THE EFFECTS OF N, P AND K FERTILIZATION ON THE LOWER STEM XYLEM OF QUAKING ASPEN IN INTERIOR ALASKA

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THE EFFECTS OF N, P AND K FERTILIZATION ON THE LOWER STEM XYLEM OF QUAKING ASPEN IN INTERIOR ALASKA

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ABSTRACT

The effects of fertilizer on the xylem of aspen growing in the subarctic are unknown. A 14-year-old post-fire sucker stand of quaking aspen (Populus tremuloides) was used to study the effects of N, P, and K fertilization on the xylem of the lower stem. The factorial experiment involved four applications of N (111 kg/ha each), K (111 kg/ha each) and P (55 kg/ha each) over three years in interior Alaska. Xylem tissue of subject trees was examined in transverse section and through maceration techniques. Fiber length was significantly decreased by N ($\bar{x}$ = .626 mm, $p<.0008$) and increased by K ($\bar{x}$ = .673 mm, $p<.0001$) fertilization compared with the controls ($\bar{x}$ = .645 mm). Vessel element length was decreased by N ($p<.0015$), P ($p<.0659$), K ($p<.0614$) and P x K interaction ($p<.0282$). Width of fibers (N) and vessels (N and K) were also increased. K increased fiber wall thickness, and N and K increased vessel wall thickness. P significantly ($p<.003$) decreased fiber wall thickness. No significant difference in the ratio of vessel to fiber area was detected from transverse sections. N and K significantly ($p<.001$ and .048 respectively) increased annual ring width, with concommitant decrease in specific gravity. An N x K interaction decreased specific gravity compared with the controls. Regardless of treatment, fiber length was 35 percent or more shorter than was reported for same age trees in other parts of the aspen range. N dominated the cellular responses. N response generally decreases the wood's desirability for pulp, but the increased productivity of the tree offsets this shortcoming.

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INTRODUCTION

Natural Range and Site Description

Quaking aspen (Populus tremuloides Michx.) is the most widely distributed tree species in North America (Viereck and Little 1972). It extends from western Alaska continuously to the maritime provinces of eastern Canada. The southern-most portion of its eastern range reaches Pennsylvania, and the northern halves of Ohio, Indiana and Illinois. In the west it extends south along the Rocky Mountains into northern Mexico (Fig. 1, Harlow and Harrar 1958).

In Alaska, quaking aspen reaches the southern slopes of the Brooks Range, and occurs throughout the interior and westward to the Koyukuk and Kuskokwim Rivers and the village of Holy Cross. From the south on the Kenai Peninsula and the base of the Alaska Peninsula it extends through the south central portion of the state north of the Chugach Mountains and joins the interior forest.

Quaking aspen is a broadleafed tree commonly found on warm, well drained, benches and southerly exposures to nearly 1000 m elevation. Although found on well drained lowland soils, Gregory and Haack (1965) found that aspen in Alaska usually occurred on slope gradients between 10 and 50 percent and aspects between 95° and 300° true north. Within this range of aspects the majority (60 percent) of stands occurred between 150° and 210°. Cooler aspects (0° to 120°, 240° to 360°) were occupied by paper birch (Betula papyrifera Marsh.). Page (1972) reported that, in Newfoundland,

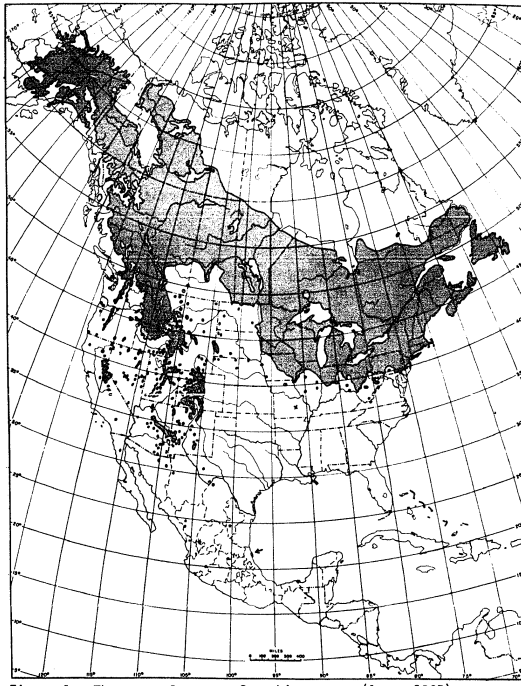

Figure 1. The natural range of quaking aspen (Anon. 1965).

aspen was almost entirely restricted to areas with a mean July temperature greater than 15.6°C, but found no correlation between aspect and aspen prevalence. Zasada and Schier (1973) found that low diurnal temperatures (20°C maximum and 10°C minimum) inhibited root suckering in three Alaskan aspen clones, whereas daily temperatures of 30°/20° and 25°/15° produced approximately equal numbers of suckers. From these laboratory data they suggested that aspen may be most common on relatively warm sites because of the importance of temperature to this form of reproduction.

Growth Rate

In interior Alaska quaking aspen is a relatively fast growing tree which can reach a diameter of 25 cm and a height of 27 m in 65 years on best sites (Gregory and Haack 1965). Lutz (1956) found 56-year-old dominant aspen 15-28 cm in diameter at breast height (1.4 m) and 20 m in height on the Kenai Peninsula.

A comparison of volume tables (Farr 1967 and Gregory and Haack 1965) reveals that aspen is superior to white spruce (Picea glauca (Moench) Voss) and paper birch (Betula papyrifera) with respect to the quantity of wood produced. On the best white spruce sites (site index 100), this species will produce 3.4 m^3/ha/yr (70 yr average, Farr 1967). Birch on better sites (index 65) can produce 3.6 m^3/yr/ha (65 yr average). By comparison aspen in the interior can produce 5.6 m^3/ha/yr (65 yr average, Gregory and Haack 1965).

Page (1972) reported that data from 94 plots in Newfoundland revealed aspen's capacity to produce 6.4 m^3/yr/ha (65 yr average).

Good sites in Saskatchewan are capable of producing 4.4 m^3/yr/ha (70 yr average, Kirby et al 1957).

Schlaegel (1971) evaluated aspen growth and yield in Minnesota. There with a site index of 90, he estimated an average of 7.4 m^3/yr/ha (60 yr average) wood production for aspen. Quaking aspen growth in interior Alaska compares favorably with growth in other portions of the aspen range.

Reproduction

This species has great potential for both sexual and vegetative reproduction. Lutz (1956) cited Reim who reported 400 - 500 x 10^6 seeds/ha in northern Europe during good seed years, with a single tree having the capacity to produce 54 x 10^6 seeds annually. Lutz (1956) reported that 41 percent of the aspen regeneration following a fire on the Kenai Peninsula were of seed origin. However, Maini (1972), found that seedling establishment under natural conditions was uncommon in Manitoba, which he attributed to short-term seed viability, and the presence of a water soluble germination and growth inhibitor in the seed hair. Zasada and Viereck (1975) obtained nearly 100 percent germination of Alaskan aspen seed under a series of temperature regimes from 5 to 25°C. However, young seedlings are extremely susceptible to damping-off and other soil fungi (Anon. 1974).

Aspen has a pronounced ability to produce adventitious root shoots (suckers). These originate from pre-existing shoot primordia, suppressed short shoots or newly initiated meristems on shallow roots (Schier 1973). Suckers emerge after a disturbance which

decreases or breaks apical dominance in the parent stem (Eliasson 1971, Steneker 1974). Schier and Zasada (1973) reported that the number of suckers produced by a root section was not correlated with root carbohydrate reserves, but found that subsequent sucker development was strongly dependent on these reserves. They also found that suckering capacity to be similar in material from Utah and from Alaska.

Light to moderate burning enhances sucker production (Shirley 1931, Lutz 1956 and Horton and Hopkins 1965), whereas intensive fires may be lethal to the sucker producing roots which are found within 5-15 cm of the soil surface (Viereck 1973). Fire is beneficial because it reduces the insulating organic mat and the blackened surface residue absorbs more solar radiation. The importance of warm temperatures to sucker production were discussed by Zasada and Schier (1973) and was suggested by Maini and Horton (1966) who reported that the greatest growth and numbers of suckers occurred at a constant temperature of 24°C. Viereck (1973) reported that 87000 stems/ha were present on areas previously occupied by aspen, following the 1971 Wickersham Dome (Alaska) fire. These stems reached a height of 2 m by 1973, despite animal browse during previous winters.

Stand Establishment

Because aspen is fast growing on better sites, and is an intolerant species, canopy closure is rapid and early mortality is high. Maini (1972) revealed that natural mortality will reduce a stand containing 99,000 stems/ha to 2470-3700 stems/ha in 30 years

and 740-1000 stems/ha at maturity (70+ years). Jones and Trujillo (1975) reported that on a stem count in a 22-year-old stand of sucker origin in Arizona, nearly 70 percent of tallied trees were dead or overtopped. They found an average of 17,908 stems/ha on four plots in the study. In areas of interior Alaska, with site index 75, Gregory and Haack (1965) reported a density of small aspen (1.27 cm diameter) to be 7474 stem/ha.

Aspen Utilization

Because of its texture, density and light color, aspen wood has good potential for utilization in particle board, excelsior, plywood, lumber core stock and furniture frames (Garland 1972) although its current use is principally pulp production. Specific gravity, fiber length and the content of lignin and other extractives are important when evaluating wood for making paper (Einspahr 1972). Wood of high specific gravity is desirable because a smaller volume of it is required for a given size batch of paper. Similarly, yield (weight of dry pulp/weight of dry wood), is associated with the suitability of wood for raw material. Extractive content (lignin, and other non-cellulosic compounds) as well as the type of paper product being produced, dictates the extent and kind of chemical process which is necessary for pulp production. Fiber length is fundamental to the strength of the final product as well as the workability of the pulp in paper making machines. Fiber cell wall thickness is also important, because thick-walled cells tend to retain their tubular form during processing, whereas thin-walled cells collapse readily. The latter contributes to better

interlacing of fibers and enhances paper strength.

Many characteristics of aspen make it an attractive tree species for commercial fiber production. Its propensity for regeneration by root suckers minimizes regeneration costs and risks, though ground scarification, prescribed burning or other techniques which disturb the forest floor enhance sucker production (Perala 1972). Mechanized harvesting such as the tree length system (skidding of limbed, tree length logs) and full tree system (skidding unlimbed logs) offer potential for disturbance which augment aspen regeneration (Zasada 1972) as well as economical harvesting.

Reference was made earlier to aspen's intolerance and resulting high early mortality of suppressed individuals. Such natural reduction of stand density diminishes the need for thinning, though Hughes and Brodie (1972) report that precommercial thinnings (yielding no commercial product) were responsible for reduced rotation time in Steneker's work and larger more sound logs for Zehngraff (1949). Such treatment, however, did not maximize profits over long rotation periods (Ibid.).

OBJECTIVES

Numerous investigators, cited herein, have studied the changes in quaking aspen xylem morphological characteristics as they occur under various growth conditions at more moderate latitudes. Because of their economic importance, fiber size, specific gravity and tree size were the main subjects of investigation. The current study, however, is more complete and is one of the first to be conducted in the sub-arctic, near the northern limit of the aspen range, where soils, temperature and light regimes are very different. It is the central hypothesis of the research that soil fertilization with nitrogen (N), phosphorus (P) and potassium (K) of native quaking aspen, growing under sub-arctic conditions, will alter the dimensions of xylem elements.

The primary objective of this study is to investigate fiber and vessel size, cell wall thickness, annual ring width and specific gravity as they are influenced in local quaking aspen by fertilization with N, P and K. Secondary objectives are to detect any differential cell responses by individual clones, to determine the fertilizer effects on the occurrence of gelatinous fibers and the percentage of growth ring cross-section occupied by respective cell types. The importance of this research is not only in determining the relationship between fertilizer treatments and tree responses, but the study may give insight into how the tree interacts with its sub-arctic environment. Because these characteristics

relate to the quality of the resource, as well as its management, such information is of practical value in view of the increasing interest in the utilization of hardwood forest resources of interior Alaska.

LITERATURE REVIEW

General

Aspen xylem is diffuse-porous with pores (vessels) distributed irregularly in clusters throughout a field of thin-to-medium-thick walled fibers when viewed in transverse section. The largest vessels are 50 to 100 microns (μ) in diameter and measure approximately .67 mm (S.D.= 0.18) in length. Fiber lengths average 1.32 mm (S.D.= 0.22) and are commonly .23 to .33 μ in diameter. Parenchyma are present in the form of rays, which are uniseriate, and terminal parenchyma which forms a narrow continuous or interrupted line of cells around the periphery of each annual ring. Specific gravity (oven dry weight/green volume) is approximately 40 g/cc (Brown et al. 1949).

WOOD PROPERTIES

Fiber Characteristics

Length -- Although Brown et al. (1949) reported that fiber lengths vary about a mean of 1.32 mm, others found this parameter more variable. Einspahr et al. (1967) reported a difference in fiber length with age. In aspen 31+ years-of-age, they recorded a mean fiber length of .93 mm; for 18 to 30-year-old trees, .97 mm and for 5-year-old trees, .67 mm. Einspahr et al. (1972a) investigated within tree variation in 10 to 17-year-old natural aspen and found that fiber length increased with age at a given level in a tree. Cell length in the outer growth rings was found to increase

from the base up to a point about 2 m above the ground, then decrease above that point. The length was found to decrease in early growth rings from base to the apex.

Johnson (1942) reported variability within the growth ring, with fiber length longest in the latewood. In addition, fiber length in Populus sp. hybrids was consistently greater in fast grown trees when compared with slower growing trees. Boyce and Kaeiser (1961) suggested that since fiber length increases from the inner to the outerpart of the ring, the wider the ring, the greater the volume of wood with long fibers and the higher the average fiber length for the tree.

Kennedy (1957) contrasted fiber length of slow growing black cottonwood (Populus trichocarpa Torr. & Gray) with untreated but fast growing trees. The slow growing trees (average age = 38 years) produced an average growth ring width of 2.73 mm; the faster growing trees, 7.1 mm wide. Fiber lengths were significantly longer in the latter group. As with Einspahr et al. (1972a), Kennedy's data revealed variation in cell length between different heights in the tree. For example, in the 10th growth ring from the pith, fibers were shorter at 5.5 m than at 1.4 or 11.0 m. This pattern was evident for both slow and fast groups.

In more recent work by Murphey and Bowier (1975), a 31 percent increase was found in the length of aspen fibers in the lower stem as a result of irrigation with municipal waste water. For eight years, at weekly intervals, the treated trees received 5.1 cm of municipal waste water which contained significant levels of

nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), chlorine (Cl) and trace elements. Einspahr et al. (1972b) tested the effects of irrigation only and irrigation plus fertilization on aspen growth. Their findings suggested that irrigation increases height growth and fertilization produces greater diameter growth. Fiber length was positively correlated with height growth. There was no significant difference in cell length between the fertilizer only and the control plots.

In a study of natural variation in fiber properties of aspen clones, Brown and Valentine (1963) found that fiber length was not related to growth as measured by ring width, and suggested that cell length is not affected significantly by environmental conditions. Further, they concluded that fiber length increases from the pith outward and is more a function of distance from the pith than the number of years of growth.

Using Populus trichocarpa and P. deltoides Marsh., Gabriel (1956) detected significant differences in fiber length between clones. He reported a 34 percent decrease in fiber length of P. trichocarpa from Alaskan clones compared with a clone from Washington state. Little information is available concerning differences in angiosperm cell length within a species as a function of latitude. However, Nylinder and Hägglund (1954) reported a decrease in tracheid length at sea level locations over a ten degree increase in latitude 55° to 65° N. Lat.) with Picea excelsa Link. A similar trend was reported by Ericson et al. (1973) with Pinus sylvestris L. over the same latitudinal range.

Foulger and Hacskaylo (1968) took another view of the environment-cell size relationship in a study of nutritional effects. Using 10 cm cuttings from eastern cottonwood (P. deltoides), they studied the effects of nutrient deficiency on stem anatomy at three heights in the subsequent growth. Deficiencies in N, K, sulfur (S) and boron (B) resulted in decreased fiber length at two or more heights in the stem. A reduction in fiber length was related to the absence of Cu, iron (Fe), Mg, manganese (Mn) and P. Fiber length, however, increased in the lower stem with the Cu and Mn deficient treatments.

Bhagwat (1967) studied the effect of mulching as well as fertilization with N, P and K in a factorial (2^4) experiment with eastern cottonwood cuttings. At the end of two growing seasons, following one application of treatments, he found a highly significant (at .01 level) increase in fiber length for all treatments, but detected no interactions the first year. In the second year, the main effects decreased in significance (to .05 level), but NxP, PxK and Kx mulching interactions became evident.

Foulger et al. (1971) investigated the effect of mineral nutrients on stem anatomy of eastern cottonwood seedlings. Though they did not quantify the relationship, they suggested that fiber length is closely associated with levels of N and K in the soil.

Width -- Using transverse sections and macerated tissue from cottonwood cuttings, Foulger and Hacskaylo (1968) found that N, K, S and B deficiency is also associated with reduced fiber length. In the same study, they found a high positive correlation between

fiber width and length in the middle and lower stem, as well as between fiber width and ring width. Although Johnson (1942) did not test for this relationship, his data support these correlations.

Bhagwat (1967) reported no nutrient effect in "percent of area occupied by lumens of fibers", but discovered that mulching has a significant (at the .05 level) effect. This parameter appears to be related to cross-sectional area, but it is not clear in the paper whether the change is the result of larger fibers or a higher percentage of fibers.

Therefore, the factors which influence aspen fiber size remain in question. The literature reveals that this characteristic varies with location within the tree, rate of growth and the type of growth, i.e., height or girth. One investigator suggested that cell size is not greatly influenced by environmental factors, and others contend that it is subject to indirect influence of soil moisture. There is reason to suggest that latitude may have an influence on cell size through its effect on such ecological factors as day length, length of growing season, summer diurnal temperatures or perhaps photoperiod.

Vessel Characteristics

Vessels form continuous ducts which transport water and dissolved nutrients from the root system into the leaves of deciduous trees. Larson (1974) described the complex patterns which trace the routing of the ducts through the stem into individual leaves. In the current study, "vessel" refers to the individual cell which is commonly termed the "vessel element" or "vessel member".

It has been my experience that few investigators have given attention to the responses of vessels to rates of growth or conditions of the environment.

Vessel length varies significantly between species. Black gum (Nyssa sylvatica Marsh.) has vessels ranging about a mean of 1.33 mm, whereas, those of osage orange (Maclura pomifera (Raf.) Schn.) and black locust (Robinia pseudoacacia L.) are near 0.18 mm in length (Brown et al. 1949). Length within a species is reported to be essentially determined by the length of the cambial initial, as lengthening is not thought to occur in the process of maturation as with fibers. To the contrary, especially in earlywood where large diameters in vessels are common, one finds vessels shorter than the cambial initials. In this case, shortening is thought to occur as the diameter increases (Brown et al. 1949).

From studies with eastern cottonwood, Larson (1974) postulated that vessel formation is controlled by the leaves (or leaf primodia) which the vessel is destined to serve. If this is correct, one would expect to find a relationship between the total leaf area in a tree and the total cross-sectional area of vessels in the sapwood. Grier and Waring (1974) found a direct relationship between the active water-conducting tissue (sapwood) and the foliage mass in Douglas-fir (Pseudotsuga mensiesii (Mirb.)Franco).

Based upon the assumption that vessels connect and form more or less continuous longitudinal elements, Taylor (1968) directly converted vessel cross-sectional area to vessel volume in his study with yellow poplar (presumably Liriodendron tulipifera L.).

Vessel volumes were greatly influenced by ring width, such that as much as 60 percent of the total wood volume as occupied by vessels in narrow rings, and as little as 30 percent in wide ones. He cited Desch (1932) who reported that the number of vessels increases with decreasing ring width. Taylor (1968) also reported an increasing percentage of vessels with increasing age, which presumably would equate with greater foliar surface.

No reference has been located which relates vessel characteristics to pulp or other product qualities. Since vessels are commonly thin walled and of comparatively large diameter, the lumen occupies the largest portion of their volume. Cell size then is of little economic importance except as it affects specific gravity, which is discussed later.

From the scientific standpoint, however, knowledge about the manner in which this cell type is controlled by the plant's environment is important since it contributes to the understanding of tree function. The literature suggests that vessel volume in a growth ring is related to ring width and age of the tree. This indicates nothing about individual cell size, since vessel volume is a composite of numerous individual cells. The implication that vessel formation may be controlled by foliar development, and the major role that vessels play in conducting water suggest that environmental influence is principally indirect. Mineral nutrition in this case may only affect vessel size as it relates to leaf size and development.

Specific Gravity

Valentine (1963) studied the natural variability in specific gravity of quaking aspen by comparing four clones in New York state. He reported that changes in specific gravity are not necessarily linear from the first formed to the other rings. This variable increases, then decreases in various portions of the ring series. Though genetic differences were apparent between clones, he concluded that this parameter in aspen is strongly influenced by the environment.

The influence of growth rate on specific gravity in poplars is not clear (Kennedy 1968). He cited Paul (1956, 1963) who summarized data from 360 specimens of poplar species and hybrids to find a negative linear relationship between growth rate and specific gravity.

Einspahr et al. (1972b) studying the effect of fertilization, irrigation and irrigation plus fertilization on 6-year-old quaking aspen reported an 8 percent decrease in specific gravity along with a 140 percent increase in volume when compared with control trees. Murphey and Bowier (1975) indicated a 2 percent decrease in specific gravity as a result of irrigation with municipal waste water. They reported that the crownwood specific gravity was 5 percent lower than that of the stem base in non-treated trees.

Johnson (1942) also reported changes in specific gravity of samples taken at various heights in Populus sp. Relatively high values were found in the stem base, but specific gravity decreased gradually to the 4.6 to 6.1 m level and then exhibited slight

increases toward the top of the tree. His study produced no significant correlations between specific gravity and growth rate. This observation was also made by Dickson et al. (1975). Kennedy (1968) who reviewed the work of Boyce and Kaeiser (1964), Farmer and Wilcox (1966) and Walters and Bruckman(1965), reached the same conclusion concerning the relationship between growth rate and specific gravity. He indicated that the latter two investigations dealt with a narrow range of growth rates and suggested that a wide range of growth rates must be studied before any effects become evident. Brown and Valentine (1963) reported negative as well as positive correlations between growth rate and specific gravity in aspen clones. Kennedy (1968) suggested that since this was the only investigation which reported positive correlations, the bulk of the evidence indicated that a negative correlation exists between specific gravity and growth rate. He further suggested that the relationship is not strong and may be of little practical importance in Populus species.

In 7-year-old sycamore (Platanus sp.), Saucier and Ike (1969) reported a lack of response of cell characteristics in individual growth rings as a result of treatment at different levels of N, and K. They found a higher specific gravity in trees showing the more vigorous growth. Wooten et al. (1973) reported a similar response to thinning of mature Liriodendron sp. In spite of increased diameter growth, the trees showed a slight increase in specific gravity.

Taylor (1968) found only a slight negative correlation (3 trees negative and 3 trees positive) between ring width and specific gravity in Liriodendron sp. His study showed a strong negative correlation between vessel volume and specific gravity. Fiber length, however, was positively correlated with specific gravity.

Cell Wall Thickness

Larson (1973) related cell wall thickness and lumen size to specific gravity in coniferous species. The phenomenon of wood cell production is basically dependent upon two separate processes in the tree. Growth regulator production which usually is increased by terminal and needle growth (Wareing et al. 1964), and photosynthesis which provides carbohydrate for cell wall synthesis are two essential factors. Larson also described three types of coniferous wood which may be formed in one growth ring. Earlywood is characterized by large diameter, thin-walled tracheids. This cell form is associated with high auxin levels, adequate water supply and low to moderate supplies of photosynthate. Transition-wood frequently found in the crown near the source of carbohydrate is characteristically composed of tracheids with large diameter but thick cell walls. This formation occurs as a result of high auxin levels, plentiful photosynthate and adequate water supply. Latewood is composed of radially narrow cells with thick walls. Conditions associated with these characteristics are high photosynthate levels (Parkerson and Whitmore 1972) as a result of a full complement of old and new needles, lower concentrations of growth regulators because of the cessation of terminal and needle growth, and

frequently lower water availability.

Echols (1972) examined the response of ponderosa pine (Pinus ponderosa) to thinning and thinning plus fertilization. He observed that untreated trees increased in specific gravity, released trees increased growth with a decrease in specific gravity and thinned plus fertilizer treated trees increased in specific gravity.

Gladstone and Gray (1973) discussed the effects of fertilization on wood quality. They described a study with slow growing red pine (Pinus resinosa Ait.) in which K was applied to overcome a deficiency of that element. This treatment resulted in a substantial growth increase. Though there was a lower proportion of latewood in the fertilized trees, there was essentially no difference in specific gravity. The authors cited Gray (1970) who investigated the K effect on the stem anatomy of the same trees. Gray related that the latewood of the treated trees had 20 percent thinner cell walls than the control trees, but that earlywood tracheids walls were 200 percent of the controls.

No literature was found which relates growth rate to cell wall thickness in hardwood species. It is likely that similar relationships exist in hardwoods as in coniferous species and that these would help explain the controversy which exists concerning relationships between growth and specific gravity.

Gelatinous Fibers

Tension wood is characteristically found on the upper side of branches and leaning stems of hardwood species. Its presence is

usually associated with eccentric growth in the area of maximum development (Brown et al. 1949).

According to Wardrop and Dadswell (1948, 1955), who were cited by Isebrands and Parham (1974), tension wood in Populus ssp. is characterized by fibers having a gelatinous innermost layer of the cell wall. Isebrands and Parham described the gelatinous layer as being cellulosic, highly crystalline, and loosely attached to the innermost cell wall layer. Isebrands and Bensend (1972) contended that the occurrence of gelatinous fibers is not restricted to branches or leaning stems, but is commonly found in the crown-formed wood of eastern cottonwood. They cited Berlyn (1961) and suggested that tension wood may be associated with rapid growth in straight erect stems.

Kennedy (1968) stated that few data are available on the comparative mechanical characteristics of tension wood versus normal wood. He indicated a higher specific gravity for tension wood, but suggested that the strength characteristics may be reduced. Isebrands and Parham (1974) comment that pulp made from tension wood usually results in paper with reduced strength resulting from bulkiness associated with the gelatinous layer. This condition hinders fiber collapse, limits inter-fiber bonding and, because of discontinuities such as slip planes and minute compression failures, decreases the strength of individual fibers. Perem (1964), however, found no difference in the average length of fibers from tension wood when compared with normal wood.

NUTRITION

The primal source of most essential mineral nutrients to plant growth is the earth's crust. An abundance of individual nutrients is by no means universal, though in time, through weathering and translocation they may enter the realm of organic tissue.

In the forest ecosystem, the organic layers on and in the forest floor represent an important reservoir of nutrients which are necessary for plant growth. They are considered to be a major source of essential macro- and micro-nutrients (Buckman and Brady 1969, Van Cleve 1971), but the elements are incorporated in complex substances which must be decomposed before the nutrients are available for plant uptake.

It is through the activity of a host of soil organisms that this process takes place. Two important factors which influence such activity are temperature and moisture (Rode 1955, Van Cleve 1971). According to the Thornthwaite (1931) evapotranspiration system, the climate of interior Alaska is classified as semi-arid with little or no excess rainfall. Though dryness may be critical within the area in soils of steep south facing bluffs along the river systems, such sites occupy a relatively small percentage of interior Alaska. More common, on north aspects and lowlands are perched bogs, underlain by permafrost (perennially frozen soil) that prevents surface water infiltration. Between these two extremes are the more moderate south slopes or coarse river alluvial deposits were no permafrost occurs and best tree growth is to be found (Viereck 1973).

Krause et al. (1959) discussed the dramatic influence of north and south aspect topography on soil characteristics and forest growth in the uplands of interior Alaska. Much of the difference that they reported is the result of temperature and its interaction with vegetation. Soils were colder and wetter and available nutrients and soil pH were reduced on north slopes where open, low growing spruce forests (Viereck and Little 1972) persisted. The partially frozen soil was covered by 25 cm of slightly decomposed mosses and 7 cm of living Sphagnum spp. mosses. In contrast, on the southerly exposure, the site supported a stand of white spruce with dominant trees approaching 28 m in height. Mineral soil in this stand was covered by 5 cm of partially decomposed moss and other plant parts, and a 3 cm thick layer of living Hylocomium spp. mosses.

Scotter (1971), also working in coniferous stands, reported higher midday summer temperatures in burned-over areas where the insulating, unincorporated organic material had been consumed by fire than in unburned, but unshaded areas of a mature forest. The blackened surface of the former absorbed more heat during the long summer days, though this was thought to be offset by increased reradiation at night. He found that soil temperature was 5.85°C warmer at 2.5 cm depth and 5.44°C warmer at 7.6 cm depth in areas which had been burned 5 to 22 years previously, than in unburned areas. Barring complete combustion of organic matter, Lutz (1956) suggested that soil nutrient status can be improved by burning, due to increased nitrification and release of nutrients by increased populations and activity of soil organisms.

In aspen stands of interior Alaska organic matter varies in thickness from 5 to 10 cm (Lutz 1956). Van Cleve and Noonan (1975) studied the litter fall and nutrient cycling for four years in three different aged aspen stands of interior Alaska. Table 1 reveals the mass of mineral nutrients which accumulates over time in this forest type. In a different study, Van Cleve and Noonan (1971) investigated the mineral content of different organic layers of seven aspen stands of ages between 20 and 120 years. Highest concentrations of nutrients were consistently found in the deeper humus layers.

As suggested earlier, the availability of mineral nutrients can be altered by forest fire, which has been an important part of the Alaskan forest environment (Viereck 1973). Fire can drastically change the status of mineral nutrient of the soil, thickness of the organic layers and soil organism activity, but its effect is varied due to different soil types, slopes, intensity of burn and material consumed (Lutz 1956, and reviewed by Viereck 1973). Horton and Hopkins (1965) reported that aspen stands in Ontario (Canada) were generally found not to support high intensity fires, due in part to the lack of sufficient fuel and moist organic matter (25 percent or greater moisture content) which is common in that locality. In Minnesota, Perala (1974) found that in aspen prescribed burning had no significant effect on the organic horizon characteristics when compared with only clearcut. Removal of overstory, however, was reported to accelerate organic matter decomposition and its incorporation into mineral soil.

Table 1. Average mass and nutrient content of aspen forest floor in different age classes (from Van Cleve and Noonan 1975).

Status (g/m^2)	Age in years		
	10	50	120
N	8.9	76.1	107.5
P	0.7	8.1	8.6
K	0.8	8.8	13.0
Ca	11.2	68.0	78.6
Mg	0.8	10.8	16.7
Fe	0.9	27.9	27.6
Mn	0.1	9.4	7.8
Zn	0.1	0.3	0.6
Biomass (ashfree)	508.2	3828.0	5922.6

Nitrogen

According to Auchmoody and Filip (1973) who reviewed forest fertilization in northeastern United States, nitrogen is the soil nutrient which most limits the productivity of hardwood forests. Van Cleve (1973) suggested that the status of post-fire nitrogen is a critical factor in subsequent forest development. Ellenberg (1971) emphasizes this nutrient's importance by stating that, after temperature and water, the N supply is the most important environmental factor limiting the productivity of green plants.

Hacskaylo et al. (1969) studied the effect of nutrient deficiencies on growth and foliage color of eastern cottonwood seedlings. Seedlings with N deficiency were half the height of controls (complete nutrient complement) after 77 days of growth. Supplied with N, however, the P-deficient and K-deficient plants were 3/4 and 7/8 the height of the control, respectively.

Much of the importance of N relates to its incorporation in plant cell materials such as chlorophyll, enzymes, structural proteins and nucleic acids which comprise 40 to 50 percent of the dry matter of protoplasm. This explains why plants demand such an abundant supply of this element (Hacskaylo et al. 1969).

Except in fertilization, nitrogen generally requires the activity of organisms to convert it from its elemental form (N_2) to one which is useable to higher plants. One exception is that elemental N is thought to be converted to the ammoniacal and nitrate form by electrical discharge in the atmosphere and added to the soil in precipitation. In areas of high rainfall as much as

9.4 kg/ha/year are known to be contributed from this source (Buckman and Brady 1969). In semi-arid interior Alaska this source probably is of low importance.

The fixation of atmospheric nitrogen is known to be accomplished by some fungi and blue-green algae (Wilde 1958) as well as through symbiotic activity between certain vascular plants and specific bacteria which infect the plant root system to form nodules. In addition to legumes, which are commonly known for such relationships, members of the Alnus, Elaeagnus, Myrica and Shepherdia genera also have this capacity (Buckman and Brady 1969). Since these groups are represented in the flora of interior Alaska (Hultén 1968, Viereck and Little 1972) they may be extremely important to the nitrogen balance of the forest floor in this region.

Nitrogen is most generally usable to plants in the nitrate form though the ammoniacal form and amino acids are thought to be utilized by certain genera of coniferous plants (Wilde 1958). No reference was found which indicates that aspen absorbs nitrogen in other than the nitrate form. However, under suitable conditions, amino acids decompose to yield ammonia and ammonia is oxidized to nitrite and nitrate (nitrification) by bacteria of the forest floor. This process may not proceed rapidly unless soils are aerated and acidity is moderate or adequate base elements are available (Buckman and Brady 1969). These requirements, in addition to factors of moisture and temperature mentioned earlier, suggest why nitrogen may be the nutrient most limiting aspen growth on offsite locations.

Phosphorus

No other element, with the possible exception of N, is as critical to field plants (Buckman and Brady 1969). The importance of this element is its key role in photosynthesis and respiration, as well as its incorporation in cell membranes and nucleic acids (Salisbury and Ross 1969, Conn and Stumpf 1967 and Nason and McElroy 1963).

The availability of phosphorus is primarily governed by factors which control soil pH. Buckman and Brady (1969) suggest an optimum soil pH between 6.0 and 7.0 However, Truog (1948, cited by Bould 1963) was more restrictive on the lower pH and suggested that the availability of this element drops rapidly at values below 6.5, and that it is most available between pH 6.5 and 7.5. Under acidic conditions phosporus forms insoluble compounds in complex with iron, aluminum and magnesium ions. Conversely, strongly alkaline soils result in the formation of insoluble calcium phosphates (Bould 1963, Buckman and Brady 1969).

Organic matter is a principal source of phosphorus which, as with nitrogen, is released during decay. Unlike nitrogen, however, some phosphorus may be supplied from certain parent material, but this process is slow. Here soil bacteria and fungi may be involved, due to the release of organic acids and CO_2 originating from microbial metabolism (Murometsev 1955, cited by Nicholas 1963). Other bacteria are capable of releasing phosphorus from iron phosphates as well as calcium phosphates (Nicholas 1963). Rode (1955) suggested that mycorrhizae play an important role in phosphorus uptake.

Gessel (1962) advised that phosphorus availability to forest trees is a perplexing problem in soil analysis. He related that under similar conditions one species responds to P treatment, whereas another does not. He described the experience of Tidball (1957), who found that heating soil, as by forest fire, made P available when tested by common extraction methods. Phosphorus uptake on these soils by Douglas-fir, however, was decreased.

Potassium

This mineral is usually present in plants in greater quantities than any other element derived from the soil except hydrogen and nitrogen (Black 1968). Gessel (1962) uses data from Ovington and Madgwick (1959) to show that 42 and 22 percent, respectively, of potassium in a Pinus resinosa ecosystem are incorporated in litter and the boles of trees. Another 21 percent was tied up in living leaves. Potassium has been shown to accumulate in aspen litter (Table 1) and is a component of ash residue following forest fire.

Potassium is generally present in mineral soils in greater amounts than are nitrogen or phosphorus, particularly in soil of feldspar and mica origin. It is released in weathering or other breakdown from such material (Black 1968). Acidic conditions favor the replacement of K^+ ions from adsorption sites by aluminum (Al^{+++}) and hydrogen (H^+) and favors their leaching from the soil.

The specific role of potassium within the plant is unknown. It is thought to play an important part as an enzyme activator, particularly with enzymes concerned with protein synthesis. deficiencies of this element are associated with such problems as

disturbed carbohydrate metabolism, decreased photosynthesis and insufficient chlorophyll production. Potassium is found in plants in the form of inorganic salts and salts of organic acids, particularly in areas of high metabolic activity (Nason and McElroy 1963). This contrasts with the previous elements which are commonly incorporated in structural compounds.

DESCRIPTION AND HISTORY OF THE STUDY AREA

The study plots are located in the upper Chena River basin approximately 40 km northeast of Fairbanks, Alaska (64° 53' N. Lat. and 147° 57' W. Long.) on a well-drained level lowland site at 240 m elevation. Mean precipitation and temperature for the growing season (May 2 to Sept. 14) over the past five years at the study site are 22.6 cm and 11.9°C.

The original forest cover was destroyed by fire in 1958[1/]. The present stand is of sucker origin. Age of the forest at the time of the fire was approximately 35 years (Van Cleve 1973). Site index of an unburned portion of the original aspen stand is near 50 (Gregory and Haack 1965).

Soil of the study area is very deep (>2 m) well drained Salchaket sandy loam (texture: 30 percent sand, 60 percent silt and 10 percent clay[2/]). The bulk density is 1.13 g/cc at the surface and increases to 1.46 g/cc near the 1 m depth. Soil pH is slightly to moderately acid with values ranging from 5.2 to 6.5 (Table 2 and 3).

1/ Personal communication: Mr. Carl Jeglum, Chief, Division of Resource Management, Bureau of Land Management, Fairbanks, Alaska 99701.

2/ Unpublished data provided by Dr. Keith Van Cleve, Forest Soils Laboratory, University of Alaska, Fairbanks, Alaska 99701.

Table 2. Status of selected soil nutrients and soil pH prior to fertilizer treatments.[2/]

Nutrient	Depth		
	0-2.5 cm	2.5-20 cm	at 38 cm
N (percent)	0.16	0.40	0.15
P (percent)	0.15	0.075	0.075
K me/100 g*	1.05	0.72	0.075
pH	5.2	6.1	6.3

* Exchangeable, per 100 g of dry soil.

Table 3. Soil respiration, percent organic matter and pH at two depths on the study area after six years of fertilization [2/].

Treatment	Depth of sample (cm)	Respiration (μl of O_2 uptake 100/hr)°of soil ($\bar{x}$)	Organic Matter ($\bar{x}$)	pH ($\bar{x}$)
N	0-15	258.4	4.6**	6.1**
	15-30	55.8**	2.5	6.5
P	0-15	327.5*	4.7**	6.2
	15-30	108.4	2.6	6.5
K	0-15	176.8	4.0	5.9**
	15-30	35.6	2.0	5.9**
NP	0-15	339.7	5.2	6.0
	15-30	49.2	2.6	6.3
NK	0-15	254.8	4.9**	5.6**
	15-30	109.2**	2.5	5.8**
PK	0-15	209.3	5.3*	5.9**
	15-30	48.5	2.8	5.7**
NPK	0-15	209.5	5.0*	5.8**
	15-30	91.3	2.6	5.9**
Control	0-15	179.8	3.5	6.4
	15-30	23.1	2.5	6.3

* Difference between treatment and control is significant at 5 percent level.

** Difference between treatment and control is significant at 1 percent level.

Pretreatment cation exchange capacity (C.E.C.) was high, 29.5 milliequivalents/100 g (dry soil) in the first 2.5 cm of depth, but dropped to 12.0 milliequivalents/100 g at 20 cm. At the depth of 80 cm, C.E.C. was 7.0 milliequivalents/100 g of soil. Table 2 shows the pretreatment nutrient status for selected minerals.

During the fall of 1969, a complete factorial fertilizer trial was established using a randomized block experimental design replicated three times. Only two of the three replications were used in this study. Nitrogen at 111 kg/ha, N as NH_4NO_3, phosphorus at 55 kg/ha, P as treble super phosphate and potassium at 111 kg/ha, K as KCl were applied four times; at the end of the 1969 growing season and before tree growth started in the springs of 1970, 1971 and 1972. A total of 444 kg/ha N and K and 220 kg/ha P had been applied in the three applications prior to the 1972 growing season.

Site Research History

Van Cleve (1973) initiated the study in 1969 and investigated the growth response after two years of fertilizer application. He reported that N produced a 12.6-fold increase in tip growth over control. Combinations of P and/or K produced no significant increase over the N effect. Stem diameter at breast height (1.4 m) was significantly (at .01 level) increased by each nutrient and interactions were found to occur in NP and NPK treatments.

In 1974 Coyne and Van Cleve (1977), studied the chemical and leaf morphological responses of quaking aspen to mineral nutrient treatments. By sampling leaves from only the N, NP, NPK and

control plots they found that N fertilization resulted in a greater than two-fold increase in leaf area and biomass. This increase was the result of increased leaf numbers and not increased leaf size. Foliar mineral nutrient content/gram of leaf weight was higher in fertilized versus control plots, though non-structural carbohydrates were found to be lower in N treated than in control plots. Foliar content of N, P, and K was increased in all cases where these nutrients were applied to the soil, however, N significantly reduced K, Ca and Mg in the leaves.

In 1975, soil samples were collected from each plot to determine the influence of six years of annual fertilization on selected qualities of the site (Table 3 and Table 4).

Table 4. Concentrations of N, P and K in soil from N, P_2/K and control plots after six years of fertilization[2/].

	Percent Total N		Percent P		K(me/100 g)	
Depth (cm)	Control	N plot	Control	P plot	Control	K plot
0-15	0.054	0.082**	0.11	0.14	0.14	0.41
15-30	0.028	0.035	0.09	0.10	0.11	0.18

** Difference between treatment and control is significant at 1 percent level.

METHODS

Clone Delineation

Aspen differs from other tree species in Alaska because of its capacity to produce root suckers prolifically following the destruction of an original stand. Thus the subsequent stand consists of genetically identical groups of individuals (clones) which range in size from several stems to clusters covering two or more acres (Steneker (1973a) cites Blake 1964). One objective of this study was to separate responses due to clonal differences.

Clone delineation can be based on sex of tree, phenology (ie. flowering, bud break, autumn color) and various morphological traits such as bark color and texture, shape of floral bracts, number of leaf margin serrations, leaf shape and petiole length (Barnes 1969). In the present study flowering and sex were of no use since only six trees, all males in an NP treatment, produced flowers. Phenological observations disclosed only very general differences between trees and were not useful in determining clones on an individual tree basis.

Six dominant or co-dominant aspen were selected from within each treatment plot. Each tree was evaluated for this selection based upon its crown stem bark color, stage of bud development (opening) and/or bark color on the north and south sides of the lower stem.

On June 6 and 21, 1972, nine leaves were collected from the

lower crowns of selected trees on the following predetermined basis:

1. Three leaves were collected from each of three origins; a branchlet < 2.5 cm long, a branchlet > 2.5 cm but < 12.5 cm in length, and one ≥ 12.5 cm long (Barnes 1969).

2. The branchlets were to be located on the same major branch, which was the lowest one greater than 50 cm long and containing 5 or more branchlets. In the event the major branch lacked sufficient branchlets of the prescribed size, a branchlet was selected on the nearest major branch. Leaves from each collection date were pressed and dried. Subsequently, measurements were made of blade width, blade length and petiole length. Serrations were counted along one-half the margin of each leaf.

An analysis of variance was performed on the measured leaf variables. Petiole length was found not to be useful in clone delineation with these trees. However, the statistical analysis of leaf blade ratio (width/length) and serrations allowed the selection of two or more trees of different clonal origin within each treatment. On the advice of Dr. Harbo, [3/] in cases where the analysis revealed two or more trees to be members of the same clone, a second tree was selected to be used as an alternate, or to detect within clone variation. If needed, in cases where a second ramet was not found through the analysis, an alternate was selected at the time of sampling on the basis of root connections, bark characteristics and/or proximity to the previously selected tree.

[3/] Dr. Samuel J. Harbo, Chairman, Program in Wildlife and Fisheries, University of Alaska, Fairbanks, Alaska.

Two ramets of two clones were selected from each treatment plot within each replication.

Sample Collection and Processing for all Xylem Cell Characteristics

During the last week of September 1972, a 10 cm section was removed from the lower 20 cm of the stem of each tree. An effort was made to avoid collecting portions of the lower stem which revealed butt swell or bend. Each stem sample was placed in an appropriately marked plastic bag, transported to the laboratory and stored at -17°C.

Each 10 cm sample provided three radial sectors for transverse sections, three for maceration and three for specific gravity determinations. After the ends of each sample were squared, a straight reference mark was scribed down the end of the section (Fig. 2). The squared end was subdivided into 6 equal sectors. Alternate sectors were marked I, II, or III. The length was then cut 4 cm from the squared end, and corresponding sectors were marked on the newly cut surface of the 4 cm long piece. The extra piece was saved in case additional material was needed. Then the 4 cm length was cut into two 2 cm lengths and each 2 cm piece was cut along the marks which separate the six sectors.

From A, sectors I, II, and III were used for transverse cell measurements. Sectors I, II and III from B were used for maceration and the three remaining sectors of B were used for specific gravity determinations.

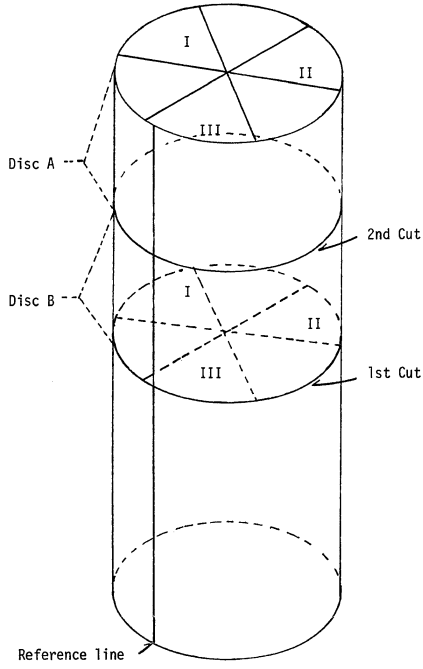

Figure 2. Diagram of the pattern used to cut samples from stem sections.

Transverse Sections

Sample Preparation -- Each sector was trimmed with a razor blade so that the radial sides were smooth, and the surface to be microtomed was flat and parallel to the labeled bottom surface. All bark was removed. It was found that slicing was facilitated by saturating the sectors with water. Saturation was accomplished by placing the sectors from a given tree in a 50 ml beaker containing distilled water and exposing it to a vacuum of 686 mm of mercury. Vacuum treatment was repeated until all sectors sank when returned to atmospheric pressure.

The sectors were then individually attached, with the labeled surface contacting the freezing stage of a sliding microtome using a 5 percent solution of gelatin as a bonding agent. The gelatin was liberally applied to the stage and the surface of the sector. During cooling, additonal solution was applied to the junction of stage and sector in order to strengthen the bond. Cooling was applied to the stage only to affix the sector to the stage during microtoming. The surface to be cut was not frozen.

After squaring the surface with the microtome, several 20 micron (μ) sections were sliced from the sector and placed in a container of distilled water. These were placed in a 2.5 cm x 2.5 cm Lab-line tissue carrier, which had been marked to indicate the sector number, tree number, treatment and replication number corresponding to the section's origin (Fig. 3).

The tissue carrier containing the sections was then submerged for 10 minutes in a .5 percent safranin O stain solution

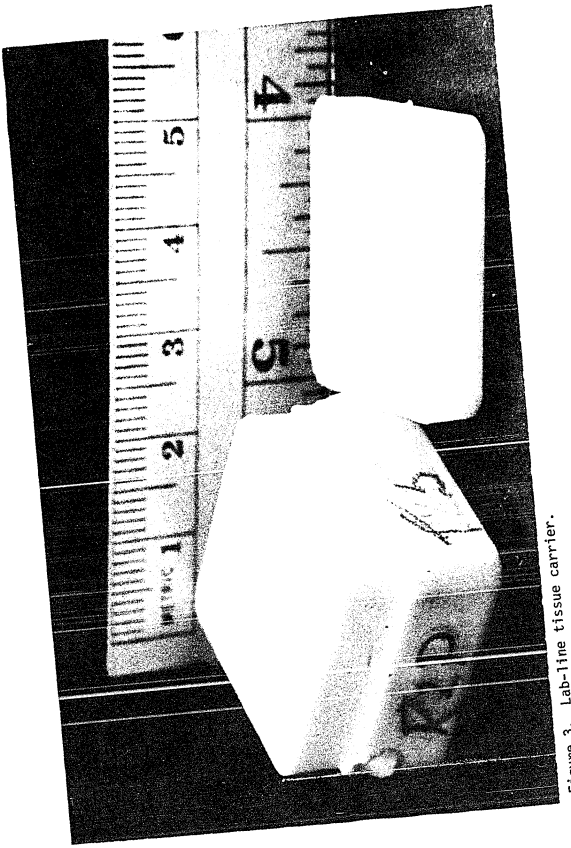

Figure 3. Lab-line tissue carrier.

(Johansen 1940). Destaining was accomplished with three one minute rinses in 50 percent ethanol baths. The sections were removed from the carrier and placed in distilled water from which they were mounted individually on labeled microscope slides. After one drop of glycerine was applied to each section, it was covered with a cover slip. This staining was found to be sufficient to provide the contrast necessary for subsequent photomicrography.

Photomicrography -- All photomicrographs were taken through a compound stereo-microscope using a 10X objective lens and with a 12.5X eyepiece mounted in the camera adapter. Exposures of 1/60th second on Kodak Panatomic X black and white film were made with a 35 mm single-lens-reflex camera body with built-in exposure meter. Light intensity for each exposure was controlled by use of the microscope sub-stage diaphragm and an attenuated light source. The film was given normal development in Kodak Microdol X developer at 25.6°C.

A series of photomicrographs was taken starting at the outside edge of the 1972 growth ring and progressing radially to include the entire 1967 ring. Within a sector a complete series included three rings of fertilizer treated, and three rings of pre-fertilizer treated growth, except where, for reasons discussed later, it was difficult to distinguish positively the 1970 from the 1969 growth. In this case the series was extended to include what may have been pre-1967 growth rings. Each developed roll of film was cut into 5 exposure strips, catalogued and stored in a negative holder.

In order to take measurements from the negatives, a negative

holder was constructed to fit a 35 mm slide projector, so that the negatives could be projected (Fig. 4). In addition to photographing the transverse sections, a photomicrograph was taken of an object micrometer, which is a .10 and .01 mm scale in the form of a microscope slide. Since the optics of the microscope-camera combination were the same as for the transverse sections, the resulting negative was used to calibrate a hand-held scale with which cell measurements were taken from the projected images.

Growth Ring Width Measurement -- The 1972 and 1971 growth rings were also measured using the series of photomicrographs. Again, the object micrometer negative was used to calibrate a hand-held scale. Ring widths were measured to the nearest .01 mm in the three sectors from each tree.

Cell Sampling and Measurement Techniques -- To obtain a random sample to determine frequency and dimensions of vessels, gelatinous fibers and normal fibers a grid was constructed and attached to the surface on which the photomicrographs were projected. The grid was drawn on transparent plastic and was constructed so that a dot screen could be placed behind it.

Five random dot screens were made to fit behind the grid. Each screen had 100 dots randomly located on it using computer generated pairs of random numbers. Each dot represented a potential sample point. The dot screens were arbitrarily numbered 1 thru 5 and one was randomly selected for each transverse section. When a dot screen was placed behing the grid, one would see a field of random dots upon which the grid was superimposed.

Figure 4. Slide projector with negative carrier.

Cell Frequency and Dimensions -- Twenty points within the 1971 and 1972 growth rings of a radial series were sampled to determine the frequency as well as radial and tangential dimensions of each of the cell types. To select a sample point, pairs of computer generated coordinates were used. Each pair designated a point on the line grid. The nearest random dot was used as a sample point and the cell type and the dimensions of the cell which was projected on that point were recorded. Dimensions were measured to the nearest micron (μ). For each growth ring in the tree there were 60 sample points (3 sectors X 20 points/sector = 60).

Cell Wall Thickness -- To sample for vessel and fiber wall thickness, only the line grid was used. In this instance 10 vessels and 10 fibers were randomly selected from the 1971 and 1972 growth rings of the photomicrograph series. There were 30 wall thickness points (10 points/sector X 3 sectors = 30 points) for each (1971 and 1972) growth ring. As before, a pair of random coordinates was drawn to determine a sample point. At each point, four cell wall measurements were taken from the vessel and four from the fiber whose center was nearest the sample point. Thicknesses were measured in microns and represented half the distance between the lumen edge of the sampled cell and the lumen edge of the adjacent cell.

Maceration

Considerable effort was expended to develop a satisfactory maceration technique for the aspen tissue. Initial efforts followed suggestions by Dr. A. N. Foulger[4/] which involved treating the wood

with a solution which was composed of equal volumes of glacial acetic acid and hydrogen peroxide (30 percent strength). The tissue was boiled in the solution over a hot water bath. After the tissue took on a bleached appearance, it was stirred periodically with a glass rod in order to break apart intact pieces. The treatment was continued for different periods, some as long as six hours. The process met with moderate success, resulting in incomplete separations of cells at one extreme and complete digestion of vessel elements at the other. The most successful treatment schedule produced a high percentage of fragmented cells. After some experimentation it was determined that the process described below resulted in more complete maceration with a low percentage of damaged cells. Tissue from the three sectors of each tree was pooled and macerated as a composite sample. Pre- and post-fertilization rings were treated separately, such that 1971 and 1972 rings were treated together as one sample and the 1968 and 1969 rings were treated as another sample.

One transverse surface of each sector from a tree was trimmed using a razor blade. Then, using a dissecting microscope, the 1971 and 1972 rings were separated from the earlier formed rings. An effort was made to place the separation cut in the earlier portion of the 1970 ring so that tissue from this fertilization year would be included with the 1971-1972 tissue. This was often difficult

4/ Dr. A. N. Foulger, Technologist, Quality and Yield Improvement in Wood Processing, Timber Utilization Research, U. S. Forest Service, Forest Products Laboratory. P.O. Box, Madison, Wisconsin 53705.

since the 1970 ring was often indistinct.

The tissue was then oven-dried at 105°C for 24 hours or, until weight stabilized. Shavings approximately 1-2 mm thick were then cut radially from each piece so that all growth periods of each growth ring were represented in the maceration. Each shaving was then cut tangentially so that the resulting pieces were approximately 1 x 2 x 20 mm (l x w x h) in size. Fifty to sixty mg of this material were combined from each sector into an appropriately marked test tube. A 6 mm glass bead weighing 285 mg (±5mg) and 3.0 ml maceration solution (60 percent acetic acid and 40 percent H_2O_2 (30 percent) were added to each tube. The tubes were placed in a bath of ethylene-glycol at 105°C for 2.5 hours. At the end of the 2.5 hours, the contents of the tube were washed with three 30 ml aliquots of distilled water. Between washes the macerated tissue was concentrated in the bottom of the tube by centrifugation, and the supernatant was discarded.

After the washes, the tube, containing the glass bead and digested tissue, was gently shaken with a minimum of water so that the bead moved around the bottom of the tube breaking up the particles of digested tissue.

When it appeared that the tissue was separated, the contents of the test tube were poured into a beaker and brought up to a volume of 75 ml with distilled water. The 75 ml volume was stirred to assure a homogeneous suspension of cells, and one ml of the suspension was introduced into an appropriate compartment of the sedimentation chamber.

The sedimentation chamber was a 28(l) x 20(w) x 20 cm deep tank (Fig. 5). It contained a 15 compartment insert, which would support, in a horizontal position, standard 25 x 75 mm microscope slides. Each slide was supported 7 mm above the compartment floor which contained 12-2.5 mm holes in the bottom of each compartment for drainage.

In operation, labeled slides were positioned in the bottom of each compartment of the chamber. The chamber then was placed inside the tank and the tank partially filled with water gradually so as not to disturb the slides. An aliquot of macerated tissue was introduced to each compartment, and 10 minutes were allowed for the cells to settle onto the slides. A tap on the tank, below the level of the slides was opened to allow the tank to drain slowly, without causing turbulence in the compartments. After the water level dropped below the level of the slides, the slides were removed and air-dried.

Measurements of Macerated Tissue

Forty vessels and forty fibers were measured from each dried slide of tissue from fertilized as well as pre-fertilized growth rings using a compound microscope with a ground glass viewing screen (Fig. 6). After calibrating a rule using the object micrometer, it was used to take all measurements.

Starting in the upper left hand corner of the specimen area on the slide, sampling was accomplished by scanning across the width of the slide, then shifting one view field to the right and scanning

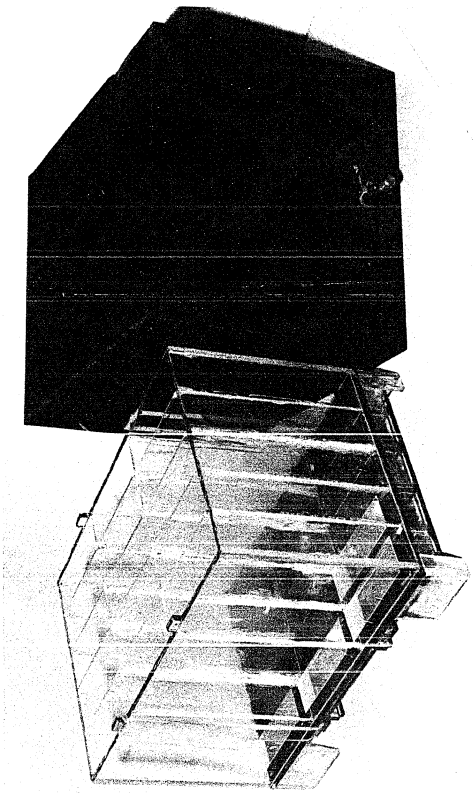

Figure 5. Sedimentation chamber and tank.

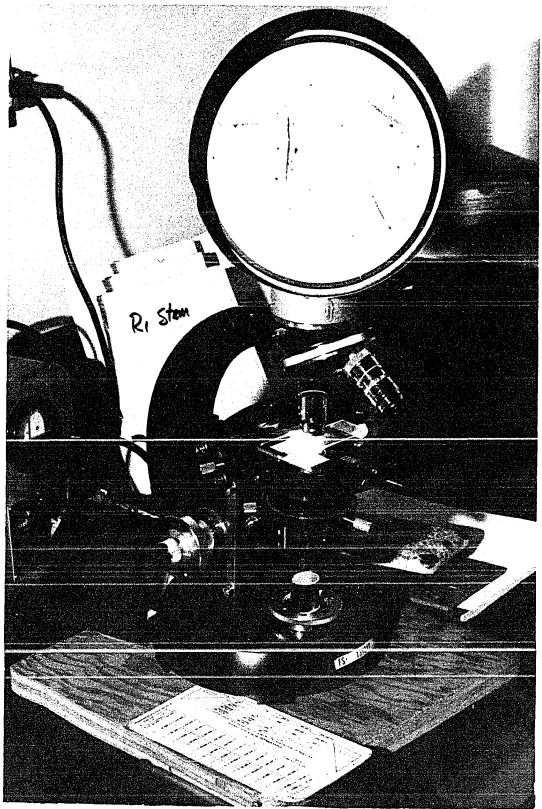

Figure 6. Compound microscope with viewing screen.

back across the slide, and so forth until 40 of each cell type were measured.

Fiber Measurements -- Total length and maximum width measurements were taken only from intact fibers, and ones which were distinctly not two joined fibers. An occasional fiber was encountered which showed indistinct lines longitudinally. Since such lines could be portions of the cell wall between two unseparated fibers, cells with such lines were omitted from the sample.

Vessel Measurements -- Only complete separate vessels were measured. On each cell, total length, trunk length and maximum width (Fig. 7) were measured.

Specific Gravity

Specific gravity determinations were made on only the 1971 and 1972 annual rings from each tree. As with the maceration proceedure, the 1971-1972 growth rings were separated from earlier formed wood using a dissecting microscope and razor blade. The three samples were saturated as described under Transverse Sections and Measurements.

To determine saturated volume, each sample was wiped to remove excess surface water and affixed to a dissecting needle. The sample was then immersed in a beaker of distilled water on a 160 gram capacity top-loading balance. By subtracting the water weight from the weight after immersion, the weight of the displaced water was determined. Since distilled water weighs (at 20°C) 1 gram/cubic centimeter, the volume in cubic centimeters was determined. Volume was recorded to the nearest .001 cc (1.0 μ^3).

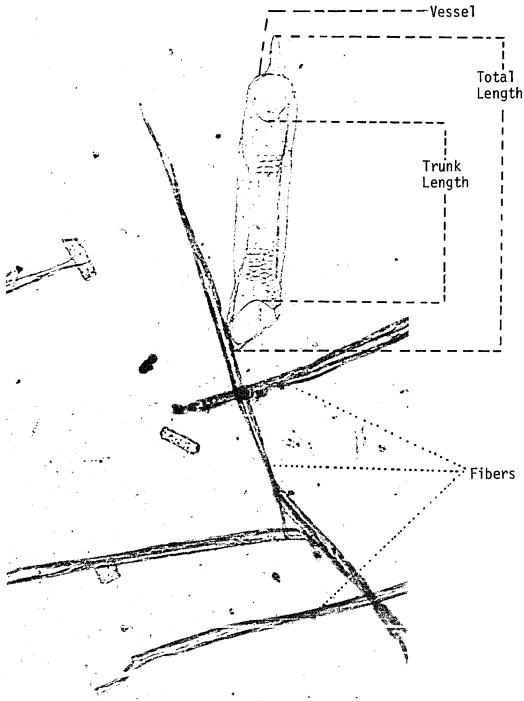

Figure 7. Vessels and fibers from macerated tissue.

To determine dry weight, the samples were oven-dried at 105°C until weight loss was no longer detected. Each sample was then quickly weighed to the nearest milligram. Specific gravity was calculated by dividing dry weight by wet volume.

Statistical Analysis

All of the data from the transverse sections were entered on standard computer cards and processed by computer.

Cell Frequency and Dimensions -- The type of cell (i.e. vessel, fiber or gelatinous fiber) and its dimensions were recorded from 20 sample points per sector in the 1971 and 1972 growth rings. This resulted in unequal numbers of observations for each cell type within a ring, but allowed for an assessment of size and frequency of each type to be recorded in one sampling. Individual cell cross-sectional areas were computed and are the product of the two dimensions from each cell.

Cell Wall Thickness -- Four cell wall thickness measurements for 10 fibers and 10 vessels within the 1971 and 1972 growth rings of each sector were recorded. The four wall measurements from each cell were averaged to provide a mean wall thickness for that cell and it was processed as an observation for that cell.

Specific Gravity -- Although specific gravity determinations were not taken from the transverse sections, the data were processed in the same manner. One determination was made from each sector and contained 1971 and 1972 growth ring tissue. Each determination represented one observation.

Processing -- Data from each of the transverse sections and specific gravity were submitted to a computer for multivariate analysis of variance. This procedure provides for testing the significance of main effects (N, P and K separately) as well as interactions, such that the response of a combination of two or more nutrients is significant only if it is different from the sum of the responses of the individual nutrients. In addition, the analysis tests significance between growth rings (years) and replications (blocks).

Maceration Data Analysis -- Since tissue was macerated from pre-fertilized as well as fertilized years, in each tree a covariate analysis of variance was used. This analysis adjusts the treatment means to account for differences within the tree and allows for more precise comparisons among treatments (Snedecor and Cochran 1968). A multivariate analysis is performed on the adjusted means so that the significance of interactions and block effects are also tested.

RESULTS AND DISCUSSION

Clone Delineation

Clone delineation in this study concerned only the clonal structure of individual treatment plots. As a result no relationships are known between plots. For this reason it was considered statistically impractical to separate clonal variation in response to treatments across all treatments.[5/] The exercise, however, did reveal that clones were numerous and small on the study site. Frequently, three or more of the six originally selected stems in each 405 m^2 plot were different in leaf characteristics, which, according to Barnes (1969), are good criteria for clone separation.

An analysis of variance was performed on fiber lengths taken from maceration data to test for clonal influences on fiber length. All clones in the NPK were used and separate analyses were performed on pre- and post-fertilization data. F-values were 18.13 and 13.65 respectively significant at the .01 level of probability. Tukey's ω procedure (Steel and Torrie 1960) was used to test differences between means.

It will be noted (Table 5) in block 1 that before treatment, clones 1 and 2 did not have significantly different fiber lengths, but that clones 3 and 4 from block 2 did. Clones 1 and 2, however,

5/ Dr. John Hazard, Biometrician, Pacific Northwest Forest and Range Experiment Station, P. O. Box 3141, Portland, Oregon 97208

Table 5. Fiber length of four aspen clones before and after fertilization with NPK.

	Block 1		Block 2	
	Clone 1	Clone 2	Clone 3	Clone 4
Pretreatment lengths (mm)	0.6484*	0.6488*	0.6126	0.5375
NPK-treatment lengths (mm)	0.6911	0.6609*	0.6550*	0.5795

* Mean values which share the same underline are not significantly different at the .01 level.

are significantly different according to the test from 3 or 4. After NPK treatment, however, a different pattern became evident. Clones 2 and 3 were not significantly different, despite being located in different blocks.

Ring Width

The addition of nitrogen in any treatment yielded a 228 percent or greater increase in mean ring width over the control (Table 6). These findings agree with the diameter growth response observed by Van Cleve (1973). Similarly, Bhagwat (1967) shows the highest F-value for N in the first year diameter growth responses.

In the current study only N and K produced significant growth ring responses, with no interaction indicated. Though the K response is significant at the .048 level, it produced only a 18.5 percent increase over the control.

Although no significance is indicated for the P effect, P produced growth rings which were 17 percent less than control. This is contradictory to the findings of Saucier and Ike (1969) and appears to disagree with findings of Van Cleve (1973) and Bhagwat (1967) who report significant increases in stem diameter as a result of P fertilization. However, in this study only xylem responses were measured whereas diameter growth, as measured by Van Cleve, incorporated phloem production and tissue formed by a second meristem, the phellogen (cork cambium). This cambium produces phellum (cork) to the outside and phelloderm, which resembles cortical parenchyma to the inside (Esau 1967).

Table 6. Summary of ring width analysis and stem diameter growth.**

Treatment	Ring width Treatment Means (mm)	Percent of Control	F-Value	p<	Stem diameter increase (cm)**
N	2.86	156.9	108.924	.001*	0.61
P	0.93	-17.0	0.634	.452	0.26
K	1.32	118.5	5.720	.048*	0.30
NP	3.36	202.0	0.277	.615	0.77
NK	3.62	225.0	0.035	.857	0.65
PK	1.62	145.3	0.001	.975	0.26
NPK	3.66	228.5	1.352	.283	0.93
Control	1.11	------	-------	----	0.21
Year	-----	------	187.113	.001**	----
Block	-----	------	5.422	.053*	----

* Significance at level indicated.
** Stem diameter increase is the mean of 1970 and 1971 growing seasons from trees in the same study plot as used in this study (Van Cleve 1973).

Wareing et al. (1964) suggested that growth regulator imbalance can alter the normal production of xylem and phloem by the vascular cambium. From work with Acer, Populus and Fraxinus they found that application of only auxin to the cambium zone resulted in production of predominantly xylem tissue, the addition of only gibberellin favored phloem production and the combination of the two resulted in the production of both tissues simultaneously.

Auxin transport is basipetal in the stems of most plants and the growing apical meristem is the main source of supply of this growth regulator (Leopold 1964). In Van Cleve's (1973) study, tip growth was not significantly greater in the P treatment than in the control, so that the auxin status may have been low. No information is available which suggests the status of gibberellin in trees of the P treatment.

Viro (1974) found with two species of birch that, depending upon the rate of application, P fertilization had suppressing effects on stem diameter growth. With Betula verrucosa Ehrh. a total treatment of 40 kg/ha of P_2O_5 produced increased stem diameters over six years. However, 80 kg/ha of the same fertilizer produced stems which were smaller than the controls over the same time span. With Betula pubescens Ehrh., both levels of P were found to reduce stem diameters.

Specific Gravity

Nitrogen fertilization decreased the specific gravity of the xylem. An average 5 percent decrease in specific gravity is evident in all treatments containing N (Table 7). The NK interaction

Table 7. Summary of specific gravity analysis.

Treatment	Treatment Mean (g/cc)	Percent less than control	F-Value	p<
N	.407	4.7	6.816	.035*
P	.424	0.7	0.649	.447
K	.407	4.7	0.331	.583
NP	.397	7.0	1.218	.306
NK	.415	2.8	5.994	.044*
PK	.414	3.0	0.296	.603
NPK	.407	4.7	0.086	.776
Control	.427	---	-----	-----
Block	----	---	0.731	.421

* Significant at level indicated.

however, counters this trend. NK produced the second largest ring width (Table 6), 225 percent wider than the controls, but the smallest reduction in specific gravity among the N containing treatments. The K treatment showed a significant ($p<.048$) increase in ring growth, although it was only 18 percent greater than the control. The specific gravity of the K treatment is less than the control by about the same amount as are the N, NP and NPK treatments, which exhibited a 200 percent or greater increase in ring width over the control. This is contrary to the findings of Bhagwat (1967), who reported an increase in diameter growth and specific gravity as a result of K fertilization, but no change of specific gravity by N or P in spite of significantly increased diameter growth. P produced no significant positive growth responses and did not significantly alter specific gravity. In general the finding in this study agree with Kennedy (1968) who suggested that specific gravity is negatively correlated with rate of growth.

Cross-sectional Area of Individual Cells

Fibers -- Among all the fibers, gelatinous as well as normal, individual cell cross-sectional area is increased by N treatment. The N effect is strongest with the gelatinous fibers ($p<.016$ in Table 8d). Interaction of NxK also shows high significance ($p<.027$) in all fibers, but the greatest interaction response is among the normal fibers (Table 8c). Though no interaction is indicated for NxK on gelatinous fibers, that treatment produced the largest response in the gelatinous fibers ($281.2\mu^2$). The highest

Table 8a. Summary of combined (normal and gelatinous) individual fiber cross-sectional area analysis.

Treatment	Treatment Mean Area (μ^2)	Percent of Control	F-Value	p<
N	279.8	135.9	7.46	.027*
P	216.9	105.3	0.21	.659
K	232.5	112.9	0.12	.731
NP	254.0	123.4	4.17	.081*
NK	254.8	123.7	7.74	.027*
PK	253.8	123.3	0.08	.785
NPK	230.7	112.0	0.05	.834
Control	205.9	-----	----	----
Block	-----	-----	4.81	.064*
Year	-----	-----	31.449	.001*
Year X treatment		-----	3.196	.063*

* Significant at level indicated.

Table 8b. Mean individual normal fiber cross-sectional area by treatment in the 1971 and 1972 growth rings with respective percentage increase over control cells.

Treatment	1972 Treatment Mean Area (μ^2)	1972 Percent of Control	1971 Treatment Mean Area (μ^2)	1971 Percent of Control
N	307.5	145	250.7	129
P	224.8	106	197.2	101
K	235.0	111	236.5	122
NP	268.3	126	242.1	124
NK	250.0	118	246.9	127
PK	254.6	120	257.9	132
NPK	233.5	110	228.3	117
Control	212.6	---	194.5	---

Table 8c. Summary of individual normal fiber area analysis.

Treatment	Treatment Mean Area (μ^2)	Percent of Control	F-Value	p<
N	280.6	138.4	7.01	.033*
P	213.0	105.0	0.15	.709
K	236.6	116.7	0.15	.710
NP	255.5	126.0	3.03	.126*
NK	248.3	122.4	10.94	.013*
PK	257.4	126.9	0.23	.645
NPK	231.3	114.1	0.01	.922
Control	202.8	-----	----	----
Block	-----	-----	6.85	.035*
Year	-----	-----	29.54	.001*
YearXtreatment	-----	-----	5.42	.015*

Table 8d. Summary of individual gelatinous fiber area analysis.

Treatment	Treatment Mean Area (μ^2)	Percent of Control	F-Value	p<
N	276.2	126.1	10.11	.016*
P	231.7	105.8	0.69	.434
K	218.7	100.2	0.02	.882
NP	248.4	113.4	8.24	.024*
NK	281.2	128.3	0.36	.566
PK	241.8	110.4	0.14	.720
NPK	226.9	103.6	0.75	.415
Control	219.1	-----	-----	----
Block	-----	-----	0.185	.680
Year	-----	-----	23.998	.001*
YearXtreatment		-----	1.066	.460

* Significant at level indicated.

of all significant responses on the cross-sectional area of individual normal fibers is that of NK ($p<.013$).

In addition to fertilizer effects, the analysis of individual normal fiber area (Table 8c) indicated treatment x year interaction ($p<.015$). This effect is not indicated for the gelatinous fibers, but is strong enough to be significant ($p<.027$) when the combined normal and gelatinous fiber data are analyzed (Table 8a).

Mean individual normal fiber areas were calculated separately for 1971 and 1972 growth rings (Table 8b). Among the main effects, it will be noted that nitrogen increased normal fiber area by 45 percent in 1972, and only 29 percent in 1971. P produced a similar response, but K gave increased percentages in 1971 over 1972. In interactions, the NxP increases are about the same in each year. PxK, NxK, and NxPxK produced larger increases in 1971. Temperatures were cooler in 1971 (discussed later in Year Effects) which puts the responses in an interesting perspective. The percentages over the control are consistently higher for treatments containing K in the cooler year.

Vessels -- Nitrogen is the only treatment which induced a significant increase in individual vessel cross-sectional area (Table 9). In spite of the tendency of P and K to reduce vessel area, NPK increased this characteristic by 31 percent over the control compared to an increase of only 22 percent for N alone. No interaction, however, is indicated for this combination of nutrients. Similarly, NP produced vessels with the largest cross-sectional area, with a 37 percent increase over the control, but with no

Table 9. Summary of vessel cross-sectional area analysis.

Treatment	Treatment Mean Area (μ^2)	Percent of Control	F-Value	p<
N	1785.8	121.5	13.65	.008*
P	1332.8	-9.3	0.50	.502
K	1432.5	-2.5	0.10	.767
NP	2006.6	136.5	0.56	.478
NK	1791.2	121.9	0.34	.598
PK	1570.1	106.8	0.20	.669
NPK	1921.7	130.7	0.63	.454
Control	1469.8	-----	-----	----
Block	------	-----	.001	.975
Year	------	-----	21.026	.002*
YearXtreatment		-----	0.893	.553

* Significant at level indicated.

interaction evident.

Several problems exist with respect to use of individual cell cross-sections to measure cell characteristics. Fibers are cells with tapered forms that are widest near the cells mid-point when viewed longitudinally. Therefore, any transverse section of the stem reveals numerous fibers, each cut at a different point on its longitudinal axis, so what appears to be a small fiber, in reality may be a cross-section from the tapered end of a large fiber. To a limited extent the same problem may exist with vessels. Though these cells are characteristically cylindrical, a section through the juncture of two vessel elements may give an erroneous image of the true cross-sectional area of the vessels involved.

From a statistical standpoint, it will be noted that the techniques used for sampling cell frequency and dimensions (Methods) resulted in an unequal number of observations per mean (See Appendix). As a result, standard deviations for the observations which contribute to the means are of less value for comparing treatment means than if a better sampling scheme had been utilized.

In addition, individual cell cross-sectional area used in the analysis is the product of two dimensions taken from each sampled cell. While one may expect that a sizeable sample of tangential or radial dimensions will produce a normal (bell shaped) distribution curve, the product need not be normally distributed. A curve was drawn for vessel and fiber area frequencies from all treatments which revealed some skewness. After consultation with biometricians

(Dr. Harbo[3] and Dr. Hazard[5]) it was concluded that the skewness would not greatly alter the results of an analysis. It is, nevertheless, felt that a better assessment of changes in cell characteristics was derived from measurements of macerated tissue (See Cell Width).

Cell Wall Thickness

Fibers -- Both N and K treatments produced approximately 5 percent increases in fiber wall thickness, but the K response ($p<.038$) has a higher level of probability than N ($p<.142$, Table 10). The K effect, which also significantly increased vessel wall thickness, was reported by Gray (1970) for red pine tracheids. Bhagwat (1967) found that N, P and K significantly increased fiber wall thickness.

Phosphorus produced the greatest significance level ($p<.003$), but its effect was to decrease wall thickness by 2 percent when compared with the controls. Its negative effect can be detected in the NP treatment, which produced cell walls 1 percent thinner than the controls in spite of the presence of N. Though NPK cell walls were thicker than those of the controls, they were thinner than in either N or K treatments, which further suggests the negative effect of phosphorus in that treatment.

Vessels -- Vessel walls, as with previous parameters, were significantly increased by N treatments (4 percent, Table 11); K also produced a significant increase (2 percent). P treatment reduced wall thickness by 2 percent, and though no strong interaction was apparent ($p<.111$), PK produced a 2 percent increase. It may be noted that the NPK treatment produced cell walls which

Table 10. Summary of the fiber wall thickness analysis.

Treatment	Treatment Mean (μ)	Percent of Control**	F-Value	p<
N	3.8	105.0	2.74	.142*
P	3.5	-2.0	19.77	.003*
K	3.8	104.8	6.47	.038*
NP	3.5	-1.4	0.73	.420
NK	3.7	104.1	2.42	.164*
PK	3.6	100.4	0.12	.740
NPK	3.6	101.3	2.82	.137
Control	3.6	-----	----	----
Block	-----	-----	21.79	.002*
Year	-----	-----	10.62	.012*
YearXtreatment		-----	0.67	.692

Table 11. Summary of vessel wall thickness.

Treatment	Treatment Mean (μ)	Percent of Control**	F-Value	p<
N	2.9	104.2	7.447	.029*
P	2.7	-1.8	0.204	.655
K	2.9	102.4	5.945	.045*
NP	2.8	100.6	0.352	.572
NK	2.9	103.3	0.010	.925
PK	2.8	101.8	3.338	.111*
NPK	3.0	107.2	1.814	.220
Control	2.8	-----	-----	----
Block	-----	-----	48.246	.001*
Year	-----	-----	18.355	.003*
YearXtreatment		-----	1.594	.263

* Significance at level indicated.
** Percentages are based on treatment means carried to three decimal places.

are 7 percent greater than the controls, but this response was not significantly different from the means of the elements supplied separately.

Cell Length

Fibers -- Fiber length in this study was closely associated with nitrogen and potassium. This is in agreement with Foulger et al. (1971), who found in eastern cottonwood seedlings that with low levels of K, increasing levels of N decreased fiber length, and that with moderate to high levels of N, an increase in K induced longer fiber formation. In this study N was found to decrease fiber length significantly (-2.9 percent, $p<.0008$) compared with the control (Table 12). K, on the other hand, increased ($p<.0001$) cell length by 4.3 percent. No significant interactions were indicated, but the depressing effect of N can be seen in the resulting lower mean fiber lengths in NK and NPK treatments.

In the current study N treatments resulted in formation of the largest ring width (Table 6) and also reduced fiber length. These findings are contrary to the findings of some workers (Johnson 1942 Kennedy 1957, 1968) who found positive correlation between ring width and fiber length, and Bhagwat (1967) who found that N soil enrichment enhanced fiber length as well as diameter growth in young eastern cottonwood. This study is not in total disagreement with that concept, since K (Table 6, Table 12) produced larger rings with longer fibers.

Johnson (1942), who reported that in Populus spp. the length of fibers formed increased toward the end of the growing season,

Table 12. Summary of fiber length analysis.

Treatment	Adjusted Treatment Mean (mm)	Percent of Control	F-Value	p<
N	.626	-2.9	39.307	.0008*
P	.646	100.1	2.017	.205
K	.673	104.3	89.829	.0001*
NP	.618	-4.1	1.456	.2730
NK	.657	101.0	0.664	.4463
PK	.670	103.9	0.130	.7312
NPK	.649	100.7	0.106	.7562
Control	.645	-----	------	-----
Block	-----	-----	1.7835	.2302

* Significant at level indicated.

suggests that a relationship exists between the shorter fibers of earlywood and the more rapid rate of growth during that portion of the growing season. It is plausible to suggest that the same relationship exists with increased growth as a result of fertilization.

Vessels -- All fertilizer treatments resulted in shorter total vessel length than the control. Of the individual elements, N was responsible for the most significant ($p<.0015$) change with an 8.8 percent decrease in vessel length (Table 13a). P and K reductions were significant ($p<.07$) and decreased length by 7.9 percent and 1.6 percent respectively. A PxK interaction was significant ($p<.0282$) but resulted in cells only 1.2 percent shorter than in the control.

Vessel trunk length (Table 13b) showed similar percentage decreases with fertilizer treatment, but only N produced a main effect with significance ($p<.0178$). An interaction of PxK is revealed, as it was with total vessel length, but in this case the mean trunk length was longer than in the control. Both cases suggest that the combination of P and K will produce a response less than the sum of separate responses of P and K.

Bhagwat (1967) found significant changes in vessel length (total) of young cottonwood plants as a result of fertilization with N, P and K. The second year after treatment he reports significant (at .05 level) NxP and PxK interactions though none were evident the first year. He suggested in his discussion that the changes in cell length were positive, but provides no data for fertilization.

Table 13a. Summary of total vessel length.

Treatment	Adjusted Treatment Mean (mm)	Percent of Control	F-Value	p<
N	.404	-9	30.50	.0015*
P	.408	-8	5.04	.0659*
K	.436	-2	5.28	.0614*
NP	.387	-13	0.97	.3634
NK	.406	-8	0.02	.8855
PK	.438	-1	8.29	.0282*
NPK	.411	-7	0.51	.5021
Control	.443	----	-----	-----
Block	-----	----	2.60	.1579

Table 13b. Summary of vessel trunk length analysis.

Treatment	Adjusted Treatment Mean (mm)	Percent of Control	F-Value	p<
N	.215	-9	10.47	.0178*
P	.216	-8	0.82	.3994
K	.226	-4	0.82	.4002
NP	.204	-13	0.04	.8543
NK	.212	-10	0.13	.7353
PK	.238	+1	4.41	.0804*
NPK	.212	-10	0.92	.3754
Control	.235	--	----	-----
Block	-----	----	0.90	.3807

* Significant at level indicated.

Foulger et al. (1971) found that N and P were each influential in determining vessel length. The N effect was reported to be quite distinct, such that as N increased, vessel length decreased. Phosphorus effects were not as conclusive, but findings suggested that above a threshold level of P, further increase can result in a reduction of length. They reported no K effect on vessel length.

Cell Width

Fibers -- In spite of the fact that all fertilizer treatments resulted in the formation of wider fibers, only N produced significant ($p<.0130$) differences (Table 14). Though no significance is given to the K response, the probability level ($p<.3444$) is much lower than that for other non-significant treatments ($p<.56$ or greater). This suggests that a K effect exists. Though no interactions were observed, it will be noted that combinations of nutrients containing N and K produced the largest percentage of fiber width increase over the control. Fiber cross-sectional area (Tables 8a and c) shows significant NxK interaction, which further suggests K has an influence on cross-sectional dimensions.

Foulger and Hacskaylo (1968) report N, K and S deficiencies were associated with the decreased fiber width. They also report a high correlation between fiber length and width. This would support the concept that suggests the existence of a K effect on fiber width, since K produces the most significant ($p<.0001$, Table 11) increase in fiber length. However, the correlation does not hold true for N, since it significantly decreased fiber length and

Table 14. Summary of fiber width analysis.

Treatment	Adjusted Treatment Mean (μ)	Percent of Control	F-Value	p<
N	18.7	113	12.19	.0130*
P	17.4	105	0.01	.9190
K	17.8	107	1.05	.3444
NP	18.7	113	0.02	.8909
NK	19.4	117	0.08	.7852
PK	16.9	102	0.38	.5602
NPK	19.7	119	0.33	.5857
Control	16.6	---	----	-----
Block	-----	-----	2.81	.1446*

* Significant at level indicated.

increased fiber width in this study.

Vessels -- As with fiber width, N produced the largest significant ($p<.0004$) increase in vessel width (Table 15). However, K also produced significantly ($p<.0731$) wider vessels. Once again, the combination of N and K produced the greatest increase over the controls, though no interaction is indicated.

Foulger and Hacskaylo (1968) reported that N deficiency significantly decreased vessel widths at all levels of the stem. K deficiency produced this effect in samples from the middle and top of the stem. Foulger et al. (1971) reported that P had the most profound effect on determining vessel width in cottonwood seedlings. They also reported that N and K played a role, but only in interaction with P. Nothing in the current study suggests that such an interaction relationship exists.

One would expect to find a relationship, such as the N effect, to exist between cross-section area (Table 9) and vessel width, since width is one of the dimensions used to determine area. Except for N, however, such a relationship is not evident. Where K significantly increased vessel width (Table 15), it, as well as P, produced smaller vessel areas than for the controls. While such an apparent discrepancy tends to cast doubt on the influence of P and K in effecting the width and breadth of vessels, the consistency of the N effect suggests that N has a dominating effect on these dimensions.

Occurrence of Gelatinous Fibers

Gelatinous fibers occur on the upper side of a stem which has

Table 15. Summary of vessel width analysis.

Treatment	Adjusted Treatment Mean (μ)	Percent of Control	F-Value	p<
N	77.7	116	50.34	.0004*
P	67.2	---	0.08	.7877
K	71.1	106	4.71	.0731*
NP	77.0	115	0.002	.9622
NK	79.6	119	0.23	.6510
PK	70.0	104	0.02	.9013
NPK	79.6	119	0.13	.7277
Control	67.0	---	----	-----
Block	-----	-----	0.02	.9064

* Significant at level indicated.

been leaning (Brown et al. 1949) and this occurrence is usually consistent for two or more rings. That was seldom the case, as nearly all of the fibers were found to be gelatinous on one side of the 1972 and none were found in that side of the 1971 ring. The 1971 ring frequently had one or more patches elsewhere in the ring.

An analysis of variance was performed on the percentage of fibers which were gelatinous from the 1972 growth ring. Variance was great and means were not significantly different, but differences do exist (Table 16). It will be noted that N and NPK contained the lowest percentage values, and that the control is near the overall mean (22.7 percent). It was noted that gelatinous fibers were not as common in control sectors, but when they were encountered, they frequently exceeded 50 percent of the fibers which were sampled.

Kennedy (1968) suggested that higher specific gravity occurs in poplar xylem with gelatinous fibers than in xylem without these fibers. The values found here agree with Kennedy, since N, NP and NPK had the lowest percentage of gelatinous fibers and also had the lowest specific gravity (Table 7).

It is not possible, using these data, to definitely associate any treatment with the occurrence of gelatinous fibers. The N and NPK treatments which resulted in the highest growth rates produced the lowest percentage of gelatinous fibers. This is contrary to the suggestion by Berlyn (1961), who reported that tension wood is associated with rapid growth in straight erect stems. The fact that P, PK and K (Table 16) had the highest percentage of gelatinous

Table 16. Percentage and occurrence of gelatinous fibers.

Treatment	Percent of fibers sampled which were gelatinous.	Occurrence of sectors with no gelatinous fibers sampled.
N	15.9	3 of 48
P	26.1	3 of 48
K	28.6	1 of 48
NP	20.2	5 of 48
NK	24.1	2 of 48
PK	28.0	4 of 48
NPK	14.9	8 of 48
Control	23.9	11 of 48

fibers suggests that a relationship may exist between P and K, and the formation of gelatinous fibers.

Total Vessel Area

An analysis of variance was performed to determine if the total cross-sectional area of vessels within a tree changed as a result of treatment with N, P or K.

After converting the percentages from the 1972 growth ring of each sector by angular transformation (Steel and Torrie 1960), the data were submitted to a one-way analysis of variance. There were 24 values per treatment. No significant difference was detected between treatment means.

Mean values were calculated for all treatments (Table 17), but no consistent trends were observed except that most treatments containing nitrogen had a smaller area occupied by vessels than did other treatments or control. Considering the observation by Coyne and Van Cleve (1977) that nitrogen treated trees had almost twice the leaf area of control trees, and the realization that the increased surface represented increased transpiration surface, it was desireable to compare water conducting (ie. vessel) areas.

Assuming an initial stem diameter of 4 cm, an annual increase in stem cross-sectional area was calculated for N treatment and control trees. Using the mean ring width (for 1971 and 1972, Table 6.) as an increment of radius expansion, an increase in stem cross-sectional area was calculated for two growing seasons. The added area was multiplied by the respective percentage of area occupied by vessels (Table 17) to give an indication of higher water

Table 17. Average area occupied by vessel + fibers which was occupied by vessels.*

Treatment	Percent Average	Standard Deviation
N	70.3	10.2
P	71.3	11.7
K	75.8	9.2
NP	70.4	11.4
NK	70.6	12.5
PK	72.2	10.7
NPK	77.4	10.2
Control	75.7	10.2

* Calculation for percent vessel area:

$$\text{Percent Area (each sector)} = \frac{\Sigma(\text{area each vessel sampled})}{\Sigma(\text{area each fiber sampled}) + \Sigma(\text{each vessel sampled})}$$

conducting potential. On that basis, N treated trees increased vessel area by 5.77 cm^2 in two years as compared with 2.28 cm^2 for control trees. This represents a 2.5-fold increase for N treated trees. Considering the observation of Coyne and Van Cleve (1976) this increase suggests that in aspen as with conifers (Grier and Waring 1974), increased foliar transpirational surface is supported by increased water conducting capacity of the vascular system.

Year Effect

Year effect was significant at the .01 level or higher in each analysis where it was tested. Temperature data from the study site[2/] between May 20 and July 20 show that portion of the 1971 growing season to be cooler than 1972. The average of weekly high temperatures during that period was 29.8°C in 1972, but only 26.6 in 1971. It is likely that the difference is a major cause of the year effect.

Although the average of the weekly low temperatures was about the same (+.22°C for 1972 and +.57°C for 1971), 1972 had minimums below 0°C through June 12. In contrast, 1971 had more fluctuating low temperatures. May 18 had a low of +12°C, followed the next week by -7°C. Again on June 6, the low for the week was +3°C, followed by a week in which -5°C was recorded. It was probably the freezing temperatures which occurred during a period of rapid cambial activity that caused a band of distended irregular cells about midway in the 1971 growth ring (Figure 8). The band closely resembles frost damage which is depicted and described by Brown et al. (1949). The damage was not evident in all trees within a

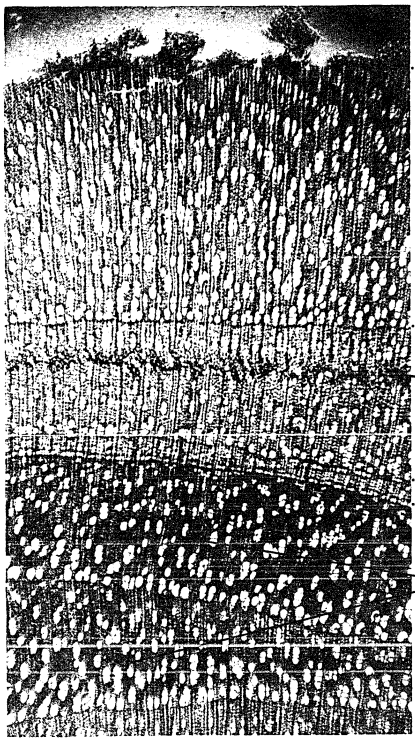

Figure 8. Transverse section showing frost damage, areas of gelatinous fibers and irregular growth rings.

treatment, or always present in each sector of an affected tree. No treatment was immune, but in no treatment did every tree reveal damage, which suggests that there was no special treatment effect involving frost hardiness.

Block Effect

A block effect is significant at the 5 percent or higher level in four of the fifteen analyses. Van Cleve (1973) detected a similar condition. Clonal differences between trees in the two areas might explain some of the differences, but unfortunately, the experimental design could not detect this.

Unpublished data[2/] suggest that factors other than clonal differences are responsible for this effect. Although the percent organic matter is an average 3.3 percent higher (at 0-15 and 15-30 cm depth), soil respiration is nearly 50 percent higher (at 0-15 cm) in block 1 than in block 2.

Soil texture is uniform over the area, though the percent clay and silt differ slightly at the 15-30 cm depth. A difference in intensity of burn in the 1958 fire may have differentially affected soil nitrogen or other nutrients in the two areas. Another possibility is that an undetected but very slight slope across the approximately 100 m wide strip on which the blocks are located may place block 1 closer to sub-surface water, which could increase soil respiration and enhance tree growth when the soils are dry. Although such explanations are purely speculative, the fact that two biological activities respond similarly to each other suggests that such environmental factors may be involved.

Nutrients

Nitrogen -- In this study, nitrogen essentially dominated the responses of aspen to fertilization. It not only produced in general the largest responses, but when it shared a response with another element, N usually produced the greater significance level. Only in the case of fiber wall thickness, did another element, potassium, rival N in significance level (Table 10 and 18).

Nitrogen greatly increased the amount of xylem in the stem of the tree. This suggests that greatly elevated levels of photosynthesis existed, which is supported by the findings of Coyne and Van Cleve (1976). On all but the earliest sampling date, they found consistently higher foliar levels of chlorophyll in N treated trees when compared with trees without N fertilization. In addition, as stated earlier, N treated trees had substantially increased leaf area and biomass and these leaves revealed an improved nutrient status when compared with the control trees. The authors reported that fertilization produced trees with pronounced vertical differentiation, such that the top of the canopy contained large, dense leaves which were in a better position to capture available light.

Van Cleve[2/] provided further data which suggested that N produced trees with a superior nutritional status. He found that twig nitrogen was significantly higher in the N treated trees. Also, bud lipid content was found to be higher before bud break than in the control trees. Kramer and Kozlowski (1960) considered lipid to be storage product in the wood of trees and cited Arrhenius (1942) who reported elevated lipid levels in aspen in the spring. They

Table 18. Recapitulation of nitrogen responses from selected summary of analysis tables.

Parameter	Percent of respective control	p<
Ring width	156.9	.001*
Specific gravity	-4.7	.035*
Vessel area	121.5	.008*
Fiber area**	135.9	.027*
Fiber wall	105.0	.142*
Vessel wall	104.2	.029*
Fiber length	-2.9	.0008*
Vessel length (total)	-9.0	.0015*
Fiber width	113.0	.0130*
Vessel width	116.0	.0004*

* Significant at level indicated.
** Area of combined gelatinous and normal fibers.

suggested that lipid, as well as starch, is a storage product in Populus sp. If this is correct, then Van Cleve's data suggest that N treated trees enter the winter with greater energy reserves than do the untreated trees. The magnitude and significance of tree responses to nitrogen treatments suggests that nitrogen availability in the stand was low and that this element is the mineral nutrient most limiting aspen productivity of the site.

Phosphorus -- The morphological responses to soil enrichment with P were not nearly as great as those with nitrogen. Six of the ten mean values (Table 19) were less than for the control mean values and two of these were significantly less. Einspahr and Benson (1967) correlated soil texture, organic matter content and soil nutrient status with tree characteristics in five aspen stands at each of five areas in Wisconsin and Michigan. They found a negative correlation between soil phosphorus levels and such properties as tree volume, height growth and fiber length. They however, ascribe this to other correlations between phosphorus levels and soil texture.

White and Carter (1970) conducted foliar analyses on six to nine-year-old Populus deltoides of river floodplains in southwestern Alabama. Leaf P (on an ashed basis) averaged from .18 percent for suppressed trees, to .20 percent for dominants. Coyne and Van Cleve (1976) found .29 percent (dry weight) P content in the control, .26 percent in the N treatment and .32 percent in NP treatment leaves of this study area. It is interesting, but unexplained, that foliar P is elevated at low soil nitrogen (control) levels, but

Table 19. Recapitulation of phosphorus responses from selected summary of analysis tables.

Parameter	Percent of respective control	p<
Ring width	-17.0	.452
Specific gravity	-0.7	.447
Vessel area	-9.3	.502
Fiber area**	105.3	.659
Fiber wall	-2.0	.003*
Vessel wall	-2.0	.655
Fiber length	100.1	.205
Vessel length (total)	-8.0	.066*
Fiber width	105.1	.919

* Significant at level indicated.
** Area of combined gelatinous and normal fibers.

highest when P is added with N (NP). A similar condition was reported for foliage of eastern cottonwood seedlings by Broadfoot and Ike (1968) and Hacskaylo et al. (1969). The latter authors revealed the same relationship to be true for black locust (Robinia pseudoacacia L.), but found the opposite to be true for Scots pine (Pinus sylvestris L.) and black walnut (Juglans nigra L.).

No data were found which defined soil nutrient requirements for aspen and which were useful for comparisons with pre-treatment nutrient status in this study area. The pre-treatment pH was more favorable for P uptake and soil P at this site was higher in the 0-2.5 cm and greater depths (Table 2) than in the 50 and 120-year-old upland aspen stands of interior Alaska[2/]. The litter fall and nutrient cycling in these older stands is described by Van Cleve and Noonan (1975). The results of this study, Van Cleve's work (1973) and the comparisons suggest that P was not limiting growth prior to fertilization.

Ash residue from the 1958 fire could have caused a surplus of available phosphorus on the site. Further application of this element through fertilization would further increase the surplus and result in no P response. Buckman and Brady (1969) suggested that with high P availability, and with pH between 6-7, higher plants do not absorb even one-third of the available phosphorus. Within this soil pH range, excess P can be incorporated with calcium to form calcium phosphates and with iron, aluminum or manganese to form hydrous oxides and complexes with silicate minerals.

Potassium -- This nutrient is median in the responses it produced in this study. Of the ten major responses which were measured, six are significant (Table 20). The largest effect of K was to increase fiber length, though nothing was found in the literature which suggests any special relationship between this nutrient and that parameter.

The fact that K was consistent in producing significantly thicker cell walls, longer fibers and increased ring width suggests that carbohydrates, as the principle substrate for cellulose synthesis, were high. The increased cell wall in K treated trees is in agreement with Gray (1970) who reported increased wall thickness of earlywood tracheids of Pinus resinosa when fertilized with this element.

Potassium levels prior to the fertilizer treatments were higher in the first 2.5 cm of soil than in either the 50 or the 120-year-old aspen stands which were mentioned earlier. At 12 cm the study site showed exhangeable potassium at 0.72 milliequivalent/ 100 g of soil, whereas the 50 and 120-year-old stands had 1.32 and .55 milliequivalents/100g respectively. Foliar potassium was comparable to levels found in P. deltoides by White and Carter (1970).

While K levels prior to fertilization were not optimum, as judged by the fact that addition of this element produced numerous significant responses, this study suggests that potassium levels were not limiting tree growth at the study area.

Interaction -- Auchmoody and Filip (1973) suggested that nitrogen deficiency must be overcome before P responses can be

Table 20. Recapitulation of potassium responses from selected summary of analysis tables.

Parameter	Percent of respective control	p<
Ring width	118.5	.048*
Specific gravity	-4.7	.583
Vessel area	-2.5	.767
Fiber area**	112.9	.731
Fiber wall	105.0	.038*
Vessel wall	103.0	.045*
Fiber length	104.3	.0001*
Vessel length (total)	-2.0	.061*
Fiber width	107.0	.344
Vessel width	106.0	.073*

* Significant at level indicated.
** Area of combined gelatinous and normal fibers.

realized. This would lead one to anticipate a high incidence of NxP interactions from the statistical analyses. That is not the case in this study. If, however, the pre-treatment soil level of P were high, interaction responses would be diluted and the combined response of N to elevated P would be revealed as a high N effect. In this study the only NxP interactions are associated with individual fiber cross-sectional area (Table 21). The most significant increase is among the gelatinous fiber area.

The NxK interaction was strongest in increasing the cross-sectional area of individual normal fibers. The response was strong enough to be significant in the combined (gelatinous + normal) fiber areas, even though this interaction was not of apparent influence on gelatinous fiber area. Most noteworthy of the NxK interactions are their relation to specific gravity (Tables 6, 7 and 21). The ring width increase of the NK treatment was one of the largest in the study, but the specific gravity decrease was among the lowest.

Table 21. Recapitulation of interaction responses from selected summary of analysis tables.

Parameter	Interaction	Percent of respective control	p<
Ring width	none	-----	-----
Specific gravity	NxK	-2.8	.044*
Vessel area	none	-----	-----
Fiber area**	NxP	123.4	.081*
	NxK	123.7	.027*
Gelatinous fiber area	NxP	113.4	.024*
Normal fiber area	NxP	126.0	.126*
	NxK	122.4	.013*
Fiber wall	NxPxK	101.0	.137*
Vessel wall	PxK	102.0	.111*
Fiber length	none	-----	-----
Vessel length	PxK	-1.0	.028*
Fiber width	none	-----	-----
Vessel width	none	-----	-----

* Significant at level indicated.
** Area of combined gelatinous and normal fibers.

MANAGEMENT IMPLICATIONS

As evidenced by growth of aspen in an adjacent site which was unburned in 1958, site quality of the area is low. However, trees that were not part of this study, which received NPK applications annually since 1968 are nearly 1.5 times the height of untreated trees. By projecting such growth for an additional 35 years, it is easy to visualize a potential site index near 75 with increased availability of nitrogen. Aspen site indexes of 75 and 65 are capable of producing 302 and 224 m^3/ha of wood respectively in 60 years (Gregory and Haack 1965). By comparison, sites similar to the one in this study with a site index of 50 produce only 102 m^3/ha of wood in the same period of time. Depending upon management objectives, it is likely that such low quality sites would receive little more than the lowest intensity management for aspen fiber production. An appropriate alternative would be conversion of the site to grow trees of a species better adapted to grow on the site.

The influence of fire, as it relates to soils and vegetation in interior Alaska has been discussed. Fire effects in many ways moderate conditions which are unique to the subarctic. Burning in conjunction with harvesting may therefore become a valuable tool for managing Alaskan aspen. Combustion of surface organic matter will result in the immediate release of most essential nutrients. Warmed soils, beneath the blackened surface residue, enhance

nutrient cycling, nitrification and encourage sucker production. Removal of stems of the competing shrub species will further improve growth of aspen suckers which are known for their intolerance. Historically, fire has perpetuated aspen, and may prove to reach its ultimate management utility in the culture of subarctic aspen.

CONCLUSIONS

There is little doubt from the findings in this study that the lack of nitrogen is limiting growth and affecting cellular development of the aspen in the study area. This study revealed that a sizeable increase in tree stem volume was the result of N fertilization. Nitrogen was also shown to decrease specific gravity, fiber length and increase fiber wall thickness. As was discussed earlier, wood of reduced specific gravity produces a lower yield of pulp for a given volume of raw material. However, in view of the sizeable increase of wood volume from N fertilization, the small reduction in specfic gravity is of little importance when one considers the increased site productivity.

Decreased fiber length and increased cell wall thickness concern the strength of paper products which are derived from the pulp. Longer fibers have larger surface area for adhesion between processed cells. Thinner walls are more easily crushed during processing which improves microfibril contact.

The addition of potassium to N treatment was found to improve wood characteristics over addition of N alone. NxK interaction resulted in improved specific gravity over N and K treatments. The K treatments produced the longest fiber in the study and the NK treatment offset the nitrogen effect and produced fibers longer than those of the control plots. The NK treatment also decreased fiber wall thickness below the level of either individual treatment. NK

produced the third thickest fiber walls in the study.

Two characteristics of the aspen tissue in this study were strikingly different from what is reported in the literature for elsewhere in the aspen range. Fiber length is consistently greater elsewhere and is reported to be 1.5 times the length of fibers in the control trees. Because of the magnitude of the difference, it is likely to be more important to pulp technologists than would be the relatively small, though significant, effects of fertilization. Since the current study is near the northern limit of the aspen range, environmental factors associated with the northern latitudes may be responsible.

Specific gravity of the wood in this study (near .43 g/cc) was higher than that reported elsewhere (.40 g/cc or lower). A relationship may exist between the shorter fibers and the higher specific gravity in this tissue. Slow growth which was apparent in the control trees may also be a contributory factor, since a negative correlation is thought to relate these two characteristics. Further research, to ascertain the influence of latitude on fiber length and specific gravity is warranted.

The majority of P effects were negative. This is particularly noteworthy in regard to cellulose deposition (cell wall thickness and ring width). As was discussed earlier and is suspected to be the case with this study, soil conditions with adequate available P, but with low N resulted in a high P/N ratio in the leaf. This condition was also found in the stem and root of eastern cottonwood

(Hacskaylo et al. 1969). Since this situation exists with a decreased cellulose deposition, it is appropriate to suggest that high plant P/N ratios may interfere with photosynthesis, the transport of photosynthate or its conversion to cell wall material. Phosphorus is intimately associated with energy relations, and a high respiration rate may be accompanying the high P/N ratio, resulting in a loss of photosynthate.

An inherent difficulty in all field fertilizer studies is that the investigator has little ability to manipulate the natural factors of the site such as temperature, rainfall and pretreatment nutrient status. As a result he must temper his conclusions based upon what is known about the field site. In this light, little knowledge was gained concerning the effects of P fertilization on stem morphology when this element is limiting. For many of the same reasons, K is not thought to have been a factor which limited growth under pre-treatment conditions, though in view of the numerous NxK interactions, it probably would limit growth under an N fertilization regime.

The effect of colder 1971 temperatures on ring width growth when compared with 1972 indicates the importance of temperature to tree growth. In view of the few weeks in the growing season, which were frost free in 1971, it is likely that photosynthetic efficiency was impaired by cold nights in spite of the warm day temperatures. It is plausible to propose that cold soil temperatures were responsible in large part for a nitrogen deficiency on the

study site. Cold soil temperatures are known to decrease soil organism activity, some of the most important of which are those responsible for nitrification. On south facing slopes, where best aspen growth is typically found, soil temperatures are likely higher and more rapid nutrient cycling and nitrification are likely to occur. A fertilizer study in which a non-nitrate source of N, such as diammonium phosphate is applied would test the importance of nitrification on the study site.

Further aspen fertilizer study is warranted. A study is needed to assess the fertilizer influence on stem growth and stem morphology of aspen growing on high productivity sites. By incorporating a prescribed burn in such a study, the utility of fire for management of Alaskan aspen would be determined.

APPENDIX

MEANS, STANDARD DEVIATIONS AND ANALYSIS RESULTS FROM DATA USED IN THIS STUDY

Means ($\bar{x}$) and standard deviations (S.D.) from ring width data. Each mean is from 12 observations (3 observations/tree X 4 trees/block treatment). Units are in millimeters (mm).

Treatment	Block (Replication)	1971 growth ring		1972 growth ring	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.
N	1	1.475	1.060	3.322	1.033
	2	2.398	0.538	4.254	1.401
P	1	0.620	0.254	0.950	0.277
	2	0.831	0.185	1.298	0.426
K	1	0.957	0.361	1.547	0.319
	2	1.254	0.269	1.522	0.548
NP	1	2.718	0.977	3.562	1.282
	2	3.382	1.259	3.792	1.304
NK	1	2.272	1.713	3.488	1.364
	2	3.917	1.343	4.802	1.654
PK	1	1.212	0.663	2.031	1.064
	2	1.443	0.651	1.792	0.844
NPK	1	2.929	1.199	3.548	1.390
	2	3.663	2.280	4.497	1.620
Control	1	1.112	0.252	1.417	0.588
	2	0.637	0.143	1.288	0.558

Ring width multivariate analysis of variance.

Source of variation	Sums of Squares	Degrees of Freedom	Mean Squares	F-Value	Probability less than
Error 1	28.040	7	4.006		
Block	21.717	1	21.717	5.422	.053
N	436.310	1	436.310	108.924	.001
P	2.542	1	2.542	.634	.452
K	22.913	1	22.913	5.720	.048
NP	1.109	1	1.109	.277	.615
NK	.140	1	.140	.035	.857
PK	.004	1	.004	.001	.975
NPK	5.415	1	5.415	1.352	.283
Error 2	2.422	8	.303		
Year	56.642	1	56.642	187.113	.001
YearXtreatment	19.746	7	2.821	9.319	.003

Means ($\bar{x}$) and standard deviations (S.D.) from specific gravity data. Each mean is from 12 observations (3 observations/tree X trees/block treatment). Specific gravity is expressed as a ratio of weight (grams of oven dry tissue) divided by volume (cm^3) of saturated tissue.

Treatment	Block (Replication)	1971 + 1972 growth rings $\bar{x}$	S.D.
N	1	0.407	0.009
	2	0.408	0.014
P	1	0.414	0.026
	2	0.434	0.026
K	1	0.402	0.015
	2	0.416	0.025
NP	1	0.395	0.022
	2	0.399	0.029
NK	1	0.405	0.024
	2	0.424	0.023
PK	1	0.422	0.038
	2	0.407	0.021
NPK	1	0.407	0.018
	2	0.407	0.025
Control	1	0.433	0.031
	2	0.421	0.024

Specific Gravity Multivariate analysis of variance.

Source of variation	Sums of Squares	Degrees of Freedom	Mean Squares	F-Value	Probability less than
Error	.007	7	.001		
Block	.001	1	.001	.731	.421
N	.007	1	.007	6.816	.035
P	.001	1	.001	.649	.447
K	.000	1	.000	.331	.583
NP	.001	1	.001	1.218	.306
NK	.006	1	.006	5.994	.044
PK	.000	1	.000	.296	.603
NPK	.000	1	.000	.087	.770

Means ($\bar{x}$) and standard deviation (S.D.) from individual fiber cross-sectional area data by year. They include data from normal and gelatinous fibers. Units are square microns (μ^2). The number of observations per mean are indicated in parentheses.

Treatment	Block (replication)	Area of individual fibers			
		1972 growth ring		1971 growth ring	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.
N	1	267.290(176)	123.941	220.907(161)	86.485
	2	343.195(169)	195.405	285.640(161)	153.794
P	1	216.280(164)	89.957	184.107(149)	70.091
	2	247.952(166)	101.827	215.908(174)	94.195
K	1	198.884(155)	81.123	214.477(151)	88.977
	2	260.950(160)	115.409	254.745(153)	105.407
NP	1	274.920(175)	127.273	234.148(169)	107.499
	2	260.857(182)	127.468	245.070(172)	124.117
NK	1	270.372(172)	123.115	247.554(177)	114.806
	2	253.884(173)	106.930	247.377(167)	106.309
PK	1	250.206(165)	115.828	240.712(163)	111.844
	2	257.497(163)	120.856	265.954(174)	134.885
NPK	1	216.698(159)	89.897	208.327(168)	94.476
	2	255.307(176)	123.694	240.447(170)	158.324
Control	1	212.170(147)	98.153	207.060(167)	89.493
	2	224.476(168)	114.852	181.146(171)	98.536

Individual fiber cross-sectional area multivariate analysis of variance.

Source of variation	Sums of Squares	Degrees of Freedom	Mean Squares	F-Value	Probability less than
Error 1	953965.531	7	136280.790		
Block	655502.648	1	655502.648	4.810	.064
N	1016637.754	1	1016637.754	7.460	.029
P	28891.968	1	28891.968	.212	.659
K	17404.750	1	17404.750	.128	.731
NP	568135.592	1	568135.592	4.169	.081
NK	1054907.387	1	1054907.387	7.741	.027
PK	10964.360	1	10964.360	.080	.785
NPK	6460.446	1	6460.446	.047	.834
Error 2	136789.412	8	17098.676		
Year	537735.757	1	537735.757	31.449	.001
Year X Treatment	382504.008	7	54643.430	3.196	.063

Means ($\bar{x}$) and standard deviation (S.D.) from individual normal fiber area data by growth ring. Units are in square microns (μ^2). The number of observations per mean is indicated in parentheses.

Treatment	Block (replication)	Area of individual normal fibers 1972 growth ring		1971 growth ring	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.
N	1	266.225(138)	120.569	216.609(128)	86.789
	2	348.766(141)	203.330	284.746(141)	153.462
P	1	204.340(106)	76.137	178.513(113)	69.856
	2	245.215(135)	93.849	215.877(163)	96.096
K	1	205.883(111)	85.829	212.750(120)	93.100
	2	264.175(114)	121.268	260.180(133)	110.395
NP	1	271.906(139)	134.454	238.029(140)	111.778
	2	264.740(146)	133.864	246.219(128)	136.424
NK	1	252.694(124)	113.888	245.951(144)	118.053
	2	247.232(138)	107.405	247.918(147)	110.746
PK	1	248.191(115)	122.510	246.564(117)	120.487
	2	261.042(119)	122.576	269.250(160)	136.171
NPK	1	211.390(136)	85.548	209.185(151)	96.411
	2	255.640(150)	130.357	247.351(148)	167.401
Control	1	203.582(122)	97.295	206.076(145)	91.795
	2	221.600(120)	122.824	182.958(142)	98.572

Normal fiber area multivariate analysis

Source of variation	Sums of Squares
Error 1	780968.660
Block	763829.014
N	782389.927
P	16808.036
K	16697.500
NP	337505.586
NK	1220508.408
PK	25812.152
NPK	1144.356
Error 2	80855.442
Year	298511.252
Year X Treatment	383684.681

s of variance.

Degrees of Freedom	Mean Squares	F-Value	Probability less than
7	111566.951		
1	763829.014	6.846	.035
1	782389.927	7.013	.033
1	16808.036	.151	.709
1	16697.500	.150	.710
1	337505.586	3.025	.126
1	1220508.408	10.940	.013
1	25812.152	.231	.645
1	1144.356	.010	.922
8	10106.930		
1	298511.252	29.535	.001
7	54812.097	5.423	.015

Means ($\bar{x}$) and standard deviation (S.D.) from individual gelatinous fiber area data by growth ring. Units are in square microns (μ^2). The number of observations per mean is indicated in parentheses.

Treatment	Block (replication)	Area of individual gelatinous fibers 1972 growth ring $\bar{x}$	S.D.	1971 growth ring $\bar{x}$	S.D.
N	1	271.158(38)	137.150	237.576(33)	84.522
	2	315.143(28)	149.112	290.074(27)	158.304
P	1	238.103(58)	108.226	201.667(36)	68.848
	2	259.871(31)	132.313	216.364(11)	64.442
K	1	181.227(44)	65.412	221.161(31)	71.727
	2	252.957(46)	100.208	218.600(20)	51.328
NP	1	286.556(36)	95.265	215.414(29)	82.903
	2	245.111(36)	97.313	241.727(44)	79.231
NK	1	316.042(48)	135.084	254.545(33)	100.756
	2	280.114(35)	102.337	243.400(20)	66.911
PK	1	254.840(50)	99.767	225.826(46)	85.403
	2	247.909(44)	116.911	228.286(14)	116.919
NPK	1	248.087(23)	109.206	200.706(17)	77.139
	2	253.385(26)	76.281	194.000(22)	54.479
Control	1	254.080(25)	93.146	213.545(22)	74.009
	2	231.667(48)	92.738	172.276(29)	99.610

Gelatinous fiber multivariate analysis of variance.

Source of variation	Sums of Squares	Degrees of Freedom	Mean Squares	F-Value	Probability less than
Error 1	187406.740	7	26772.391		
Block	4942.462	1	4942.462	.185	.680
N	270607.942	1	270607.942	10.108	.016
P	18462.436	1	18462.436	.690	.434
K	630.035	1	630.035	.024	.882
NP	220559.289	1	220559.289	8.238	.024
NK	9716.422	1	9716.422	.363	.566
PK	3743.310	1	3743.310	.140	.720
NPK	20131.463	1	20131.463	.752	.415
Error 2	93806.575	8	11725.822		
Year	281395.272	1	281395.272	23.998	.001
YearXTreatment	87517.275	7	12502.468	1.066	.460

Means ($\bar{x}$) and standard deviation (S.D.) from individual vessel cross-sectional area data by year. The units are in square microns (μ^2). The number of observations per mean is indicated in parentheses.

Treatment	Block (replication)	Area of individual vessels 1972 growth ring		1971 growth ring	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.
N	1	1666.531(64)	718.138	1292.329(79)	623.625
	2	2238.507(71)	1079.129	1968.987(79)	882.823
P	1	1639.895(76)	657.173	1201.582(91)	649.109
	2	1366.432(74)	565.952	1122.545(66)	527.523
K	1	1371.447(85)	689.839	1442.180(89)	577.249
	2	1693.200(80)	779.071	1242.552(87)	622.969
NP	1	1926.231(65)	1244.052	1931.127(71)	855.871
	2	2311.724(58)	1247.121	1901.941(68)	785.186
NK	1	1982.412(68)	996.865	1834.317(63)	841.626
	2	1837.075(67)	911.570	1533.753(73)	645.183
PK	1	1599.347(75)	696.442	1430.610(77)	607.022
	2	1587.896(77)	736.002	1678.697(66)	605.575
NPK	1	2168.222(81)	893.255	1809.389(72)	782.793
	2	2099.766(64)	906.748	1589.086(70)	731.779
Control	1	1696.860(93)	603.926	1635.890(73)	748.787
	2	1284.667(72)	631.419	1181.072(69)	468.492

Individual vessel area multivariate analysis of variance.

Source of variation	Sums of Squares	Degrees of Freedom	Mean Squares	F-Value	Probability less than
Error 1	54427995.761	7	7775427.966		
Block	8280.440	1	8280.440	.001	.975
N	106094575.982	1	106094575.982	13.645	.008
P	3897434.996	1	3897434.996	.501	.502
K	735935.177	1	735935.177	.095	.767
NP	4358371.433	1	4358371.433	.561	.478
NK	2651472.804	1	2651472.804	.341	.578
PK	1549267.404	1	1549267.404	.199	.669
NPK	4887019.455	1	4887019.455	.629	.454
Error 2	11588165.102	8	1448520.638		
Year	30456097.984	1	30456097.984	21.026	.002
Year X Treatment	9056074.936	7	1293724.991	.893	.553

Means ($\bar{x}$) and standard deviations (S.D.) from fiber wall thickness data. Means are derived from 120 observations each. Units are in microns (μ).

Treatment	Block (replication)	1972 growth ring $\bar{x}$	1972 growth ring S.D.	1971 growth ring $\bar{x}$	1971 growth ring S.D.
N	1	3.690	0.549	3.560	0.539
	2	4.121	0.620	3.752	0.466
P	1	3.462	0.473	3.485	0.456
	2	3.715	0.471	3.448	0.390
K	1	3.662	0.407	3.717	0.389
	2	3.917	0.474	3.787	0.515
NP	1	3.525	0.490	3.465	0.448
	2	3.621	0.512	3.585	0.520
NK	1	3.887	0.557	3.602	0.466
	2	3.783	0.480	3.719	0.520
PK	1	3.544	0.460	3.563	0.429
	2	3.756	0.428	3.598	0.455
NPK	1	3.548	0.449	3.521	0.492
	2	3.796	0.549	3.712	0.551
Control	1	3.575	0.413	3.481	0.559
	2	3.698	0.626	3.642	0.677

Fiber wall thickness multivariate analysis of variance.

Source of variation	Sums of Squares	Degrees of Freedom	Mean Squares	F-Value	Probability less than
Error 1	6.723	7	.960		
Block	20.930	1	20.930	21.793	.002
N	2.630	1	2.630	2.739	.142
P	18.984	1	18.984	19.767	.003
K	6.216	1	6.216	8.472	.038
NP	.704	1	.704	.733	.420
NK	2.326	1	2.326	2.421	.164
PK	.115	1	.115	.120	.740
NPK	2.709	1	2.709	2.821	.137
Error 2	7.806	8	.976		
Year	10.365	1	10.365	10.623	.012
Year X treatment	4.600	7	.657	.673	.692

Means ($\bar{x}$) and standard deviations (S.D.) from vessel wall thickness data. Means are derived from 120 observations each. Units are in microns (μ).

Treatment	Block (replication)	1972 growth ring $\bar{x}$	1972 growth ring S.D.	1971 growth ring $\bar{x}$	1971 growth ring S.D.
N	1	3.035	0.331	2.919	0.371
	2	2.912	0.346	2.783	0.337
P	1	2.854	0.394	2.852	0.455
	2	2.688	0.299	2.579	0.286
K	1	2.950	0.323	2.992	0.344
	2	2.771	0.347	2.735	0.313
NP	1	2.929	0.352	2.881	0.326
	2	2.733	0.271	2.704	0.269
NK	1	3.200	0.402	3.000	0.370
	2	2.696	0.320	2.644	0.276
PK	1	2.925	0.373	2.933	0.333
	2	2.783	0.306	2.731	0.268
NPK	1	3.181	0.444	3.104	0.473
	2	2.940	0.470	2.754	0.375
Control	1	2.887	0.393	2.892	0.394
	2	2.725	0.326	2.671	0.329

Vessel wall thickness multivariate analysis of variance.

Source of variation	Sums of Squares	Degrees of Freedom	Mean Squares	F-Value	Probability less than
Error 1	7.390	7	1.056		
Block	50.934	1	50.934	48.246	.001
N	7.862	1	7.862	7.447	.029
P	.215	1	.215	.204	.665
K	6.277	1	6.277	5.945	.045
NP	.371	1	.371	.352	.572
NK	.010	1	.010	.010	.925
PK	3.519	1	3.519	3.334	.111
NPK	1.915	1	1.915	1.814	.220
Error 2	1.752	8	.219		
Year	4.020	1	4.020	18.355	.003
Year X treatment	2.444	7	.349	1.594	.263

Means ($\bar{x}$) and standard deviations (S.D.) of fiber dimensions from maceration data.
The means are derived from 160 observations each. Units are in millimeters (mm).

Treatments	Block	Fiber length				Fiber width			
		pre-fertilization		post-fertilization		pre-fertilization		post-fertilization	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
N	1	0.6297500	.0200883	0.6359375	.0349788	0.0159375	.0014987	0.0165937	.0009540
	2	0.6382500	.0489970	0.6490625	.0052336	0.0186875	.0019432	0.0223437	.0025339
P	1	0.5786250	.0585820	0.6128750	.0642850	0.0151687	.0014823	0.0155000	.0013578
	2	0.6018125	.0386622	0.6381875	.0463161	0.0167812	.0009207	0.0175937	.0007526
K	1	0.6168125	.0282101	0.6811875	.0930937	0.0157500	.0010052	0.0153750	.0012624
	2	0.6135625	.0645004	0.6651250	.0700100	0.0169375	.0017984	0.0193750	.0011319
NP	1	0.6603125	.0933980	0.6543125	.0398468	0.0167812	.0005896	0.0181562	.0014045
	2	0.5903125	.0443975	0.6000625	.0138359	0.0173437	.0013516	0.0201875	.0027205
NK	1	0.6245625	.0559979	0.6593750	.0477557	0.0163437	.0013361	0.0184375	.0042896
	2	0.6238750	.0213722	0.6711250	.0255159	0.0170312	.0006404	0.0203437	.0004130
PK	1	0.5961250	.0667172	0.6502500	.0228108	0.0173125	.0015894	0.0168750	.0007971
	2	0.6136250	.0598228	0.6728750	.0246361	0.0185312	.0007172	0.0199375	.0017215
NPK	1	0.6485625	.0164347	0.6760000	.0425603	0.0149687	.0006240	0.0153750	.0012416
	2	0.5750625	.0440617	0.6172500	.0472467	0.0155312	.0008315	0.0204687	.0027279
Control	1	0.6431250	.0366609	0.6637500	.0444756	0.0166875	.0007939	0.0164375	.0005637
	2	0.5876250	.0381447	0.6271250	.0370723	0.0173125	.0014631	0.0175000	.0012374

Means ($\bar{x}$) and standard deviations (S.D.) of vessel total length and width from maceration data. The means are derived from 160 observations each. Units are in millimeters (mm).

Treatments	Block	Total vessel length				Vessel width			
		pre-fertilization		post-fertilization		pre-fertilization		post-fertilization	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
N	1	0.3753125	.0195910	0.3980625	.0262642	0.0659688	.0031875	0.0753438	.0062943
	2	0.4175625	.0574080	0.4138750	.0469013	0.0691813	.0065329	0.0811566	.0039043
P	1	0.3631875	.0482560	0.3995000	.0387045	0.0611876	.0076625	0.0647813	.0058687
	2	0.3846875	.0090769	0.3904375	.0184418	0.0679688	.0034692	0.0668750	.0043625
K	1	0.4115000	.0262774	0.4620000	.0309886	0.0678125	.0031300	0.0732813	.0067557
	2	0.3846875	.0309895	0.4158125	.0377996	0.0645313	.0050450	0.0683438	.0028438
NP	1	0.4263125	.0198813	0.4043125	.0157366	0.0700313	.0018325	0.0764625	.0025215
	2	0.3836875	.0301948	0.3839375	.0174730	0.0655625	.0063815	0.0790625	.0118623
NK	1	0.3931250	.0357477	0.4062500	.0287496	0.0666250	.0066152	0.0814688	.0091546
	2	0.3998750	.0454508	0.4093125	.0449543	0.0669375	.0055757	0.0779063	.0042111
PK	1	0.3826250	.0554393	0.4265000	.0202937	0.0657500	.0054343	0.0690313	.0079670
	2	0.4118750	.0157962	0.4538750	.0329580	0.0654688	.0052155	0.0606563	.0052395
NPK	1	0.4123125	.0069143	0.4297500	.0122014	0.0656875	.0009816	0.0777813	.0033887
	2	0.3744375	.0088279	0.3908750	.0089571	0.0677188	.0063675	0.0815000	.0048251
Control	1	0.3975000	.0267823	0.4476875	.0207167	0.0711875	.0098861	0.0710000	.0032740
	2	0.3788750	.0371722	0.4317500	.0271224	0.0648750	.0095884	0.0646563	.0069518

Means ($\bar{x}$) and standard deviation (S.D.) of vessel trunk length (fig. 7) from maceration data. The means are derived from 160 observations each. Units are in millimeters (mm).

Treatment	Block	Vessel trunk length			
		pre-fertilization		post-fertilization	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.
N	1	0.2098750	.0219293	0.2170625	.0227691
	2	0.2300000	.0339338	0.2305625	.0352286
P	1	0.1863750	.0365140	0.2170000	.0184876
	2	0.1975625	.0132025	0.1946875	.0136265
K	1	0.2252500	.0197009	0.2440625	.0247162
	2	0.1985000	.0176316	0.2151250	.0207299
NP	1	0.2188125	.0088421	0.2139375	.0199179
	2	0.2048125	.0230121	0.2008750	.0175991
NK	1	0.2058750	.0310064	0.2080625	.0085911
	2	0.2087500	.0310517	0.2158750	.0199181
PK	1	0.2037500	.0325147	0.2311875	.0070722
	2	0.2112500	.0105258	0.2443125	.0268323
NPK	1	0.2226875	.0145335	0.3383750	.0096188
	2	0.1985625	.0162370	0.2005625	.0101743
Control	1	0.2081875	.0240376	0.2334375	.0113089
	2	0.1835625	.0192065	0.2199375	.0183614

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