).

Table 7. Articles on the hydrology of the aspens categorized by location and component of the hydrologic cycle.

		Hydrologic Component					
Vegetation	Location	Soil moisture	Interception Stem Flow	Runoff	Evapotranspiration	Stream Flow	Authors
Populus tremuloides	Utah	x			x		Johnston & Doty (1969)
	Utah	x			x		Johnston (1969, 1970)
	Utah	x			x		Tew (1967)
	Utah	x	x	x		x	Croft & Monniger (1953)
	Utah			x	x		Marston (1958, 1966)
	Utah	x					Hart *et al*. (1969)
	Utah		x				Johnston (1971)
	Colorado	x			x		Brown & Thompson (1965)
	Colorado					x	Bates & Henry (1928)
	Colorado		x				Dunford & Niederhall (1944)
	New Mexico		x				Gary (1972)
	Minnesota	x			x		Mital & Sucoff (in press)
	Minnesota		x				Verry & Timmons (1977)
	Minnesota		x	x		x	Verry (1972)
	Minnesota		x				Verry (1976)
	Michigan				x		Miller & Gates (1967)
Populus Grandidentata	Ontario		x				Clements (1971a, b, c; 1972)
Populus tremula	USSR	x		x	x		Smirnov & O'dinokova (1954)
	USSR		x				Rhamanov (1958)
	USSR				x		Bocharov (1976)
	USSR				x		Rauner (1976, 1977)

III. EXPERIMENTAL DETERMINATION OF WATER IN PLANT CELLS

The preceding section described the uptake, internal transport, and loss of water by aspens. This section summarizes research on the status of water in the aspens. Two representations of water status have been used. The first gives the chemical potential of water for tissues, cells, or parts of cells.

$$\Psi_{plant} = \Psi_s + \Psi_p + \Psi_m \quad \text{(Slatyer 1967)}$$

where s, p, and m refer to solute, turgor, and matric potentials. The second characterizes the water content, with the measure relative water content (RWC), defined as:

$$RWC = \frac{\text{Fresh weight} - \text{Dry weight}}{\text{Turgid weight} - \text{Dry weight}} \times 100 \quad \text{(Slatyer 1967)}$$

The research has focused on measuring leaf Ψ or leaf RWC and relating leaf Ψ or RWC to soil moisture and plant behavior. The relation of water status to behavior is discussed in Secs. IID6, IVB3, and VA1.

A. Leaf Ψ on Moist and Dry Soils

Leaf Ψ in TA (Brown and McDonough 1977; Mital et al. 1978) and in EA (Fluckiger et al. 1977) share the diurnal pattern (Figure 6) common to other mesic species. Leaf Ψ progressively declines after dawn as stomates open and evaporative demand increases, while with darkness leaf Ψ increases abruptly as the two processes reverse. In a dry-down study using 2-year-old TA in 10-inch pots, Brown and McDonough (1977) showed that both dark and daytime leaf Ψ decreased as soil Ψ_m decreased (Figure 6). The results resemble those of other species (e.g., Gardner and Nieman 1964) except that the nighttime differences between leaf Ψ and soil Ψ were much higher in TA. The larger-than-usual difference could result from the psychrometric technique or from high nighttime transpiration (Sec. IID5). The author replotted the data from Figure 6 and found that soil Ψ, leaf Ψ at dawn, and leaf Ψ at midday are linearly related to each other (Figure 7). Such estimations are useful in models of SPAC and growth.

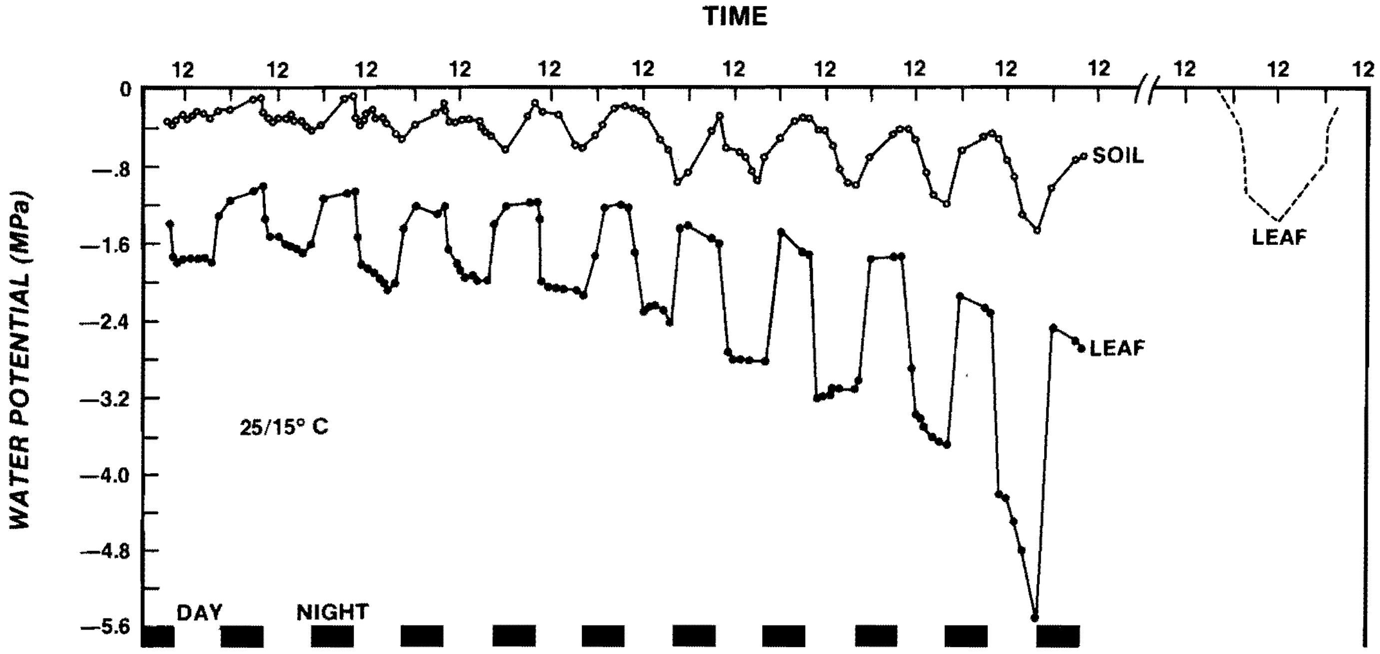

Figure 6. Diurnal soil Ψ_m and leaf Ψ of Populus tremuloides in controlled conditions (Brown and McDonough, 1978) and leaf Ψ on forest saplings on a clear day in Minnesota (Mital et al. 1978). Brown and McDonough measured leaf Ψ with in situ thermocouple psychrometers while Mital et al. used a Scholander type pressure chamber. (Courtesy of Plant and Soil.)

Jarvis and Jarvis (1963d, 1965) determined leaf RWC and leaf Ψ for EA growing under four soil moisture regimes (Table 2) or three hydroponic media Ψs. When the media Ψs was reduced to -0.32 MPa, leaf Ψ (both day and night) dropped about 1 MPa, a much larger decrease than necessary to maintain the soil to leaf gradient (Jarvis and Jarvis 1965), in the absence of stem resistance.

Media Ψs (MPa)	Leaf Ψ (MPa)	Leaf RWC
-0.05	-0.1 to -0.3	99
-0.32	-1.2 to -1.3	93

Eubanks (1969, 1971), using hydroponics with TA (Table 6), also found that daytime leaf Ψ was lower when media Ψ was lower, but he did not find the large drop in leaf Ψ noted by Jarvis and Jarvis (1965).

Unfortunately, this information obtained in the growth chamber cannot be transferred to the forest. First values of media Ψ in small pots or solutions are not equivalent to values of bulk soil obtained in field measurements; root density, hydraulic conductivity, and soil moisture diffusivity differ. Further, in the forest the rapidly changing radiation and humidity alter leaf Ψ independently of soil moisture. Finally, small plants have a different frictional potential and a lower buffering capacity.

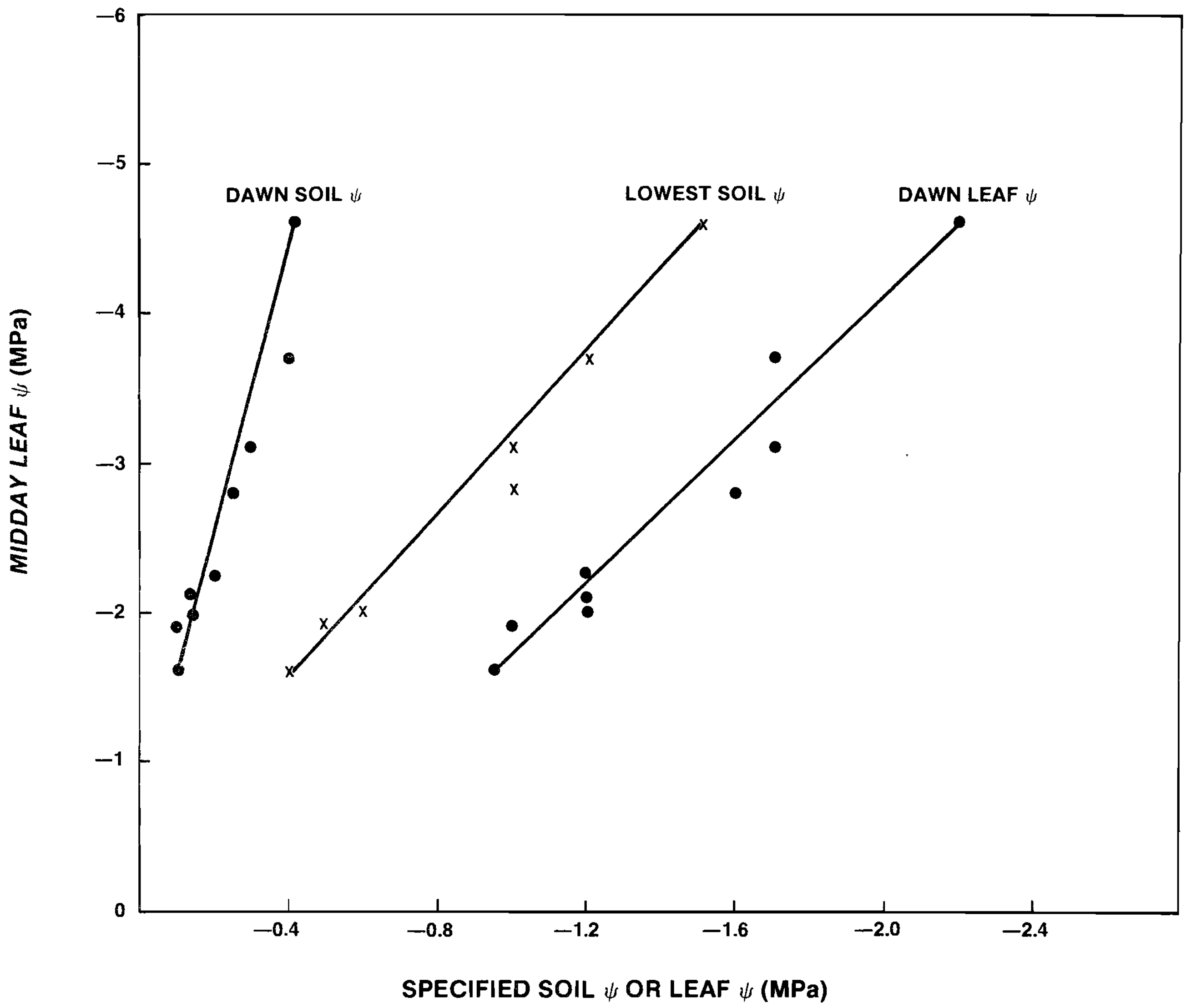

Figure 7. The relation of leaf Ψ at midday to leaf Ψ at dawn or soil Ψ at dawn or lowest daily soil Ψ. Data are from Brown and McDonough, 1978 (Figure 6).

To date, Federer (1977) has most completely related leaf Ψ to soil Ψ_m in natural settings; the lower leaf Ψ's in Figure 4 are associated with soil Ψ's at an unknown level below -0.08 MPa. During the driest period in Figure 4, the leaves of BTA lost greenness and many BTA lost leaves from their lower branches; TA was not as affected (Federer, personal communication). Exposed leaves of TA contorted when predawn leaf Ψ was -1.5 MPa (Tobiessen and Kana 1974).

B. Variation in Leaf Ψ at a Sampling Time

The author explored within and among tree variation of leaf Ψ for TA, measuring individual leaves in a pressure chamber. Three trees 2 to 3 m tall were analyzed one day and six similar trees on another day. Based on 19 leaves collected from three trees with two to three branches per tree, coefficients of variation in Ψ were 28 to 31% between 0900 and 1400, and 17 to 25% earlier and later in the day. The standard errors were 0.12 MPa or less. Differences in Ψ between two leaves on the same long shoot averaged 0.26 ± 0.17 MPa or 26% of the higher Ψ.

The largest and most consistent difference was between leaf Ψ on long shoots and short shoots. On the same TA tree, between 1200 and 1600 hours, leaf Ψ on short shoots averaged as much as 1.1 MPa lower. These results differ from those in the simulated dry-down of TA (Sec. IID5), where leaf Ψ was similar on long and short shoots. The difference between long and short shoots may be related to xylem conductance (Sec. IIC1).

Changes in stem Ψ over very short periods were noted by Hayden (1968) who implanted small plaster-encoated resistors into the branches of BTA saplings. The stem Ψ responded within 15 seconds to wind changes of less than 0.02 m/sec, and within 1 minute to abrupt increase in radiation.

C. Leaf Ψs

Eubanks (1969, 1971) using rough quantitative methods examined leaf Ψs of TA seedlings grown in 18 environments, six levels of polyethylene glycol in solution at each of three light intensities (Table 6). As the measurements were made during the light period, leaf Ψs near full turgor is unknown. Leaf Ψs was higher in shade-grown plants, which may indicate that shaded leaves in the forest would be poorer competitors for water. Although leaf Ψs was lowered as media Ψs decreased from -0.05 to -1.5 MPa, the maximum decrease was only 0.4 MPa, assuming constant RWC.

Rakhi et al. (1978) measured Ψs of several EA leaves with pressure-volume curves. The Ψs at zero turgor was -1.9 MPa; and at full turgor, -1.7 MPa. Thirteen percent of total plant water was lost between full and zero turgor. Using refractometry, Scheumann (1965) determined that the cell sap expressed from EA leaves on optimum soil moisture was 20.8 "dry substance percent" and the sap from droughted leaves near death was 31.1%.

D. Summary

The components of leaf water status respond to environment as would be anticipated from studies with other species. Leaf Ψ follows the normal diurnal curve. Leaf Ψ, leaf Ψs, and RWC decrease as media Ψ decreases. Visible drought damage to leaves occurs at predawn leaf Ψ of -1.5 MPa or midday leaf Ψ near -2.0 MPa. Leaf Ψ at a sampling time may vary by 0.1 MPa within and among neighboring saplings. Leaves on short shoots can display a very different water balance than leaves on long shoots. Little is known about Ψs and Ψp.

IV. PLANT RESPONSES TO WATER DEFICITS

This section is divided into five parts, the first three of which examine direct responses to water deficits. The fourth part examines the water factor in site quality and the fifth the response of aspens to dry situations.

A. Specific Physiologic Processes

The physiology of any plant can be profoundly altered by water deficits, but little is known specifically for aspens. As already discussed, leaf water deficits control stomatal aperture and in turn the resistance to CO_2 uptake and photosynthetic rate (Holmgren et al. 1965; Laisk and Oja 1971). Jarvis and Jarvis (1963a) found that net assimilation rate was reduced about 20% in moderately dry soil (Treatment D, Table 2). In other research Jarvis and Jarvis (1965) noted for EA that root respiration decreased as the Ψs in the bathing media dropped from -0.05 to -1.4 MPa.

B. Growth and Water Deficits

The relation of aspen growth to water deficits has been examined in four types of studies which are listed below and then discussed in more detail.

(1) Forest studies correlating growth to soil moisture, climate. In these studies, climate is statistically related to growth obtained by periodic measurements or by stem analysis.

(2) Field irrigation studies.

(3) Controlled environment studies. In most of these, seedlings are grown at various levels of soil moisture with all other factors nonlimiting. In these environments, where genetic nutrient, temperature, and disease variables are controlled, very close relations between growth and water can be established.

(4) Studies correlating growth with transpiration.

1. Forest growth, climate, soil moisture, and tissue water.

The quantification of the moisture factor in the growth of aspen stands has been blocked by the lack of plots with long-term growth, mortality, and climatic records. Using one of the better data sets, Perala (1978) correlated growth from eight 5-year periods on seven thinning plots with concurrent soil moisture. Average monthly soil moisture was reconstructed from soil properties and historic records of climate. His prediction equation for basal area growth was improved by including the variable $M(\mathrm{lnF})_{\mathrm{june}} + M(\mathrm{lnF})_{\mathrm{july}}$ where M is the monthly available water over the 5 years and F is $\frac{\text{temperature} - 50}{10}$. M by itself did not improve the fit. Perala (1978) then selected the best, average, and worst 5-year climate and grew the stands for 40 years at each of these three regimes with other variables held constant. Basal area growth in the best climate was almost twice that in the average and worst climates. The higher growth would not occur in nature (Perala 1978) if only because it would lead to higher mortality than predicted.

Taking a simpler approach, Duncan and Hodson (1958) examined 10 years of annual growth on 77 sites. They found a positive correlation between diameter growth of dominant TA and April through July rainfall. Growth in the wettest year (24 inches) was about 35% more than that in the driest year (8 inches). Kazadaev (1974) noted a similar reduction (41%) in diameter growth of EA as a result of two consecutive drought years. In contrast, Fraser (1959) over a 5-year period found no relation between radial growth of TA and rainfall. Qualitative evaluations of the effects of drought on aspens relative to other species indicated that growth of EA was less affected than that of balsam poplars (Belgium 1977) and more affected than that of *Quercus robur*, *Betula verrucosa* (Kazadaev 1974), *Pinus sylvestris*, *Fraxinus excelsior*, or *Tilia cordata* (Raskatov and Eremin 1973). BTA was less affected by drought than such nominally drought-hardy species as *Quercus macrocarpa* and *Pinus banksiana* (USDA 1931).

Data relating growth reductions to tissue water balance are unavailable for forest conditions unless the leaf Ψ's at which stomates close are used to indicate reduced photosynthesis. In that case, leaf Ψ's below 1.3 to 1.8 MPa are associated with reduced photosynthesis in TA and BTA (Federer 1977).

2. Irrigation

Murphey and Bowier (1975) applied effluent to a TA stand with trees 6 to 20 years old. During the 10-year period, 20 m of water, 1,500 kg of N, 280 kg of K, 335 kg of P, 1,075 kg of Ca, and 450 kg of Mg and unspecified quantities of micronutrients were sprayed on each ha. Based on measurements of 12 trees of similar dbh at harvest (25 to 32 cm), it was concluded that treatment more than doubled volume growth per tree, increased fiber length about 20% and did not change specific gravity. The effects of water and fertilizer cannot be separated in this study, but the research discussed next indicates that water could have been an important contributor to the increased growth.

Einspahr and Wyckoff (1978) and Einspahr *et al*. (1972) irrigated and/or fertilized native aspen stands growing on a Vilas fine sand, an unproductive site. The irrigation was timed to keep the soil from dropping below 60% of field capacity, which probably means the soil Ψ was still above -0.1 MPa. This required 8 to 23 cm of water per year. The fertilizer was given in two applications each of 1,120 kg per ha of N_{20} P_5 K_{20} Ca_{20} Mg_{20}. The researchers concluded that young aspen sucker stands growing on low quality upland sands and averaging about 3 m^3/ha/year increased their growth about 35% from fertilization, 50 to 80% from irrigation and 100-150% from irrigation plus fertilization (Table 8). Irrigation increased fiber length 10%, but had little effect on specific gravity and the vessel to fiber ratio. The response to irrigation appears greater in stands 7 to 13 years old than in stands 1 to 7 years old.

3. Controlled Environment Studies

Results from three studies agree that moderate moisture deficits reduce short-term growth of aspen seedlings by 10 to 25% and severe deficits reduce growth still more. As already discussed, these results cannot be transferred to the forest with anticipation that similar growth reductions will occur at the same media Ψ.

In one experiment with TA, several concentrations of polyethylene glycol were added to nutrient solutions (Eubanks 1969, 1971). Approximate weight growth over the next 16 days was reduced 15% at -.3 MPa and between 25 and 50% at -1.5 MPa (Table 6. The reduced growth was associated with lower Ψ, Ψs and Ψp (Table 2). In a similar experiment, Jarvis and Jarvis (1965) compared EA seedlings grown for 12 days on hydroponic media of -0.05, -0.22 and -0.32 MPa. Net assimilation rate, relative growth rate, and leaf number did not vary with treatment, but the area of individual leaves was progressively

Table 8. Growth response of P. tremuloides sucker stands to fertilization and irrigation (after Einspahr and Wyckoff 1978).

Treatment	No. of Trees/ha	Height Growth[a]	Volume[a]	Volume Growth
		(m)	m^3/ha	m^3
	Growth from ages 1 through 7			
Control	12,800	4.7a	20a	8a
Fertilizer (F)	13,800	5.3c	32b	16b
Irrigation (I)	14,400	5.0b	25ab	12ab
F and I	12,700	5.4c	34b	18b
	Growth from ages 7 through 13			
Control	11,200c	5.2a	32a	4a
Fertilizer (F)	9,400b	5.9b	40a	9ab
Irrigation (I)	11,600c	5.9b	51ab	10ab
F and I	7,800a	7.0c	65b	15b

[a] Means within a column within a trial followed by the same letter are not significantly different.

reduced from 13.1 cm^2 at -0.05 MPa to 8.2 cm^2 at -.32 MPa. The coincident change in the relative water content of the leaves was from 97 to 93%. In contrast to the leaves, roots grew as fast or faster at lower media Ψ. The results suggest that moisture deficits would be critical during leaf expansion in older trees since almost all leaves enlarge within a 3-week period.

Jarvis and Jarvis (1963a) found a 23% reduction in the relative growth rate on soils cycling from field capacity to -0.5 MPa (Table 2). Net assimilation rate and leaf area were also reduced. The shoot:root ratio was higher at lower soil Ψ, a result contrary to the findings in hydroponics (Jarvis and Jarvis 1965; Eubanks 1969).

4. Growth and Transpiration

In many agronomic crops, especially within a site, transpiration is directly related to dry matter production. Just such a relationship was found between transpiration and current annual volume increment among four EA stands 8, 25, 37, and 63 years old (Smirnov and Odinokova 1954), but age and transpiration may have been confounded. Jarvis and Jarvis (1963a) found no strong relation between transpiration and 20-day growth for EA, but growth was too little to expect one.

Eidman (1943) calculated that EA consumed more water (5.8 g/day) per gram of growth than most other species, and Holmgren et al., using entirely different techniques, showed that the instantaneous water use efficiency of EA was relatively low. He divided the sum of air and leaf resistances to vapor transfer by the sum of air, leaf and mesophyll resistances to CO_2 transfer. Betula verrucosa and EA had ratios of about 0.21 compared to 0.34 for Quercus robur and Acer platanoides.

5. Summary

In forest conditions, aspens grow more when moisture is favorable. One model predicts a doubling of growth with sustained favorable soil moisture and air temperature compared to periods of average climate. Irrigation, when applied to keep the available water content of a sandy soil at 60% or higher, increases growth 50 to 80%. Fertilization plus irrigation approximately doubles the increase obtained with irrigation alone.

Pot studies indicate that when soil Ψ averages -0.3 MPa and cycles between -0.01 and -0.5 MPa, growth will be reduced about 23%. Modest growth reductions occur in hydroponic solutions with media Ψs of -0.3 MPa. However, the growth reductions associated with low values of soil Ψ in the forest remain unknown. Nor is it yet possible to associate forest measurements of leaf Ψ or RWC with specific reductions in growth.

C. Mortality and Water Deficits

No one has reported direct drought kill of entire stands or even small groups of trees, although several papers relate natural thinning to moisture. Taking an overview, Graham et al. (1963) suggested that moisture deficits interacting with pests accounted for the wave-like pattern of mortality in precommercial aspen stands on light soils in Michigan. They suggest that as the stand develops, the increasing foliage area increases transpiration to the limit of available water. As a result, natural thinning occurs and a period of rapid growth ensues until water again becomes critically limiting. This natural thinning, according to Graham et al. (1963) depends in part upon insects and diseases, specifically leafhoppers, leaf diseases, aphids, and root Agrilus in younger stands and Saperda, Agrilus, other borers, and Hypoxylon cankers in older stands. At least three reasons have been offered by various authors to explain why pests induce more mortality during dry periods. It is proposed that the same amount of damage is more destructive when the tree is already stressed, that pest invasions are often more successful when the tree is growing slowly (Sec. VB2), and that weather can directly affect the pathogen or insect.

The wave-like pattern complicates simple statistical correlation between mortality and climate. For example, mortality might be reduced during a moist period, leaving the stand overstocked and subject to abnormally high mortality during an ensuing period of average precipitation. Despite these problems, Perala (1978) very cautiously noted a relation between current mortality and lnM/F for June and July of earlier years. M and F were previously described (Sec. IVB1).

Heavy mortality are also observed as mature TA stands decline over a 3- to 8-year period in Wisconsin and Michigan (Graham _et al_. 1963; Fralish 1972). While a role of dry soil or increased exposure of residual crowns may be proposed as contributors to this rapid decline, data are lacking.

D. Water as a Factor in Site Quality for TA

The importance of water to the distribution and productivity of aspens has been long and repeatedly emphasized (Heinselman and Zasada 1955), and while much can be learned by focusing on water alone, neither the water regime nor its contribution to productivity can truly be isolated from other factors. For example, soil texture, which is used to assess soil water-holding capacity, also determines the cation exchange capacity.

1. Early Statements on Water and TA Site Quality

Early evaluations of site quality were based on visual observations of where TA occurred and grew well (Weigle and Frothingham 1911; Kittredge and Gevorkiantz 1929; Gates 1930; Moss 1932). Baker's (1925) study provides an outstanding example. He noted that altitudinal distribution varied with moisture in the central Rocky Mountain region. Aspen reached its lowest altitudinal limit as a scrubby tree along creeks in the chaparral and ponderosa pine types. At higher elevations, it spread out along the creek banks and into moist pockets; in the Douglas-fir zone, it spread further to the flats and moist slopes. Baker also described aspen "islands" on dry hillsides where long, horizontal patches of aspen marked the occurrence of water-bearing strata beneath the surface. The best aspen sites had "plentiful moisture," while on dry sates growth was poor and decay occurred early.

In total, the early studies suggested that aspen is a moisture-demanding species which can survive on drier sites only with significant loss of growth.

2. Factors Influencing Site Quality (1935-1960)

The relation of water to aspen site quality was confirmed from 1935 to 1960 with studies showing that productive sites generally had soil properties associated with favorable moisture conditions: high organic matter, moderately high silt plus clay, and an appropriately high water table. These results form the basis for current management guides (Perala 1977).

Among the first and best studies of this type was that of Kittredge (1938) involving 277 field plots in Wisconsin and Minnesota. He related TA site quality to (1) soil texture groups, (2) surface geological formation groups, (3) combined texture and geological formation groups, (4) soil profile groups, and (5) associated vegetation.

In general, soils of moderate texture were the most productive. Among geological formations, dry outwash and impermeable lake-bed clays were the worst and moderately heavy morainic and till soils the best. However, the highest correlations were with soil profiles grouped by such moisture-related properties as the thickness of the A_2 horizon, presence of gleying, and the texture and water-holding capacity of the C horizon. The least productive profile groups had properties associated with dry soils. The profiles with highest average site indexes entailed mesic or hydromesic soil conditions. The correlation coefficients in this and subsequent studies are lowered by the high genetic variation of aspens, e.g., a slow-growing clone may be the only genotype on a good site (Zahner and Crawford 1965).

The importance of ground water and soil organic matter on aspen site relations was investigated by Wilde and Pronin (1950) on infertile gley sands of central Wisconsin. On such soils, site index improved as the organic matter in the upper 18 cm increased from 1.5 to 4.5%. Stoeckeler (1948) also stressed the importance of organic matter and in particular its destruction by fire. Following fire, site index on sandy soils was reduced as much as 17 feet (5.2 m) in part through a loss in moisture-holding capacity.

Wilde and Pronin (1950) also found that site index improved with increasing depth to water table from 40 to 80 cm, but then decreased for depths below 80 cm. Not only the correct depth to water table but also lateral movement of the subsurface water were considered favorable for BTA (Graham and Harrison

1955) and TA (Graham et al. 1963) on sandy soils in lower Michigan. An impermeable layer 45 to 150 cm from the surface encouraged lateral movement and improved site index. More shallow impermeable layers, particularly those within 30 cm of the surface resulted in sites as poor as deeply drained coarse sands. Shallow layers were barriers to water percolation and root penetration, causing superficial water during high rainfall and rendering deeper soil water unavailable. The best aspen sites included the margins of seepages where even superficial water was moving.

In an extensive study, Stoeckeler (1960) related soil properties to site index in well stocked even-aged TA stands in northern Minnesota and Wisconsin. The best regression coefficients were with the moisture-related properties of texture ($r = 0.70$ to 0.89) and moisture equivalent ($r = 0.66$). Stoeckeler concluded that aspen grows best on well drained loams to silt loams with 55 to 60% silt plus clay content in the A and B horizons. The poorest sites were sands with less than 15% silt plus clay content. Stoeckeler also concluded that optimum depths to water table of 1.2 to 1.8 m improved site index on sands by 10 feet, on loamy sands by 7 feet, and on sandy loams by 5 feet. On finer soils, a high water table either had no effect or was detrimental to growth.

Textural discontinuities also affected productivity. Coarse gravel at a depth of 60 cm beneath sands or loams reduced site index by as much as 20 feet, while heavier textures beneath sands raised site index by up to 12 feet (Stoeckeler 1960). Hannah and Zahner (1970) also found that the site index of BTA on sands was raised from 46 to 60 by pedogenic bands and to 71 by till-like lenses.

3. Site Quality Modeling (1961-1981)

The new effort since 1960 has been quantitative modeling of site productivity using more than soil properties. In the central Rocky Mountain region, Jones (1971) modeled the environment as a geometric space defined by three ordinates; temperature (heat sums), nutrients, and moisture. The moisture factor was complex, incorporating into a single value monthly precipitation, monthly mean temperatures, potential direct-beam insolation, water-holding capacity of the soil, and factors influencing runoff. When tested on 57 plots in diverse aspen habitats, the model accounted for 30% of the variation in site index.

More recently in the same region, Roise and Betters (1981) examined the effect of aspect and elevation on TA. They assumed that moisture was a function of ambient and solar radiation which in turn could be calculated from elevation and aspect. The model described the occurrence of TA, but was not tested with growth. Occurrence of TA was also studied using ordination based on ecologic preference of associated species (Bakuzis and Kurmis 1978). TA was found in all moisture conditions in Minnesota except the wettest but was most common on moderately moist to moist sites.

Working in Wisconsin, Fralish (1972) and Fralish and Loucks (1967, 1975) studied both the supply and demand aspects of moisture. They concluded that site index is largely controlled by availability of water, and the following regression model is typical of their findings:

$$SI = 74.83 + 2.48\ AWC - 0.09\ WTD + 1.51\ Exposure, \quad r^2 = 0.62$$

SI is site index of TA at age 50 in feet; WTD is water table depth; Exposure is based on a rating system from 1 (exposed) to 5 (sheltered) and depends on aspect and topographic position; and AWC is available water-holding capacity (inches) to a 12-inch depth. Among individual factors, site index was most strongly correlated with exposure, which indicates the importance of considering evaporative demand in site-moisture relations. Their models seem effective and deserve testing in a broader range of situations.

4. Summary

TA is found on a wide variety of moisture conditions, but grows well only in mesic situations. TA grows well on soils of moderate texture and best with a 55-65% silt-plus-clay content. Growth on sands improves with percent soil organic matter. These effects can be partly attributed to high soil water-holding capacity. Shallow water tables improve site index appreciably on coarse-textured soils, but on fine soils, shallow water tables may reduce site index. Subsurface gravel layers under sands or loams may reduce site index while heavier soils under sands increase site index. Productivity of TA sites can be better predicted if evaporative demand is considered along with soil moisture properties.

E. Response to Dry Situations

As indicated in the previous section, TA occurs in many moisture conditions, but quality stems occur and grow rapidly only on mesic sites. BTA has a narrower geographic and ecological range than TA. In Michigan it is considered the more mesic species (Graham *et al*. 1963), while in Minnesota it is the more xeric (Bakuzis and Kurmis 1978).

The individual aspen leaf loses water more rapidly than many other temperate trees; this helps explain why growth is best on mesic sites. When water is plentiful, the transpiration rate is higher and the water use efficiency lower (Sec. IIA5 and IVA4). When the soil dries, the stomates close at a modest leaf Ψ (Sec. IIA5), but Jarvis and Jarvis (1963d) suggest that a relatively large amount of water can be lost before leaf Ψ (EA seedlings) drops. This last observation needs verification (Rakhi 1978). Even when the stomates are presumed shut, the r_d of the lower leaf surface of TA remains low, about half that of *Betula populifolia*, *Quercus coccinea*, *Q. alba*, *Populus grandidentata*, and *Prunus* spp. (Federer 1977). EA also maintained a low r_d when stressed; detached leaves with severe water deficits transpired at 20% the rate of detached leaves kept turgid (Jarvis and Jarvis 1963d). These EA leaves with closed stomates lost water faster than similar leaves of *Pinus sylvestris*, *Picea abies*, or *Betula verrucosa*.

The nighttime transpiration of TA and EA was high: 12 to 25% of daytime in EA (Jarvis and Jarvis 1963b) and 15 to 30% of daytime in TA (from curves of Kimmerer and Kozlowski 1981; Mital *et al*. 1978; Tobiessen, personal correspondence). As an aside, the author suggests that when factors in the water balance are marginal, the customary occurrence or absence of nighttime dew and saturation humidities could determine the presence or absence of TA and EA. Dew and high humidities would limit noctural transpiration.

Despite their high transpiration rates, aspens commonly occupy moderately dry sites. Many adaptations are involved. Most important is their ability to regenerate and spread from root suckers. The young stems use the root system of existing or recently detopped mature trees and therefore have very high root:shoot ratios. This permits most generations of the species to bypass the seedling stage when plants are most susceptible to drought. Since seed is usually available, initial establishment on a dry site could occur during those rare years when site disturbance and rainfall coincide.

Aspens are also able to survive in drier environments because of their extensive root systems which can deplete water from at least the upper 2 to 3 m of soils (Sec. IIB). The low leaf area of pure aspen overstories lessens the demand for water. Although the shrub, grass, and herb understories consume water, these species are often more shallow rooted, and may not severely compete for water at soil depths below 1 m. During dry periods, aspens also lower transpiration by early leaf senescence or abscission. During the drought of 1976 in Minnesota, the author observed widespread leaf browning at least 3 weeks before usual. In mid-August, during a natural drought in New England, Federer (personal communication) observed leaf abscission more in BTA than TA, and especially from the lower crown. Scheumann (1965) reported that on dry soil EA leaves withered, and on still drier soils they abscissed.

Drought hardening, still another adaptation to drought, may occur in EA. Jarvis and Jarvis (1963d, 1965) developed several lines of evidence which suggest that leaves of EA seedlings grown under supraoptimal water conditions (Treatment A in Table 2) are less drought hardy than those grown under drier conditions (Treatment B, C, and D). First, dessication damage to leaves began at a slightly higher RWC in the wettest treatment. Secondly, at the same leaf Ψ, leaves grown in lower media Ψ had higher RWC. Third, leaf Ψs at full turgor was only -1.5 MPa in the wettest treatment compared to -1.9 MPa in the other treatments. (The author estimated the leaf Ψs at full turgor by replotting Figure 4 in Jarvis and Jarvis (1963d) as a pressure-volume curve. The reciprocal of leaf Ψ was plotted as a function of 100-RWC). Fourth, in hydroponics the leaf Ψ was 0.8 MPa lower in plants at a media Ψs of -0.32 MPa compared to seedlings at -0.05 MPa. With TA, under a much wider range of media Ψs, Eubanks (1969, 1971) found little increase in leaf Ψs. All these results are preliminary, since the sample was small and improved methods are now available for measuring Ψ, Ψs, and stomatal closure.

Preliminary results are also available concerning the ability of EA leaves to tolerate low RWC. The leaf RWCs at which damage occurred were 33 to 66% (Arvidsson 1951); and 30% in growth chamber seedlings and 54 % in a forest tree (Jarvis and Jarvis 1963d).

In summary, TA and BTA successfully survive and reproduce on dry sites but do not reach large commercial size there. The TA succeeds on dry sites despite relatively high transpiration rates, probably because of its deep and extensive root system and low leaf area. Also, in times of severe drought, aspen leaves can die or abscise, conserving water in the meristems. The capacity to regenerate from root suckers best explains the widespread occurrence of aspens on dry sites; suckering allows the species to bypass the seedling stage when individuals are most susceptable to drought. EA appears to drought harden; seedlings grown at moderate deficits develop lower leaf Ψs and die at a lower leaf RWC.

V. PESTS, DESTRUCTIVE AGENTS, AND WATER

As already indicated (Sec. IVC), moisture deficits and drought may interact to cause periodic increases in the mortality of TA. This section reviews reported relationships between specific pests and the water relations of aspen. When possible, the direct effects of climate were distinguished from the effects of aspen water relations on the pest.

A. Diseases

1. Stem Cankers

Plant water influences the incidence and growth rate of stem cankers, the relation being most completely explained for *Hypoxylon mammatum* (pruinatum) on TA. Successful artificial innoculation with Hypoxylon required a moist sealed wound (Bagga and Smalley 1969, 1974), but more innoculations developed into cankers on dry soil and at low relative humidity (Table 9). Furthermore, the growth of established cankers could be reversibly promoted by watering dry soil or inhibited by drying wet soils. In well-watered soils, cankers grew twice as fast at 50% relative humidity as at 90%. The minimum bark moisture required for successful innoculation and growth of Hypoxylon was 80% "relative turgidity" (Bier 1961a, b) as determined by soaking bark discs for 24 hours. (The term "relative turgidity" was inappropriate as much of the uptake may have been apoplastic). The reasons dry soils and tissue favor canker growth remain unknown but mycotoxins may be involved since the size of lesions produced on excised leaves by metabolites of Hypoxylon varied with the moisture regime of the leaf prior to excision (Bruck and Manion 1978). Bagga and Smalley (1967) earlier demonstrated that the fungus grew well at the low external Ψ produced by an agar concentration of 8%.

Table 9. Effect of soil moisture, relative humidity (RH), and plant moisture on Hypoxylon canker development in greenhouse *P. tremuloides* (after Bagga and Smalley 1969, 1974).

Experiment	Watering	RH	Plants With Cankers[a]	Canker Length[a]	Relative Saturation Moisture[b]	Original Moisture Content[b]
		(%)	(%)	(mm)	(%)	(% ODW)
1969	Every day	40-80	50	19[c]	60-80	74-77
	Every 3rd day	40-80	67	56	50-80	69-77
	Every 5th day	40-80	90	69	---	---
1974	Continuous	50	20	12	---	---
		90	20	12	---	---
	At wilting	50	100	50	---	---
		90	100	28	---	---

[a] Each value the average of 30 seedlings.

[b] Each value, the average of 5 seedlings.

[c] In 1969 experiment LSD was 20 mm; in 1974 experiment LSD was 11 mm.

Indirect evidence suggests these laboratory results may apply to the forest. In northern Michigan, the number of new Hypoxylon infections varied inversely with May through July rainfall, the cankers grew faster in a cool dry season, and aspen mortality from cankers was higher in dry summers (Day and Strong 1959). In New York, the incidence and destructiveness of Hypoxylon was less on lowland or moister upland soils (Bruck and Manion 1980). Anderson (1972), however, found no relation between Hypoxylon and height of water table.

The wood borers whose wounds and galleries provide major infection courts (Anderson and Martin 1981) can also be considered in relating Hypoxylon to moisture. Dry summers favor several borers (Sec. VB2). However, Graham *et al*. (1963) found that Hypoxylon developed at the point of *Saperda calcarata* ovipositions only in relatively moist summers.

Other stem cankers have been studied in less detail than Hypoxylon, but the results agree that low water favors canker development. Artificial innoculations with *Fusarium lateritum*, *Cryptodiaporthe salicella*, and *Septoria musiva* were successful only when the bark of dormant cuttings of TA was dried to below 80, 80, and 71% "relative turgidity," respectively (Bier 1961a, b). Watering the cuttings arrested the growth of the cankers. Literature reviewed by Anderson (1972) indicated that drought and offsite locations predispose aspen to infection by *Cytospora chrysosperma* (*Valsa sordida*). The increased susceptibility of EA was related to lower plant water content, and a change in tannin deposition is a proposed mechanism.

2. Stem rots, decays, and diebacks

Basham (1958) found slightly higher decay and butt rot in 140 to 180-year-old trees on the driest of four sites, but the sampling system does not permit generalization. In Minnesota, foresters state that decay is more significant on sites which are too wet or too dry for good aspen growth. In EA, the incidence of the stem rot, *Phellinus tremulae*, increased with wetness of the site (Il'in 1977). The incidence of the tip dieback *Venturia tremula* was increased by irrigation of TA (Einspahr and Wyckoff 1978).

B. Insects

1. Defoliators

Outbreaks of forest tent caterpillar (*Malacasoma disstria*) infestations occur after an increase in annual cyclonic passages (Wellington 1952). No tie to plant water relations was inferred, and the increased populations may be attributable to longer feeding periods in the humid weather (Graham *et al*. 1963). Growth reductions attributable to defoliation were not significantly affected by rainfall during the growing season (Duncan and Hodson 1958), although several foresters in Minnesota (personal communications) indicated that mortality was heavier on dry sites during the outbreaks in the late 1970's. After partial defoliation by gypsy moth (*Porthetria dispar*), the residual leaves of TA had a more favorable water balance than leaves in undefoliated crowns (Stephens *et al*. 1972).

2. Stem borers

Dry summers appear to favor successful oviposition and early larval development of the poplar borer (*Saperda calcarata*) (Graham and Mason 1958; Graham *et al*. 1963). Populations are not higher, however, on dry sites. Low precipitation may explain why populations of the stem borer, aspen agrilus (*Agrilus liragus*) (Graham *et al*. 1963) peaked during the 1930s. The agrilus completes its life cycle in trees which have low vigor.

C. Pollution

The poor performance of EA growing near highways has been related to lower r_d's caused by pollutants. Particulate matter deposited in the stomatal pore inhibited closing (Fluckiger *et al*. 1977). Also, vehicle exhaust at a ratio of 1:200 with air, inhibited normal stomatal closing in dark and at a ratio of 1:10 decreased r_d in the light (Fluckiger *et al*. 1978b).

In controlled conditions, sulfur dioxide at 0.2 and 0.5 μl/l partially closed the stomates of TA (Kimmerer and Kozlowski 1981). The closure was reversible and varied with clone.

D. Wind and Temperature

The author observed an unusual amount of stem breakage during the Minnesota drought of 1976. The xylem of the broken trees was unusually brittle and dry. Although cold and heat injury vary with water status, this literature was not reviewed.

E. Summary

The little known about the interaction of aspen water balance with pests is quite intriguing. The successful innoculation and growth of Hypoxylon and other stem cankers is favored by drier bark and/or wood, lower soil moistures and lower air humidities. First-year survival of aspen borer is much higher in dry summers. Highway pollution lowers r_d while SO_2 raises r_d.

VI. TOPICS FOR FUTURE RESEARCH

Among the numerous possible problems, these were selected for their practical significance to Lake States forestry or scientific interest to the author.

Topic A - Modeling Evapotranspiration

One present need is to determine parameters which can be used in existing ET models such as PROSPER, EVTRAN, or THIRSTY (Sec. IIE). We need parameters which can be applied in forest situations where climate and stand information is usually limited. Among the parameters, the crop coefficient deserves first attention; in particular we need to learn how to predict its change with phenology, soil moisture deficits, evaporative demand, and stand characteristics such as leaf area index, stand structure, and species composition. A related need exists for long-term observations of climate and soil moisture (to at least 4 m) in representative stands.

Topic B - Growth and Water Deficits or Surplus

1. Assessing site quality

Current methods for predicting the site quality of TA in the Lake States emphasize multiple correlation with soil properties. The author propose that these same variables be processed into a simple water balance model which would include soil moisture-supplying capacity, exposure, PET, and precipitation. This model could then be incorporated in more general ecological classifications.

2. Timing of Deficits and Growth

The time during the annual cycle when water deficits appear determines how they impact growth. Deficits will affect quantitative changes (e.g., number of cambial divisions) differently in June than in August. Of greater interest is the impact of timing on such qualitative changes such as the induction of dormancy.

3. Aging and Water Relations

The author suggests the following postulates and hypothesis be tested. Short shoots impart drought resistance but have lower net assimilation rates. As at least certain clones of aspen age, increasing percentages of their crown are in short shoots. Therefore, short shoots impart both slow growth and drought avoidance to older trees.

4. Explaining Poor Growth on Wet Sites

In the Lake States poor growth and early deterioration can be attributed more to wet soils than to dry. For example, the most recent U.S. Forest Service National Forest Survey of Wisconsin found that of the 1,067,000 acres in aspen type with potential yields of 4.2 m^3/ha (60 ft^3/ac) or less, 90% were either poorly drained, usually wet or frequently flooded (Lundgren and Hahn 1978). Research is needed to further classify these poorly drained and flooded sites. There is also a need to assess why aspen growth is poor and why stands rapidly deteriorate on the various wet sites.

Topic C – *Hypoxylon* Canker

A physiological explanation is needed as to why dry conditions favor the rapid growth of stem cankers in TA. The interaction between plant stress and disease is a targeted area for basic research in food crops suggesting that the scientific community recognizes a need for more knowledge in this aspect of host-disease interactions. In aspen we already have a model system for trees since the studies of Bier and Bagga and Smalley have shown that dry air and dry aspen tissue favor canker growth. The physiologic explanation of susceptibility must then be integrated into a hypothesis which accounts for the proposed or known effects of moisture on the insect vector and the disease fungus.

Topic D - Descriptive Water Relations

1. Tissue Water Status

T. H. Hinkley (personal correspondence) suggests the usefulness of describing the seasonal and diurnal patterns of tissue water status. Such data would aid in developing parameters for crop resistance and predicting the effects of water deficiency on growth.

2. Xylem Resistance

The studies of Zimmerman (1978) on BTA should be expanded into definitive studies of how xylem resistance affects leaf water status and how water deficits and transpirational flux affects xylem resistance.

3. Strategies of Conserving Water

EA extends from northern Finland to northern Algeria and TA extends from central Alaska to eastern Mexico. A study could be done to determine how either species adapts to survive under such different durations and intensities of evapotranspiration.

REFERENCES

(Item followed by asterisk is not cited in text)

Akhromeiko, A. I. and M. V. Zhuravleva. 1957. Investigation of the velocity of the water current in woody plants. Soviet Plant Physiol. 4:164-169.

Alekseev, V. A. 1969. The microclimate in aspen stands. Lesn. Z. Arkangel'sk 12:7-10. FA 31:456 (1970).

Anderson, G. W. 1972. Diseases. In: Aspen Symposium. USDA For. Serv. Gen. Tech. Rep. NC-1, p. 74-82. North Central For. Exp. Stn., St. Paul, Minnesota.

Anderson, G. W. and M. P. Martin. 1981. Factors related to the incidence of Hypoxylon cankers in aspen and survival of cankered trees. For. Sci. 27:461-476.

Antipov, N. I. 1971. Correlation between cuticular and stomatal transpriation in woody and bushy plants. Soviet Plant Physiol. 18:1026-1030.

Arvidsson, I. 1951. Austrocknungs- und Durreresistenzverhaltnisse einiger Reprasentanten olandischer Pflanzenvereine nebst Bermerkungen uber Wasserabsorption durch oberirdische Organe. Oikos Suppl. 1:1-181. In: Levitt (1980).

Bagga, D. K. and E. B. Smalley. 1967. Water stress in relation to initiation and development of Hypoxylon canker of aspen. Phytopath. 57:802 (Abstr.).

Bagga, D. K. and E. B. Smalley. 1969. Factors affecting canker development on Populus tremuloides artificially innoculated with Hypoxylon pruinatum. Can. J. Bot. 47:907-914.

Bagga, D. K. and E. B. Smalley. 1974. The development of Hypoxylon canker of Populus tremuloides: Role of interacting environmental factors. Phytopath. 64:658-662.

Baker, F. S. 1925. Aspen in the central Rocky Mountain region. USDA Dept. Bull. No. 1291, 47 p. Washington, D.C.

Bakuzis, E. V. and V. Kurmis. 1978. Provisional list of synecological coordinates and selected ecographs of forest and other plant species in Minnesota. College of Forestry Staff Series Paper 5, Univ. Minnesota, St. Paul, Minnesota.

Balek, J. and O. Pavlik. 1977. Sap stream velocity as an indicator of the transpirational process. J. Hydrology 34:193-200.

Barnes, B. V. 1966. The clonal growth habit of American aspens. Ecology 47:439-447.

Bartos, D. L. and R. S. Johnston. 1978. Biomass and nutrient content of quaking aspen at two sites in the western United States. Forest Sci. 24:273-280.*

Basham, J. T. 1958. Decay of trembling aspen. Can. J. Bot. 36:491-505.

Bates, C. G. and A. J. Henry. 1928. Forest and streamflow experiment at Wagon Wheel Gap, Colorado. Monthly Weather Rev. Suppl. 30. 79 p.

Batzer, H. O. 1972. Insects. In: Aspen Symposium. USDA Gen. Tech. Rep. NC-1, p. 83-87. North Cent. For. Exp. Stn., St. Paul, Minnesota.*

Belgium, Centre de Populiculture du Hainaut (The effects of the 1976 drought on poplars (in Belgium)). 1977. Bulletin Trimestriel, Societe Forestiere de Franche-Comte et des Provinces de l'Est 38:111 (Fr.). In: For. Abstr. (1978) 49:2880.

Bendtsen, B. A. and L. W. Rees. 1962. Water-content variation in the standing aspen tree. For. Prod. J. 12:426-428.

Berndt, H. W. and R. D. Gibbons. 1958. Root distribution of some native trees and understory plants growing on three sites within ponderosa pine watersheds in Colorado. USDA For. Serv. Rocky Mt. For. Range Exp. Stn. Pap. 37, 14 p. Ft. Collins, Colorado.

Bier, J. E. 1961a. The relation of bark moisture to the development of canker diseases caused by native, facultative parasites. IV. Pathogenicity studies of *Cryptodiaporthe*, *Salicella* (Fr.) *Petrak*, and *Fusarium lateritium Nees.*, on *Populus trichocarpa* Torrey and Gray, *P. 'robusta'*, *P. tremuloides* Michx., and *Salix* sp. Can. J. Bot. 39:139-154.

Bier, J. E. 1961b. The relation of bark moisture to the development of canker diseases caused by native, facultative parasites. VI. Pathogenicity studies of *Hypoxylon*, *Pruinatum* (Klotzsch) Cke., and *Septoria musiva* PK. on species of *Acer*, *Populus*, and *Salix*. Can. J. Bot. 39:1555-1561.

Bocharov, V. S. 1976. Evapotranspiration on sites with different afforestation in forest-steppe with small groves of aspen (*Populus*) or birch (*Betula*). Vestn. S-Kh. Nauki. Kaz. 6:88-91. (Ru.).

Brinkman, K. A. and E. I. Roe. 1975. Quaking aspen: silvics and management in the Lake States. USDA For. Serv. Agric. Handbook No. 486, 52 p. Washington, D.C.*

Brown, A. B. 1935. Cambial activity, root habit and sucker shoot development in two species of poplar. New Phytologist 34:163-179.

Brown, H. E. and J. R. Thompson. 1965. Summer water use by aspen, spruce, and grassland in western Colorado. J. Forestry 63:756-760.

Brown, R. W. and W. T. McDonough. 1977. Thermocouple psychrometer for in situ leaf water potential determinations. Plant & Soil 48:5-10.

Bruck, R. I. and P. D. Manion. 1978. Mammotoxin bioassay for genetic and environmental predisposition of aspen to cankering by *Hypoxylon mammatum*. Proc. Amer. Phytopath. Soc. 4:184.

Bruck, R. I. and P. D. Manion. 1980. Interacting environmental factors associated with the incidence of *Hypoxylon* canker on trembling aspen. Can. J. For. Res. 10:17-24.

Buell, M. F. and H. F. Buell. 1959. Aspen invasion of prairie. Bull. Torrey Bot. Club 86:264-269.

Bylinska, E. 1975. The relationship of winter transpiration of selected species from the genera *Viburnum*, *Populus* and *Lonicera* to the northern boundary of their geographical distribution. Monogr. Bot. Vol. L., 59 p.

Clements, J. R. 1971a. Evaluating summer rainfall through a multistoried largetooth aspen community. Can. J. For. Res. 1:20-31.

Clements, J. R. 1971b. Interception per canopy in a multistoried largetooth aspen community. Can. For. Serv. Inf. Rep. PS-X-26, 13 p.

Clements, J. R. 1971c. Net rainfall in a multistoried aspen forest community. Can. For. Serv. Inf. Rep. PS-X-27, 9 p.

Clements, J. R. 1972. Stemflow in a multistoried aspen community. Can. J. For. Res. 2:160-165.

Croft, A. R. and L. V. Monniger. 1953. Evapotranspiration and other water losses on some aspen forest types in relation to water available for stream flow. Amer. Geophys. Union Trans. 34:563-74.

Danilin, M. A. 1975. Moisture content and density of wood of aspen in relation to sex. Lesn. Zh. 2:34-37. *In*: For. Abstr. (1976)37:4744.

Day, M. W. 1944. The root system of aspen. Amer. Midl. Nat. 32:502-509.

Day, M. W. and F. C. Strong. 1959. A study of *Hypoxylon* canker on aspen. Mich. Agric. Exp. Stn. Quart. Bull. 41:870-877. Univ. Michigan, Ann Arbor, Michigan.

DeByle, N. V. 1964. Detection of functional intraclonal aspen root connections by tracers and excavation. For. Sci. 10:386-395.*

Demidenko, V. P. and I. M. Gadzhiev. 1972. The effect of soil conditions on the distribution and productivity of *Populus tremula* forests of the middle Ob' region. Tr. Biol. Inst. Akad. Nauk. SSSR Sibirsk. Oto. 15:59-71. (Ru.).*

Drew, L. 1973. Vegetation-environment relationships in the prairie forest transition zone in Minnesota. Ph.D. Thesis, University of Minnesota. 405 pp.

Duncan, D. and A. C. Hodson. 1958. Influence of the forest tent catepillar upon the aspen forests of Minnesota. For. Sci. 4:71-93.

Dunford, E. G. and C. H. Niederhorf. 1944. Influence of aspen, young lodgepole pine, and open grassland types upon factors affecting water yield. J. Forestry 42:673-677.

Edgar, J. C. 1970. Density and moisture content of aspen wood and bark. 57 p. M.S. Thesis. Michigan Tech., Houghton, Michigan.

Eidmann, F. E. 1943. Untersuchungen uber die Wurzelatmung und Transpiration unserer Hauptholzarten. Akad. Dt. Forstw. Schrftr. *In*: Kostler *et al*. 1968.

Einspahr, D. W., M. K. Benson, and M. L. Harder. 1972. Influence of irrigation and fertilization on growth and wood properties of quaking aspen. 11 p. API-TAPPI For. Prod. Lab. *In*: Symp. Effects of accelerated growth on wood properties, 1971.

Einspahr, D. W. and G. Wyckoff. 1978. Growth response of hybrid aspen to intensive forest management. TAPPI 61:49-52.

Enescu, V., V. Enescu, M. Damian, A. Savulescu and N. Stanciu. 1955. The root system of certain species of trees and shrubs on marshy soils. (Rumanian). Bul. sti Acad. Repub. rom (Sect. Biol.) 7:945-980. *In*: For. Abstr. (1956)17:3715.*

Eubanks, J. O. 1969. The effect of light intensity and osmotic water stress on the water potential of *Populus tremuloides*. 86 p. The Institute of Paper Chemistry and Lawrence University, Appleton, Wisconsin. *In*: Diss. Abstr. (1970)30:4864-65.

Eubanks, J. O. 1971. Effect of light intensity and osmotic stress on the water relations of *Populus tremuloides*. For. Sci. 17:79-82.

Farmer, R. E. 1962. Depth and diameter of the parent roots of aspen suckers. Mich. For. 23. 4 pp.

Federer, C. A. 1976. Differing diffusive resistance and leaf development may cause differing transpiration among hardwoods in spring. For. Sci. 22:359-364.

Federer, C. A. and G. W. Gee. 1974. Tree water stress in relation to water yield in a hardwood forest. Res. Rep. 7, 30 p. Water Resource Res. Center, Univ. New Hampshire, Duram, NH.

Federer, C. A. 1977. Leaf resistance and xylem potential differ among broadleaved species. For. Sci. 23:411-419.

Fedorov, N. I. 1969. The water regime of aspen infected by heart rot. Naue. Dokl. Vyss. Skoly (Biol. Nauki) Moskva (9):95-99. (Ru.ru.).

Fluckiger, V. W., J. J. Oertli, H. Fluckiger-Keller. 1978a. The effect of wind gusts on leaf growth and foliar water relations of aspen. Oceologia 34:101-106.

Fluckiger, V. W., H. Fluckiger-Keller, and J. J. Oertli. 1978b. Inhibition of the regulatory ability of stomata caused by exhaust gasses. Experientia 34:1274-1275.

Fluckiger, V. W., H. Fluckiger-Keller, J. J. Oertli, and R. Guggenheim. 1977. Pollution of leaf and needle surfaces near a highway and its effect on stomatal diffusive resistance. Eur. J. For. Path. 7:358-364.

Fralish, J. S. 1972. Youth, maturity, and old age. *In*: Aspen Symposium. USDA For. Serv. Gen. Tech. Rep. NC-1, p. 52-58. North Cent. For. Exp. Stn., St. Paul, Minnesota.

Fralish, J. S. and O. L. Loucks. 1967. Prediction of aspen site index from correlation with site factors in Wisconsin. Univ. Wisconsin For. Res. Notes 132, 6 p.

Fralish, J. S. and O. L. Loucks. 1975. Site quality evaluation models for aspen (Populus tremuloides Michx.) in Wisconsin. Can. J. For. Res. 5:523-528.

Fraser, D. A. 1959. Tree growth in relation to soil moisture. P. 183-204. In: Tree Growth. (ed. T. T. Kozlowksi) Ronald Press, New York.

Gardner, W. R. and R. H. Nieman. 1964. Lower limit of water availability to plants. Sci. 143:1460-1462.

Gary, H. L. 1972. Rime contributes to water balance in high-elevation aspen forests. J. Forestry 70: 93-97.

Gates, F. C. 1930. Aspen association in northern lower Michigan. Bot. Gaz. 40:233-259.

Gibbs, R. D. 1930. Sinkage studies II. The seasonal distribution of water and gas in trees. Can. J. Res. 2:425-439.

Gibbs, R. D. 1935. Studies of wood II. On the water content of certain Canadian trees and on changes in the watergas system during seasoning and flotation. Can. J. Res. 12:727-760.

Gibbs, R. D. 1958. Patterns in the seasonal water content of trees. In: Physiology of Forest Trees (ed. K. V. Thimann). Pp. 43-69. Ronald Press, New York.

Gifford, G. F. 1966. Aspen root studies on three sites in northern Utah. Amer. Midl. Natur. 75:132-141.

Goldstein, R. A., J. B. Mankin, and R. J. Luxmoore. 1974. Documentation of PROSPER: A model of atmosphere-soil-plant water flow. EDFB-IBP 73-9. National Technical Information Service, Springfield, Virginia.

Grace, J. 1978. The turbulent boundary layer over a flapping Populus leaf. Plant, Cell, Environment 1:35-38.

Graham, S. A. and R. P. Harrison. 1955. Site identification for bigtooth aspen sucker stands. Michigan Forestry Note 10, 4 p. Ann Arbor, Michigan.

Graham, S. A. and R. R. Mason. 1958. Influence of weather on poplar borer numbers. Michigan Forestry Note 20, 3 p. Ann Arbor, Michigan.

Graham, S. A., R. P. Harrison, and C. E. Westell. 1963. Aspens. Univ. Michigan Press, Ann Arbor, Michigan. 272 p.

Grupce, R. 1967. The moisture deficit of certain woody plants. God. Zborn. Zemj-Sum. Fak. Univ. Skopje (Sum) 20:75-83 (Maced. e.).*

Gulidova, I. V. 1958. Transpiration of trees and herbaceous species in the central taiga zone, and its relation to meteorological conditions. Trud. Inst. Les. No. 41:111-121. In: For. Abstr. (1960)21:4016. (Ru.).

Gulidova, I. V. and E. V. Jurina. 1962. The water regime of the soil and the seasonal course of photosynthesis and transpiration in trees. Bjull. Mosk. Obse. Ispyt. Prir. (Otd. Biol) 67:102-112.*

Hannah, P. R. and R. Zahner. 1970. Nonpedogenetic texture bands in outwash sands of Michigan: Their origin and influence on tree growth. Soil Sci. Soc. Amer. Proc. 34:134-136.

Hart, G. E., J. D. Schultz, and G. B. Coltharp. 1969. Controlling transpiration in aspen with phenylmercuric acetate. Water Resources Res. 5:407-412.

Hayden, B. P. 1968. Wind effects on water tension in woody plants. Ph.D. Thesis, Univ. Chicago. 79 p.

Heinselman, M. L. and Z. A. Zasada. 1955. A review of literature relating to quaking aspen sites. USDA For. Serv. Lake States For. Exp. Stn. Pap. 32, 61 p. St. Paul, Minnesota.

Holmgren, P., P. G. Jarvis, and M. S. Jarvis. 1965. Resistance to carbon dioxide and water vapour transfer in leaves of different plant species. Physiol. Plant. 18:557-573.

Il'in, A. M. 1970. Dynamics of moisture of wood in male and female Populus during the growing stage. Lesn. Z. 13:25-28. In: For. Abstr. (1971)32:2180.

Il'in, A. M. 1973a. The root systems of male and female aspen. In: Lesovodstvo, lesnye kul-tury i pochvovedenie Vyp. I. Leningrad, USSR; Izdatel'stvo Leningradskogo Universiteta. p. 49-53 (Ru.).

Il'in, A. M. 1973b. Sex ratio in the aspen under different conditions of growth. Sov. J. Ecol. 2: 162-163.

Il'in, A. M. 1977. The phytopathological condition of secondary aspen stands on oal-forest soils. Lesnoi Z. 6:31-34.

Isaeva, L. N. 1966. Distribution of moisture in the stems of growing trees of the principal species in E. Siberia. In: Svojstva drevesiny, ee zascita, i novye drevesnye materialy. Izdatel'stvo 'Nauka', Moscow. Pp. 3-10 (Ru.).*

Ivanescu, D. 1967. Populus Tremula. Editura Agro-Silvica, Bucharest. 179 p. (Rum.f.ru.).*

Jarvis, P. G. and M. S. Jarvis. 1963a. The water relations of tree seedlings I. Growth and water use in relation to soil water potential. Physiol. Plant. 16:215-235.

Jarvis, P. G. and M. S. Jarvis. 1963b. The water relations of tree seedlings II. Transpiration in relation to soil water potential. Physiol. Plant. 16:236-253.

Jarvis, P. G. and M. S. Jarvis. 1963c. The water relations of tree seedlings III. Transpiration in relation to the osmotic potential of the root medium. Physiol. Plant. 16:269-275.

Jarvis, P. G. and M. S. Jarvis. 1963d. The water relations of tree seedlings IV. Some aspects of the tissue water relations and drought resistance. Physiol. Plant. 16:501-515.

Jarvis, P. G. and M. S. Jarvis. 1965. The water relations of tree seedlings V. Growth and root respiration in relation to osmotic potential of the root medium. p. 167-182. In: Water Stress in Plants (ed. B. Slavik) W. Junk, The Hague.

Jaynes, R. A. 1978. A hydrologic model of aspen-conifer succession in the western United States. USDA For. Serv. Res. Pap. INT-213. 17 p.

Jensen, R. A. and J. R. Davis. 1953. Seasonal moisture variations in aspen. Minnesota For. Notes 19, 2 p. Univ. Minnesota, St. Paul, Minnesota.

Joachim, H. F. 1953. Investigations into poplar root development and the site requirements of poplar varieties. Wissenschaftliche Abhandlungen, Deutsche Akademie der Landwirtschaftswissenschaften, Berlin. No. 7, 208 p.*

Johnston, R. S. 1969. Aspen sprout production and water use. USDA For. Serv. Res. Note INT-89, 6 p. Intermt. For. Range Exp. Stn., Ogden, Utah.

Johnston, R. S. 1970. Evapotranspiration from bare, herbaceous, and aspen plots: A check on a former study. Water Resources Res. 6:324-327.

Johnston, R. S. 1971. Rainfall interception in a dense Utah aspen clone. USDA For. Serv. Res. Note INT-143, 4 p. Intermt. For. Range Exp. Stn., Logan, Utah.

Johnston, R. S. and R. D. Doty. 1972. Description and hydrologic analysis of two small watersheds in Utah's Wasatch mountains. USDA For. Serv. Res. Pap. INT-127, 53 p. Intermt. For. Range Exp. Stn., Ogden, Utah.

Johnston, R. S., R. K. Tew, and R. D. Doty. 1969. Soil moisture depletion and estimated evapotranspiration on Utah Mountain watersheds. USDA For. Serv. Res. Pap. INT-67, 13 p. Intermt. For. Range Exp. Stn., Ogden, Utah.

Jones, J. R. 1971. An experiment in modeling Rocky Mountain forest ecosystems. USDA For. Serv. Res. Pap. RM-75, 19 p. Rocky Mt. For. Range Exp. Stn., Ft. Collins, Colorado.

Kassam, A. H. 1972. Determination of water potential and tissue characteristics of leaves of Vicia faba L. Hort. Res. 12:13-23.

Kaufmann, M. R. 1982a. Leaf conductance during the final season of a senescing aspen branch. Plant Physiol. 70:655-657.

Kuafmann, M. R. 1982b. Leaf conductance as a function of photosynthetic photon flux density and absolute humidity difference from leaf to air. Plant Physiol. 69:1018-1022.

Kaufmann, M. R. 1982c. Evaluation of season, temperature, and water stress effects on stomata using a leaf conductance model. Plant Physiol. 69:1023-1026.

Kaufmann, M. R. and C. A. Troendle. 1981. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. Forest Sci. 27:477-482.

Kazadaev, S. A. 1974. The effect of the drought of 1972 on the diameter increment in the central forest-steppe. Lesovedenie 3:92-94 (Ru.e.).

Keller, T. and H. Beda-Puta. 1973. Gas exchange of leafless shoots in winter. Schweizerischa Zeitschr. Forstwesen 124:433-441 (G).

Kimmerer, T. W. and T. T. Kozlowski. 1981. Stomatal conductance and sulfur uptake of five clones of Populus tremuloides exposed to sulfur dioxide. Plant Physiol. 67:990-995.

Kittredge, J., Jr. 1938. The interrelations of habitat, growth rate, and associated vegetation in the aspen community of Minnesota and Wisconsin. Ecol. Monogr. 8:151-246.

Kittredge, J., Jr. and S. R. Gevorkiantz. 1929. Forest possibilities of aspen lands in the Lake States. Minn. Agric. Exp. Stn. Tech. Bull. 60, 84 p. Univ. Minnesota, St. Paul, Minnesota.

Kleshnin, A. F. and I. A. Shulgin. 1957. On transpiration rate under artificial illumination. Soviet Plant Physiol. 4:522-527.*

Knutson, D. 1968. Wetwood in trembling aspen (Populus tremuloides Michx.). Ph.D. Dissertation. 152 p. Univ. Minnesota, St. Paul, Minnesota.

Kolovsky, R. A. 1973. Influence of air relative humidity on the value of trees bioelectric potentials. Lesovedenie (6):53-59 (Ru.e.).*

Koshcheev, A. L. 1955. Flooding of clearings and methods of preventing it. Acad. Sci. USSR (Ru.). Cited in Veretennikov, 1964.

Kostler, J. N., E. Bruckner, and H. Bibelriether. 1968. Die Wurseln der Walbaume. 284 p. Verlog Paul Parey, Hamburg.

Kozlowski, T. T. (ed.). 1981. Water deficits and plant growth VI. Woody Communities. Academic Press, New York. 582 p.

Kozlowski, T. T. and C. H. Winget. 1963. Patterns of water movement in forest trees. Bot. Gaz. 124: 301-311.

Krasovskii, L. I. and V. A. Chashchukhin. 1974. The state of water in plant tissues at negative temperatures under natural conditions. Soviet Plant Physiol. 21:809-812.

Laisk, A. and V. Oja. 1971. Changes of aspen mesophyll resistance in response to rapid dehydration of the leaf. Soviet Plant Physiol. 18:467-474.*

Lange, O. L., L. K. Kappen, and E. D. Schulze. (eds.). 1976. Water and plant life. Springer-Verlag, Berlin. 536 p.

Larsen, C. M. 1956. The role of stomata in the description of races and clones of forest trees. 12th Congr. Int. Union For. Res. Organ., Oxford. No. IUFRO/56/22/104:425-429.

Leaf, C. F. and G. E. Brink. 1973. Hydrologic simulation model of Colorado subalpine forest. USDA For. Serv. Res. Pap. RM-107.

Leaf, C. F. and G. E. Brink. 1975. Land use simulation model of the subalpine coniferous forest zone. USDA For. Serv. Res. Pap. RM-135.

Levitt, J. 1980. Responses of plants to environmental stresses. Vol. II. 2nd Ed. 607 p. Academic Press, New York, New York.

Lundgren, A. L. and J. T. Hahn. 1978. The extent and characteristics of low productivity aspen areas in Wisconsin. USDA For. Serv. North Central For. Exp. Stn. Gen. Tech. Rep. 45, 24 p. St. Paul, Minnesota.

Maini, J. S. 1968. Silvics and ecology of *Populus* in Canada. *In*: Growth and utilization of poplars in Canada. p. 55-57. Can. Dept. For. and Rural Dev., Dept. Publ. No. 1205.

Marston, R. B. 1958. Parrish Canyon, Utah: A lesson in flood sources. J. Soil and Water Conserv. 13:165-167.

Marston, R. B. 1966. Some comparative hydrologic characteristics of aspen and mountain brush communities on steep mountain watersheds in northern Utah. Diss. Abstr. 26:5630.

McQueen, I. S. and R. F. Miller. 1972. Soil-moisture and energy relationships associated with riparian vegetation near San Carlos, Arizona. Professional Paper, U.S. Geological Survey No. 655-E, 51 p. From Meteorological and Geoastrophysical Abstr. 24, 6-352.*

Miles, T. J. 1979. Aspen root biomass and nutrient contents. 65 p. Plan B. Paper. College of Forestry Library, Univ. Minnesota, St. Paul, Minnesota.

Miller, P. C. 1967. Leaf orientation and energy exchange. Abstr. in Bull. Ecol. Soc. Amer. 48:55.

Miller, P. C. 1969. Solar radiation profiles in openings in canopies of aspen and oak. Science 164: 308-9.

Miller, P. C. and D. M. Gates. 1967. Transpiration resistance of plants. Amer. Midl. Natur. 77:77-85.

Mital, D. 1980. Observation and prediction of soil moisture under four aspen stands. Plan B. paper xxp. Sch. For., Univ. Minnesota, St. Paul, Minnesota.

Mital, D., L. Lindholm, and E. Sucoff. 1978. Leaf diffusive resistance and leaf water potential of *Populus tremuloides*. Office Report, College of Forestry, Univ. Minnesota, St. Paul, Minnesota.

Mital, D. and E. Sucoff. 1982. Predicting soil moisture depletion beneath trembling aspen. Can. J. Forest Res. (in press).

Molcanov, A. A. 1961. Les i klimat (Forest and Climate). 279 p. Izdatel'stvo Akademii Nauk SSSR, Moscow.*

Moss, E. H. 1932. The vegetation of Alberta, IV. The poplar association and related vegetation of central Alberta. J. Ecol. 20:380-415.

Muller-Stoll, W. R. and U. Hartmann. 1950. *Cytospora* canker of poplar (*Valsa sordida* Nitschke) and the requirements for parasitic propogation. Phytopath Z. 16:443-478. (Ger.).*

Murphey, W. K. and J. J. Bowier. 1975. The response of aspen (*Populus tremuloides*) to irrigation by municipal waste water. TAPPI (Tech. Assoc. Pulp Paper Ind.) 58:128-129.

Nestsiarovich, M. D., T. F. Dziarugina, and B. S. Aliker. 1970. The effect of soil moisture on the growth of year-old seedlings of *Populus tremula* and *Ulmus laevis*. Minsk Belaruskaya Akad Navuk Vestsi Ser. Biialagichenykh Navuk 4:20-25.*

Neuwirth, G. 1958. The water balance in forest stands determined through analyses of moisture and absorption capacity. Arch. Forstw. 7(6/7):449-458.*

Parlange, J. Y., P. E. Waggoner, and G. H. Heichel. 1971. Boundary layer resistance and temperature distribution on still and flapping leaves. I. Theory and Laboratory experiments. Plant Physiol. 48:437-442.

Paul, G. and E. S. Verry. 1980. Changes in water yield resulting from changes in land use. In: Symp. North Country Futures: Industrial Impacts on Forest Resources, Communities, and You. March 27-29, 1980. Symposium Minnesota Dept. Natural Resources.

Perala, D. A. 1977. Manager's handbook for aspen in the north central states. USDA For. Serv. Gen. Tech. Rep. NC-36, 30 p. North Cent. For. Exp. Stn., St. Paul, Minnesota.

Perala, D. A. 1978. Thinning strategies for aspen: A prediction model. USDA For. Serv. Res. Pap. NC-161, 14 p. North Cent. For. Exp. Stn., St. Paul, Minnesota.

Polster, H. 1957. Transpiration rate and water requirements of Poplar clones. Wiss. Abh. Dtsch. Akad. LandWiss. Berlin No. 27 (Beitr. Pappelforsch. No. 2) p. 99-147.*

Rahmanov, V. V. 1958. Is precipitation intercepted by tree crowns lost to the forest? Bot. Z. 43:1630-3. In: For. Abstr. (1959)20:2717.

Rangelov, K. 1969. Comparative studies of certain physical and mechanical properties of wood of male and female aspens. Gorskostop. Nauka. Sofija 6(4):105-10.

Raskatov, P. B. and V. M. Eremin. 1973. Effect of the 1972 drought on the increment of certain tree species. Lesnoi Zhurnal 16(4):5-8 (Ru.).

Rakhi, M. O., I. G. Zavadskaya, and N. I. Bobrovskaya. 1978. Errors in determining components of the leaf water potential with the aid of a pressure chamber. Transl. from Fiziol. Rast 25:869-877.

Rauner, Y. L. 1976. Decidious forests. In: Vegetation and the atmosphere. Vol. 2, p. 241-264. (ed. J. L. Monteith) Academic Press, New York.

Rauner, Y. L. 1977. Heat balance of the plant cover. 219 p. TT74-52015 published for USDA ARS. Amerind Pub. Co. New Delhi. Transl. from Russian "Teplovoi Balans Rastitel'nogo Pokrova." (1972).

Rauner, Y. L. 1966. Thermal-balance observations in a deciduous forest. TT-66-51099. Transl. from Russian Isvestiya Akademic Nauk SSSR, Seriya geograficheskayr 5:79-86 (1958).

Roa, R. L. and W. F. Pickard. 1975. The applicability of the magneto-hydrodynamic technique to water flux measurements in forest trees. J. Exp. Bot. 26:469-475.

Roise, J. P. and D. P. Betters. 1981. An aspect transformation with regard to elevation for site productivity models. Forest Sci. 27:483-486.

Rushin, J. W. and J. E. Anderson. 1981. An examination of the leaf quaking adaptation and stomatal distribution in Populus tremuloides Michx. Plant Physiol. 67:1264-66.

Sandberg, D. 1951. The regeneration of quaking aspen by root suckering. 172 p. Plan B Paper, College of Forestry Library, Univ. Minnesota, St. Paul, Minnesota.

Scheumann, W. 1965. Serial studies of the hydration of forest plants. p. 99-107. In: Water Stress in Plants (ed. B. Slavik). W. Junk, The Hague.

Shirley, H. L. 1941. Restoring conifers to aspen lands in the Lake States. USDA For. Serv. Tech. Bull. 763, 36 p.

Silina, A. A. 1955. The transpiration of woody species in the Tellerman forest. Fiziol. Rast. 2:364-72. In: For. Abstr. (1956)17:1208.

Slatyer, R. O. 1967. Plant water relations. Academic Press, New York. 366 p.

Small, E. 1972. Water relations of plants in raised sphagnum peat bogs. Ecology 53(4):726-728.

Smilga, J. and I. Jervekilga. 1978. Triploid aspen in the Latvian SSR. Jaunakais mezsaimnieciba 20: 23-32. Referativnyi Zhurnal.

Smirnov, V. V. and N. S. Odinokova. 1954. Gidrologiceskaja rolj osinovyh lesov (The hydrologic role of aspen woods). Dokl. Akad. Nauk SSSR 99:849-852.

Smith, P. and L. Every. 1980. Rooting habits of selected commercial tree species of the eastern United States - A Bibliography. USDA For. Serv. Bibliographies and Literature of Agr. 10. 59 pp.*

Sokolov, A. A. 1967. Root occupation of the A_1 horizon of soddy podzolic soil beneath Norway spruce, birch and aspen canopies. Lesoved., Moskvā (2):83-86. (Ru.e.).

Stephens, G. R., N. C. Turner, and H. C. DeRoo. 1972. Some effects of defoliation by Gypsy moth (Porthetria dispar L.) and elm spanworm (Ennomos subsigarius Hbn.) on water balance and growth of deciduous forest trees. For. Sci. 18:326-330.

Stoeckeler, J. H. 1948. The growth of quaking aspen as affected by soil properties and fire. J. Forestry 46:727-736.

Stoeckeler, J. H. 1960. Soil factors affecting the growth of quaking aspen forests in the Lake States. Agric. Exp. Stn. Tech. Bull. 233, 48 p. Univ. Minnesota, St. Paul, Minnesota.

Strain, B. R. 1964. Physiological and morphological variability of local quaking aspen clones. Abstr. of thesis, in Dissert. Abstr. 25:3228.*

Strothman, R. O. and Z. A. Zasada. 1962. Silvical characteristics of quaking aspen. USDA For. Serv., Lake States For. Exp. Stn. Pap. 49, 30 p. St. Paul, Minnesota.*

Tew, R. K. 1967. Soil moisture depletion by aspen in central Utah. USDA For. Serv. Res. Note INT-73, 8 p. Intermt. For. Range. Exp. Stn., Ogden, Utah.

Tobiessen, P. 1982. Dark opening of stomata in successional trees. Oecologie 52:356-359.

Tobiessen, P. and T. M. Kana. 1974. Drought-stress avoidance in three pioneer tree species. Ecology 55:667-670.

Trappe, J. M. 1962. Fungus associates of ectotrophic mychorrizae. Bot. Rev. 28:538-606.

Troendle, C. A. and C. F. Leaf. 1980. Hydrology. In: An Approach to Water Resource Evaluation of Nonpoint Silvicultural Sources. EPA 600/8-80-102.

USDA Forest Service, Eastern Region. 1980. Root characteristics of some important trees of Eastern forests. A Summary of the Literature. 217 pp.*

USDA Forest Service. 1931. Drought resistance of forest plants. Lake States For. Exp. Stn. Tech. Note 7, 1 p. St. Paul, Minnesota.

Veretennikov, A. V. 1964. The effect of excess soil moisture on transpiration of woody plants. Soviet Plant Physiol. 11(2):231-235. (Ru.ru.e.).

Verry, E. S. 1972. Effect of aspen clearcutting on water yield and quality in northern Minnesota. Proc. Am. Water Resour. Conf. 14:276-284.

Verry, E. S. 1976. Estimating water yield differences between hardwood and pine forests. USDA For. Ser. Res. Pap. 128, 12 p. North Cent. For. Exp. Stn., St. Paul, Minnesota.

Verry, E. S. and D. R. Timmons. 1977. Precipitation nutrients in the open and under two forests in Minnesota. Can. J. For. Res. 7:112-119.

Vozzo, J. and E. Hacskaylo. 1974. Endo- and ectomychorrizal associations in five Populus species. Bull. Torrey Bot. Club 101:182-186.

Weigle, W. G. and E. H. Frothingham. 1911. The aspens: Their growth and management. USDA For. Ser. Bull. 93, 35 p. Washington, D.C.

Wellington, W. G. 1952. Air mass climatology of Ontario north of Lake Huron and Lake Superior before outbreaks of the spruce budworm and the forest tent catepillar. Can. J. Zool. 30:114-127.

Wilde, S. A. and D. T. Pronin. 1950. Growth of trembling aspen in relation to ground water and soil organic matter. Soil Sci. Soc. Amer. Proc. 13:345-347.

Zahner, R. and N. A. Crawford. 1965. The clonal concept in aspen site relations. In: Forest-Soil Relationships in N. America, p. 229-243 (ed. Youngberg). 2nd North American Forest Soils Conference, Oregon State Univ., Corvallis, Oregon.*

Zan, M. 1968. Evaluation of the effects of reduced transpiration upon soil moisture retention in an aspen stand throughout the growing season in northern Utah. Utah Center for Water Resources Research Report 14-2. 57 p.

Zasada, Z. A., M. L. Heinselman, and G. K. Voigt. 1954. Potential productivity of forest lands in Pine, Carlton, Aitkin, and southern St. Louis counties, Minnesota. USDA For. Serv. Lake States For. Exp. Stn. Misc. Rep. 30, 53 p. St. Paul, Minnesota.*

Zimmerman, M. H. 1978. Hydraulic architecture of some diffuse-porous trees. Can. J. Bot. 56:2286-2295.