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Clonal Variation of Wood Density and Fibre Length of Trembling Aspen (*Populus tremuloides* Michx.) in North-Central Alberta

by

ALVIN D. YANCHUK

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF FOREST SCIENCE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Clonal Variation of Wood Density and Fibre Length of Trembling Aspen (*Populus tremuloides* Michx.) in North-Central Alberta submitted by ALVIN D. YANCHUK in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in FOREST SCIENCE.

Bruce P. Dancik

Supervisor

Robert T. Hardin

Date 15 October 1982

To my parents, Julian and Helen, my brother,
Rob, and Brenda ...
for her patience

Abstract

Patterns of intra- and inter-clonal variation of wood density and fibre length of trembling aspen (*Populus tremuloides* Michx.) were examined in north-central Alberta. The study was conducted as two [illegible] experiments, the first dealing with within-clone variation of wood density and the second with among-clone variation and heritability of wood density and fibre length.

Four trees from each of three clones were sampled to determine the patterns of wood density variation within stems and within clones. Sample disks were removed at five heights from each tree to examine variation among cardinal directions and across the southern radius at each height. Although only three clones were sampled, there were significant differences ($P<0.05$) among clones. Wood density tends to be high at the bottom of the tree, decreases to a minimum at mid-height, then increases again near the top of the tree. In the radial direction wood density is high near the pith (at all heights), decreases substantially, then increases again in the mature wood zone (after rings 15-20+). Average wood density values varied from 0.348 g/cc to 0.402 g/cc. Although some genetic control over wood density is evident among clones, numerous factors such as tension wood organization and relative cell proportions and distribution probably contribute to the large within-tree variation in wood density. In the second study fifteen putative trembling aspen clones were sampled to examine patterns of variation and determine the heritability of wood density and fibre length among clones. Large increment cores from the southern radius at breast height of each of five to nine trees in each clone were divided into four-year sections from the pith outward. All trees sampled were at least 36 years of age. Wood density measurements were made on each four-year section, and fibre lengths were measured on every second four-year increment period. Th[illegible]e significant (P<0.05) clonal differences for both wood density and fibre length. Broad-sense heritabilities for wood density and fibre length were 0.35 and 0.43, respectively. Wood density is generally high near the pith, decreases substantially a short distance from the pith, then increases in the mature wood zone. Fibre length is short near the pith and increases markedly across the radius. There was a slight negative correlation between wood density and growth rate and a slight positive correlation between fibre length and growth rate.

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I. Introduction

A. Trembling Aspen

Trembling aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America (Cottam 1963). It occurs on a variety of sites and soil types in its large geographic range, with best growth being attained on moist well-drained loamy sands (Fowells 1965). In the prairie provinces, trees at age 70 will vary in height from 16 m on poor sites to 24 m on good sites (Steneker 1976). Trembling aspen usually occurs in young even-aged stands, but in the absence of disturbance, more shade-tolerant and long-lived tree species tend to suppress, kill and replace the shade-intolerant aspen. With periodic disturbances, aspen clones will be maintained and under certain conditions expand and increase in acreage (Barnes 1975, Kemperman and Barnes 1976).

Aspen is typically dioecious (Einsphar and Winton 1976). Although large seed crops are produced annually (Maini 1972), its primary method of reproduction is by vegetative suckering of the lateral root system, which results in trembling aspen having a clonal growth habit (Barnes 1966, Schier 1973). An aspen clone is initiated by the establishment of a seedling (the ortet), and suckers (ramets) arise from the root system of this ortet (Barnes 1966). Vegetative reproduction in this manner allows multiple stems of the same genotype to grow in proximity.

Suckering in aspen is controlled primarily by apical dominance of stems; throughout the growing season varying concentrations of growth inhibitors produced by the trees suppress sucker formation (Maini 1972, Schier 1976). Disturbances such as logging or fire remove the apical dominance, and suckering usually increases dramatically. Initial stocking of suckers after such disturbances is quite high (up to 200,000 stems/ha), but dominance is quickly restablished and stocking levels are reduced substantially through natural mortality during the first several years (Steneker 1976).

Trembling aspen is a relatively short-lived species. In the Rocky Mountains, stems commonly reach 100 years of age, whereas stands of aspen in the Great Lakes region break up by age 60 (Jones and Markstrom 1973). Because of its large geographic distribution aspen occurs with a large number of tree and shrub species. Fowells (1965) indicated that it is the minor component of 27 forest associations and the major tree species in six forest types throughout North America.

B. Variation

Considerable intra-specific variation is known to exist in trembling aspen. Among western populations of aspen, Barnes (1975) found large among-clone differences for leaf, bud and twig characters. The amount of fungal wood decay (Wall 1971), the incidence of hypoxylon canker (Copony and Barnes 1974), rooting and suckering ability (Schier 1974), nutrient and biomass content (Bartos and Johnston 1978) and resistance to air pollutants (Karnosky 1977) all have been shown to exhibit great inter-clonal variation.

The inter-clonal variation in a number of characters typically has been found to exhibit clinal patterns of variation. For example, Barnes (1975) reported that the leaf, bud and twig characters of western aspen exhibited clinal patterns of variation. Geographic variation in a number of leaf and wood characters also has been found for aspen in Wisconsin (Einsphar and Benson 1966).

Clone size was investigated by Kemperman and Barnes (1976). They reported that clones in the west were generally larger in size than clones in the east and north, with the latter averaging 0.1 acres (0.04 ha) in size. They suggested that these geographic differences may be a function of the age of the clones (primarily a function of past glaciation in the area), rate of seedling establishment, disturbances by fire and competition with conifers or other vegetation. South of the glacial boundary, very large clones were found in the west. Average clone size is quite small, but individual clones occupying more than 100 acres have been reported (Kemperman and Barnes 1976).

Trembling aspen is typically diploid (2n=38) (Einsphar and Winton 1976); however, there are reports of triploid clones in natural stands (Every and Wiens 1971). These triploid clones also have been found to exhibit better growth and wood quality characteristics than comparable diploids (Einsphar *et al.* 1963, Einsphar *et al.* 1968). Although their occurrence in nature is relatively rare, triploids are probably also present in Alberta aspen populations. Thus triploids could prove to be quite valuable in the future for genetic improvement of aspen.

C. Utility

Aspen, in comparison to other hardwood tree species in North America, should be particularly attractive to the forest industry. Along with its clonal growth habit, fast rates of growth and relative ease of propagation, it can be used as a source of pulpwood (newsprint, specialty papers) or lumber, where it is manufactered into boxes, pallets, furniture parts, excelsior, particleboard and turned products (Jones and Markstrom 1973).

Einsphar (1972) pointed out the possibilities of aspen competing favourably in the hardwood fibre market, particulary as a short rotation species. Furthermore, by reducing rotation ages of aspen to ten to 20 years, he expected only a slight decrease in wood and pulp quality using such material. This decrease is primarily due to the inclusion of the larger percentage of juvenile wood from young trees. Wood obtained from juvenile trees is typically of lower quality and utility than wood harvested from older trees (Bendtsen 1978, Zobel 1976).

D. Wood Properties

Of all the anatomical properties of wood usually investigated (e.g., proportion of cells, moisture content, etc.), specific gravity (or wood density[1]) is usually considered the most important parameter directly influencing wood quality, particularly in conifers (Zobel 1961). Wood density is a measure of the amount of wood substance per unit volume. Wood is a complex chemical material largely made of cellulose, hemicellulose, lignin and a number of extraneous compounds. The type and amount of these extraneous compounds (usually reffered to as extractives) are often distinctive in certain tree species and can have a pronounced effect on wood properties (Marra 1981). The basic density of the cellulose-lignin matrix that makes up the substance of wood remains relatively constant from species to species at approximately 1.53 g/cc. Therefore, the major difference between the wood of a "light-wooded" species and the wood of a very "dense-wooded" species is: 1) the thickness of the woody cell walls; 2) size of the wood cells, and; 3) the interrelationship between the various kinds of cell in terms of 1) and 2) (Panshin and DeZeeuw 1970).

Mitchell (1963) pointed out the practical significance of wood specific gravity for various southern pines. An

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[1] Wood density and specific gravity are terms which can be used synonymously. The first is usually expressed in units and the latter expressed as a pure number indicating relative density. Wood density will be the only term used in the results and discussion of this text.

increase of 0.02 in specific gravity leads to a dry weight increase of 100 pounds of pulp per cord of wood, and an increase of 1000 psi in modulus of rupture in solid wood. Namkoong *et al.* (1969) and Zobel (1961) reviewed the practical applications of wood density and its overall importance in tree improvement.

In *Populus* a few anomalies may alter wood density, without actually enhancing or decreasing the quality of the wood. Zones of tension wood, which are extremely variable and common in *Populus* (Kennedy 1968, Wahlgren 1957), change the structural properties of wood (Panshin and DeZeeuw 1970). Tension wood typically is associated with the upper side of leaning stems; however, its pattern of occurrence seems to be fairly random (Kennedy 1968). The tension-wood fibres are characterized by a G-layer loosely attached to the inside of the cell walls (usually replacing the normal S1 and S2 layers), and by a number of cell surface failures, which contribute to the overall lower strength of pulps containing large amounts of tension wood (Isebrands and Parham 1974, Mia 1968).

Wood decay is very common in natural stands of trembling aspen. Although many pathogens attack aspen, the most important merchantable losses are due to only a few parasitic fungi which primarily destroy heartwood. Wet wood, another problem in aspen wood, is primarily caused by a pockets of bacterial infection scattered throughout entire logs. The infected areas typically collapse when dried, resulting in reduced quality of solid wood products (Anderson 1972).

Dinwoodie (1965) reported the three principle factors controlling paper strength are fibre (or tracheid) density, fibre strength and fibre length. The first two are primarily related to overall wood density; therefore, fibre length could be considered as the second most important wood character affecting wood quality, particularly in a pulpwood species.

In trembling aspen, fibres are primarily of the libriform type and average about 1.2 mm in length. Vessel elements are numerous and relatively small in diameter and are approximately 0.7 mm long (Panshin and DeZeeuw 1970). Trembling aspen kraft pulp compares favourably in quality with most hardwood kraft pulps. It is also reported to give higher yields and pulps at a faster rate than most other hardwoods (Hatton 1974).

With the increasing interest and use of aspen in many areas of the continent, research pertaining to its wood and fibre quality, utilization and growth also has increased (Einsphar 1972, Keays 1972, Maini and Cayford 1968, Neilson 1975, Neilson and McBride 1974). However, because of the large geographic distribution of the species, information gathered concerning various aspects of aspen growth and utilization may not be reliable or relevant in other parts of its geographic range. Furthermore, because of the large phenotypic variability exhibited by the species, important characters may differ significantly in other parts of its range.

Within a species, both wood density and fibre length have been shown to vary not only within trees, but also among individual trees and geographic locations. Because of the large natural variation in both of these wood properties, a review of general patterns of wood property variation, particularly within trees, is appropriate.

E. Variation Within Growth Rings

Fibre Length

Angiosperms tend to exhibit varying patterns of fibre length variation within annual growth increments, whereas softwood species display a more consistent pattern of variation within rings. Kennedy (1966) reported that tracheid length of Norway spruce increased only slightly across increments. Others have also noted this pattern of fibre length variation in other softwoods (Anderson 1951, Bannan 1964, Dinwoodie 1960, McGuinnes 1963, Wellwood and Juraz 1968).

As mentioned previously, some species of hardwoods deviate from this trend of fibre length increasing across an individual increment. Taylor (1963, 1975a) found that fibre length of sweetgum and hickory was relatively short in earlywood, gradually increased in the middle of the ring then decreased to its original length in the latewood, or; increased until the midpoint of the ring and maintained the same length throughout the latewood (oaks). Johnson (1942) looked at fibre length variation within growth rings in *Populus tremuloides* (Michx.) and noted that fibres of earlywood were shorter than those of latewood, and those of mid-season were of intermediate length. Bisset *et al.* (1950) reported that latewood fibres averaged approximately 32-180 percent longer than earlywood fibres in the same growth ring of several angiosperms. They found that mean fibre length for earlywood fibres of aspen was 0.83 mm and for latewood fibres 1.28 mm. Kennedy (1957), Kennedy and Smith (1959) and Smith and Rumma (1971), reported similar results in fibre length variation in *Populus*. These suggest that when sampling for fibre length, entire rings or composites of rings should be used to average the affect of within-ring variation.

The effect of rate of growth on fibre length is an important question that must be addressed before any attempt is made to breed for either fibre length or volume growth. For *P. trichocarpa* (Torr. and Grey) and *P. x regenerata*, faster growing sprouts had longer fibres than did slower growing material (Kennedy and Smith 1959). Kennedy (1957) noted that fast-grown black cottonwood generally had longer fibres than slow-grown trees and growth-rate class proved to be a significant factor influencing fibre length. Spurr and Hyvarinen (1954) and Kennedy (1968) also concluded that faster grown trees usually produced longer fibres. However, they do cite several papers which indicate an inverse or no relationship to growth rate and its effect on wood fibre length.

Wood Density

Due to the difficulty of obtaining reliable estimates of wood density from small samples within rings, relatively little information is available for diffuse porous hardwoods. Smith and Rumma (1971) found an increase in specific gravity from 0.248 to 0.318 within an annual ring of Italian hybrid poplar (I-214).

Ifju *et al.* (1965) found a large increase in specific gravity from earlywood to latewood in conifers. The prominent latewood zone in the pines accounts for this well-documented increase in wood density within annual rings (Kennedy 1966, Larson 1957, McGuinnes 1963, Paul 1939).

The greatest controversy concerning specific gravity and annual growth rates is the effect ring width (or rate of growth) has on wood density. Guiher (1968) found that only eight percent of the total variation in specific gravity of *P. deltoides* (Bart.) related to rings-per-inch. In simpler terms, rate of growth had only a limited effect on wood density. Cech *et al.* (1960), Kennedy and Smith (1959), Paul (1956) and Smith and Rumma (1971) reported that slight decreases in specific gravity occurred as ring width increased. However, Kennedy and Smith (1959) suggested that the influence of growth rate on specific gravity could largely be countered by the selection of individuals having both traits at the desirable levels. It is obvious that the

question has not been thoroughly answered, but it seems that growth rate generally does not affect wood density as directly as has been assumed.

F. Variation Across a Radial Section

Fibre Length

Substantially more information is available on fibre length variation across a radial section of secondary xylem. For many softwood species, tracheid length typically increases from the pith outward (Goggans 1961, Krahmer 1966, Panshin and DeZeeuw 1970). This pattern of fibre length increase has also been noted in angiosperms (Saucier and Hamilton 1967, Taylor 1968). Van Buijtenen (1960) found that directional variation of fibre length in aspen was not significant and probably fairly random (i.e., fibre length within an annual ring with cardinal direction is rather constant). He also noted that differences in fibre length not only existed across radial sections, but that significant differences existed among trees. In addition, he suggested that initial fibre length of juvenile wood and its relative increase in length with age should be taken into account for selection purposes.

Einsphar *et al.* (1972) reported that at all sampling heights fibre length of trembling aspen increased from the pith outward.

Wood Density

Both fibre length and wood density variation typically are studied together. Most of the literature previously mentioned also contains information on variation of wood density within stems (e.g., Goggans 1961, Ifju *et al*. 1965, Krahmer 1966, McGuinnes 1963, Mitchell 1963). Most of these studies of softwoods, as well as studies of *Populus* (Brown and Valentine 1963, Guiher 1968, Johnson 1942, Kennedy and Smith 1959, Valentine 1962, Walters and Bruckmann 1965), indicate that wood density tends to increase from the pith outward. Brown and Valentine (1963) indicated that wood density dropped rapidly for the first 1.5 cm from the pith, then increased to approximately 4 cm from the pith and thereafter remained constant or increased only slightly. Although exceptions to this pattern have been reported (Taylor and Wooten 1973, Wellwood and Jurazs 1968), most tree species exhibit a general or gradual increase in wood density with age.

G. Fibre Length and Wood Density Variation Among Trees

Typically there is marked variation in fibre length and wood density among individuals within any tree species. In many studies of softwoods (Dadswell *et al*. 1961, Jackson and Greene 1958, Lee 1978, etc.) and hardwoods (Saucier and Hamilton 1967, Taylor and Wooten 1973, Van Buijtenen 1960 etc.), substantial among-tree variation of fibre length and wood density relative to within-tree variation have been reported.

In addition to tree-to-tree variation within stands, there are substantial differences between stands as well. Echols (1958), Einsphar and Benson (1966), Farmer and Nance (1969), Goddard and Strickland (1962) have reported geographic patterns of fibre length and specific gravity variation for both hardwood and softwood species. Although a majority of the studies report continuous or clinal differentiation patterns for these two wood properties, some reports indicate a random distribution of populations or stands exhibiting higher or lower than average wood density. Ledig *et al.* (1975) suggest that geoclimatic influences may account for a large proportion of this variation. Larson (1957) also indicated that various environmental factors account for geographic differences in specific gravity of slash pine.

Many factors are responsible for this variation in natural populations and it is difficult to determine what actually causes specific patterns of wood property variation. A majority of studies suggest that climatic variables play an important role in controlling wood property variation. It is uncertain whether these clinal patterns are a result of gene flow among different populations or a reflection of a continuous gradient of selection pressure (Endler 1977, Guries and Ledig 1982).

H. Inheritance of Wood Density and Fibre Length

It has been well established that wood density and fibre length exhibit moderate to strong heritabilities (Goggans 1961, Zobel 1961). Heritabilities for these two wood properties of softwood species, particularly the southern pines, frequently have been reported (Kennedy 1966, Squillace *et al.* 1962, Stonecypher and Zobel 1966, Van Buijtenen 1962. Zobel and Rhodes 1957, Zobel 1961).

Only a few reports of heritabilities of these traits exist for hardwood species, usually in poplar. Van Buijtenen *et al.* (1959) estimated broad-sense heritabilities of 0.17 and 0.35 for wood density and fibre length, respectively, for trembling aspen in Wisconsin. Einsphar *et al.* (1967) found high to moderate narrow-sense heritabilities for both wood density and fibre length of five year-old aspen. Similarly, Einsphar *et al.* (1963) reported moderate to high heritabilities for these properties in triploid clones of aspen. Similar heritabilities for wood density and fibre length have been reported for eastern cottonwood (Farmer and Wilcox 1965, Wilcox and Farmer 1967).

From these studies, it is apparent that both genetic and environmental influences cause wood properties to vary within and among trees. Most wood properties are metric characters; therefore, sampling intensity and design will dictate the success or implications that can be drawn from such studies.

I. Objectives

Little information is available on variation and heritability of wood density and fibre length of aspen in areas other than eastern North America. Furthermore, little information is available on the patterns of wood density variation within trees of trembling aspen.

The objectives of this study were to investigate wood density variation within trees and wood density and fibre length variation among clones of trembling aspen in north-central Alberta.

The specific objectives are:

1) To describe the patterns of wood density variation within stems of aspen trees. Specifically, how does wood density vary in the axial and radial directions in stems? Are there significant differences among sampling positions at a sampling height?

2) To determine the extent of variation among clones of aspen for both wood density and fibre length. Specifically, are there differences among clones for both wood properties? What are the patterns of fibre length variation at breast height in stems of aspen? Does rate of growth affect wood density or fibre length? What is the extent of genetic control as derived from broad-sense heritability estimates?

The study was conducted as two separate experiments. The first was concerned with variation of wood density within stems. Establishing the patterns of wood density variation within trees is important, because among-tree variation has little practical value if within-tree variation is not defined.

Because the clone is the basic genotypic unit of aspen, it also was important to examine the extent of inter-clonal variation for the two wood properties. Little information is presently available describing variation of these two wood characters outside of eastern North America. Therefore, the second study was primarily concerned with wood density and fibre length variation among clones at one site in north-central Alberta.

II. Intra-clonal Variation in Wood Density

A. Materials and Methods

Sampling

The sample area was located approximately five miles north of Blue Ridge in north-central Alberta (SE1/4, Sec.10, T60, R10, W5). The soils of the area are described as being in the Luvisolic order (Orthic Grey Wooded) (Wynnyk *et al.* 1969). Understory species in the stand were primarily *Rosa woodsii* (Lindl.), *Corylus cornuta* (Marsh.), *Cornus stolonifera* (Michx.), *Alnus spp.* and *Salix spp.* The area was chosen because of easy access, abundance of commercial aspen and previous mapping of clones in the area. All clones were naturally occurring trembling aspen clones, and clone delineation was based on phenotypic and phenological differences as described by Barnes (1969).

Four stems from each of three adjacent clones were selected for study. Five 6 cm thick disks were removed from each tree at heights of 0.6, 3.0, 5.5, 7.9, and 10.4 m above ground (approximately 2.4 m [8 foot] intervals). Exact height intervals were not always used since it was necessary to avoid branch stubs and knots. The 12 stems sampled were between 11 and 13 m in height and varied in age at the stump from 40 to 47 years. All trees had straight, non-leaning stems without advanced or incipient decay. Four 10-degree wedges were removed from the north, south, east and west cardinal directions of each disk. Wood density of all 240 wedges (four wedges per disk, five disks per tree, from 12 trees) was determined using the oven-dry/green volume method. Green volumes were obtained by soaking the trimmed wedges for 24 hours in water, removing excess moisture from the surface of the samples with a damp cloth, and displacing each sample in water (measured to 0.001 g/ccm), which gave green volume in cubic centimeters. The wedges were dryed for a period of 24 hours at 103 degrees C, placed in desiccators to cool (approximately 15 minutes), and weighed. Basic wood density of each sample (in g/cc) was then determined by dividing the oven-dry weight by green volume.

After wood density determination on all four 10-degree wedges from each sample disk, only wedges removed from the southern cardinal direction were used for further analysis. These sixty wedges were then divided into five-year increments or sections from the pith outwards. This was done so that rings formed at similar anatomical (or cambial) ages at certain heights up the stem could be compared. Wood density (measured and calculated as described above) values for the consecutive five-year sections along the southern radius were used to indicate wood density variation with age. One radius at each sampling height was used to represent wood density at a location, because of results from the analysis carried out on the 10-degree wedges (See Table 1). Widths of the five-year sections and the physical distance from the pith to the midpoint of each section were recorded. These two values were measured using a dissecting microscope fitted with an eyepiece micrometer.

Benzene-alcohol extractives in aspen wood are known to comprise approximately five percent of the dry weight of wood (Pearl and Harrocks 1960). Removal of wood extractives in wood density surveys is a commonly used technique (e.g., Taylor 1974). All wood samples were subjected to extraction in benzene-alcohol solutions (50:50 benzene-ethanol and 95 percent ethanol) in soxhlet apparatus for periods of eight hours. After organic chemical extraction, samples were boiled in a large volume of distilled water (for eight hours) to remove hot-water-soluble extractives.

Statistical Analyses

Data were analyzed using a split-plot analysis of variance and covariance (Steele and Torrie 1980). Sources of variation for the within-tree study were "clones", "trees within clones" and "height". The basic linear model was:

$$Y(ijkl) = u + Ci + Tj(i) + Hk + el(ijk) ,$$

where C = clones(random)
T = trees/clones(random)
H = height(fixed)
e = error

The split in the model occurred between "trees/c/a" and "height" because of the change in unit size (i.e., trees were considered as the whole plot and within trees was considered as the split-plot). Analyses of variance and covariance were computed using AOV5 (Smillie 1969) and Harvey's LSM76 (1977) program. Harvey's program is a mixed-model least-squares program capable of handling data with unequal numbers. This was required because unequal numbers of five-year sections were present among the five sample heights. Means presented in Figures 1 through 6 are simple means calculated for the four trees in each clone. Significance was tested in all cases at $P<.05$.

The source of variation "trees within clones" (e.g., see Tables 1 and 2) typically is tested against the error mean square term to determine if there is significant variation among trees within clones. This test, however, is improper in this split-plot design (Anderson and McLean 1974), because there is no valid error term for "trees within clones". This *F* ratio, if calculated, would only indicate whether or not the variation among trees is greater than the variation within trees; it indicates nothing about intra-clonal variation. Therefore, the amount of variation among clones is the only parameter which should be emphasized. Also, broad-sense heritability estimates typically are calculated from an analysis such as this; however, in this first study heritability estimates for wood density were not obtained, because variance components were all close to zero. This was probably due to the the large number of observations within trees relative to the number of clones and trees within clones sampled.

B. Results and Discussion

The results of the analysis of variance indicated that significant differences existed among the three sampled clones (Table 1). This is somewhat surprising in view of the small number of clones used in this study. Brown (1961) also found significant differences in wood density among four clones of trembling aspen in New York. If clonal differences are apparent with such small samples sizes, it is likely that inter-clonal variation is an important component of phenotypic variation of wood density of aspen in natural stands.

There also were significant differences among the five sampling heights within trees (Table 1). Wood density is quite high at the base of the tree, decreases substantially at mid-height and then increases near the top of the tree (Figure 1). This pattern of wood density variation has been reported in *Eucalyptus grandis* ex Maiden (Taylor 1973) and *Celtis laevigata* Willd. (Taylor and Wooten 1973). The most common pattern of wood density variation in hardwoods is a general decrease from the base to the top of the tree. There is some evidence to indicate that wood density is higher in the crown, but reasons for this are not clear (Panshin and DeZeeuw 1970).

Four trees in clone 2 exhibited large differences in wood density at the various sampling heights (Figure 2). Although clear or precise patterns of variation are not indicated, the variable nature of wood density at higher

Table 1 - Analysis of variance of unextracted within-stem wood wood density in aspen determined on four 10-degree wedges at five sampling heights from four trees from each of three clones in north-central Alberta.

SOURCE	DF	MEAN SQUARES	F
Clones	2	0.003084	4.85*
Trees/Clones	9	0.000636	
Height	4	0.004173	12.35**
Direction	3	0.000167	0.49
Ht. x Direc.	12	0.000338	1.60
Clone x Ht.	8	0.001123	5.32**
Trees/C x Ht.	36	0.000384	1.82
Clone x Direc.	6	0.000221	1.04
Trees/C x Direc.	27	0.000140	0.66
Error	132	0.000211	

TOTAL SS = 0.088923

** significant at the 1% level.
* significant at the 5% level.

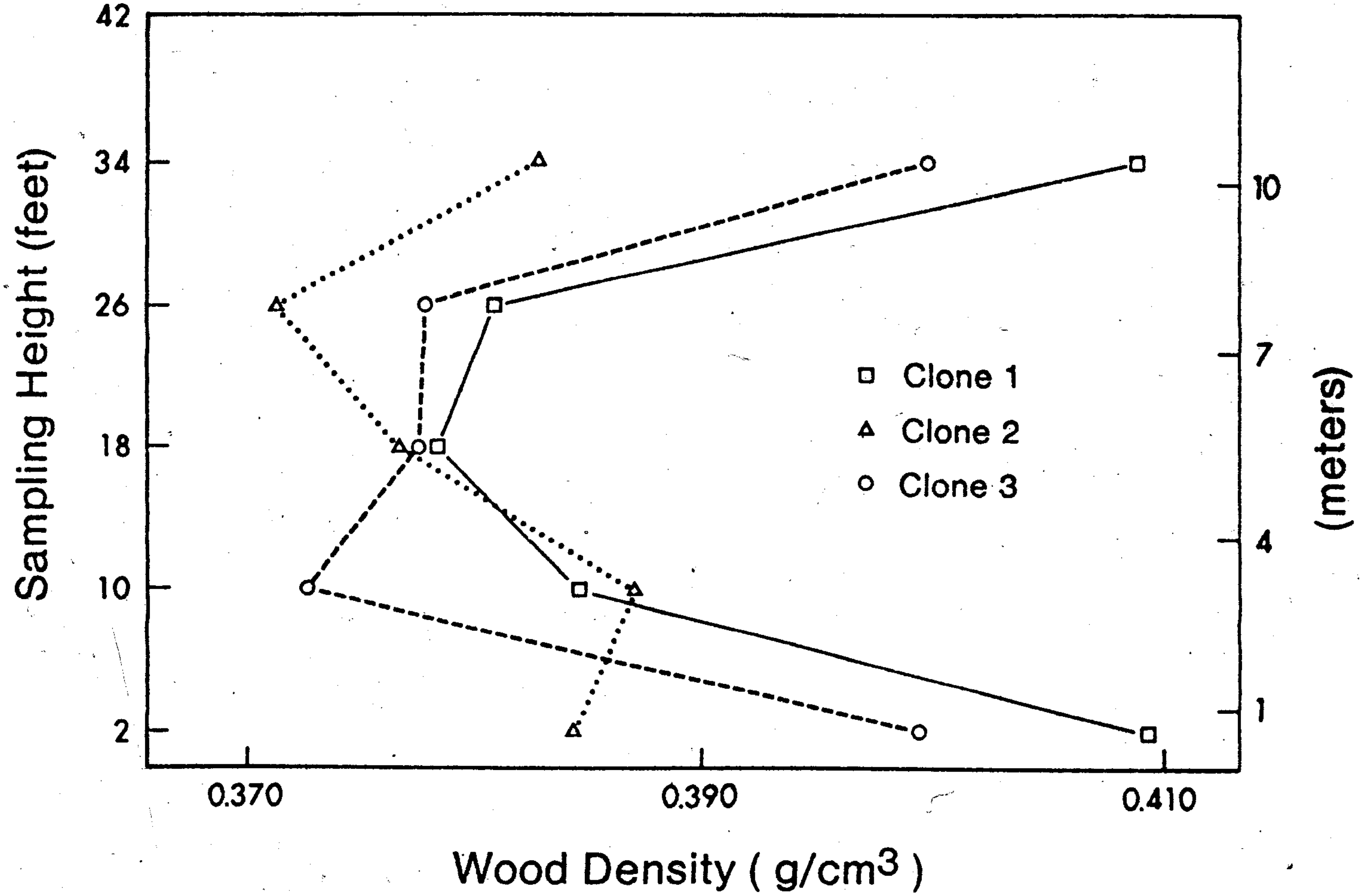

Figure 1 - Unextracted wood density variation within stems of aspen at at five sampling heights for three clones in north-central Alberta. Each plotted value is the mean for the 16 10-degree wedges.

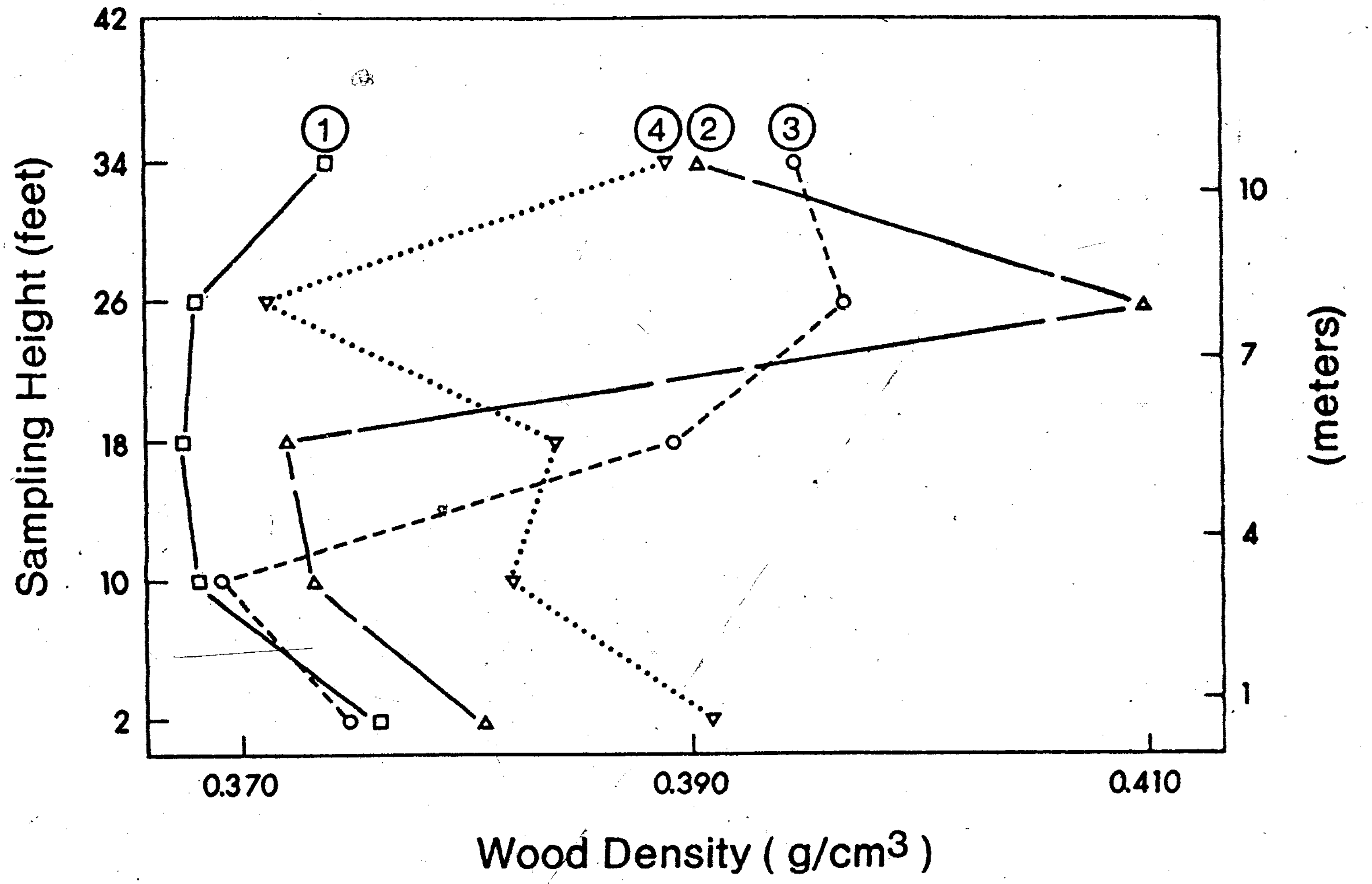

Figure 2 - Extracted wood density variation with height within four stems of aspen from one clone (clone 2). Each plotted value is the average wood density of the four 10-degree wedges at each height.

sampling locations in proximity to the crowns is quite evident. The varying wood densities at higher heights may be due to variation in size and structure of the crowns. Interaction terms for the various sources of variation were not significant, with the exception of "clone x height" (Table 1). This variation (evident in Figure 1) may not be very meaningful, because the samples at fixed height intervals did not correspond to similar crown positions in all trees. The interaction, therefore, may be due to the confounding effects of samples containing crown-formed versus non-crown-formed wood.

No significant differences among radial directions within sampling height were found (Table 1). Walters and Bruckmann (1965) also found no differences between north and south samples of wood at the same height in *Populus deltoides* (Bartr.). These suggest that sampling from one radius adequately represents wood density at any height in the tree.

In all three clones, wood density was high near the pith, dropped substantially a short distance from the pith, and again increased near rings 15-20 (approximately 30mm from the pith) (Figure 3). Variation across the southern radius at five sampling heights for the three clones was generally quite similar (Figures 4, 5 and 6). This pattern of high wood density near the pith and decreasing wood density throughout rings 15-20 usually occurred at all sampling heights.

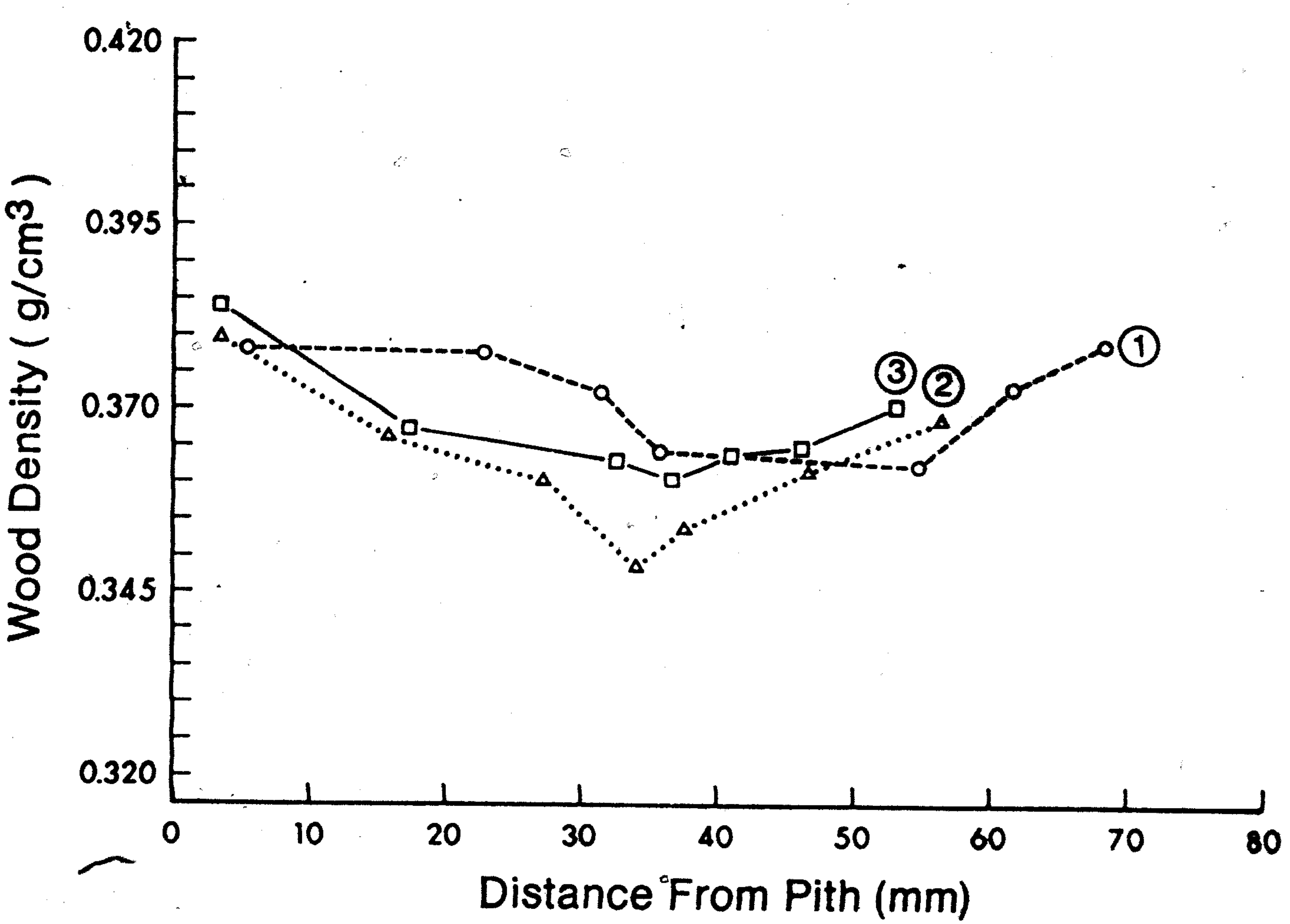

Figure 3 - Extracted wood density variation in aspen for three clones in north-central Alberta. Each plotted value is the average of all five-year increments for each clone at the average distance from the pith the sections occured.

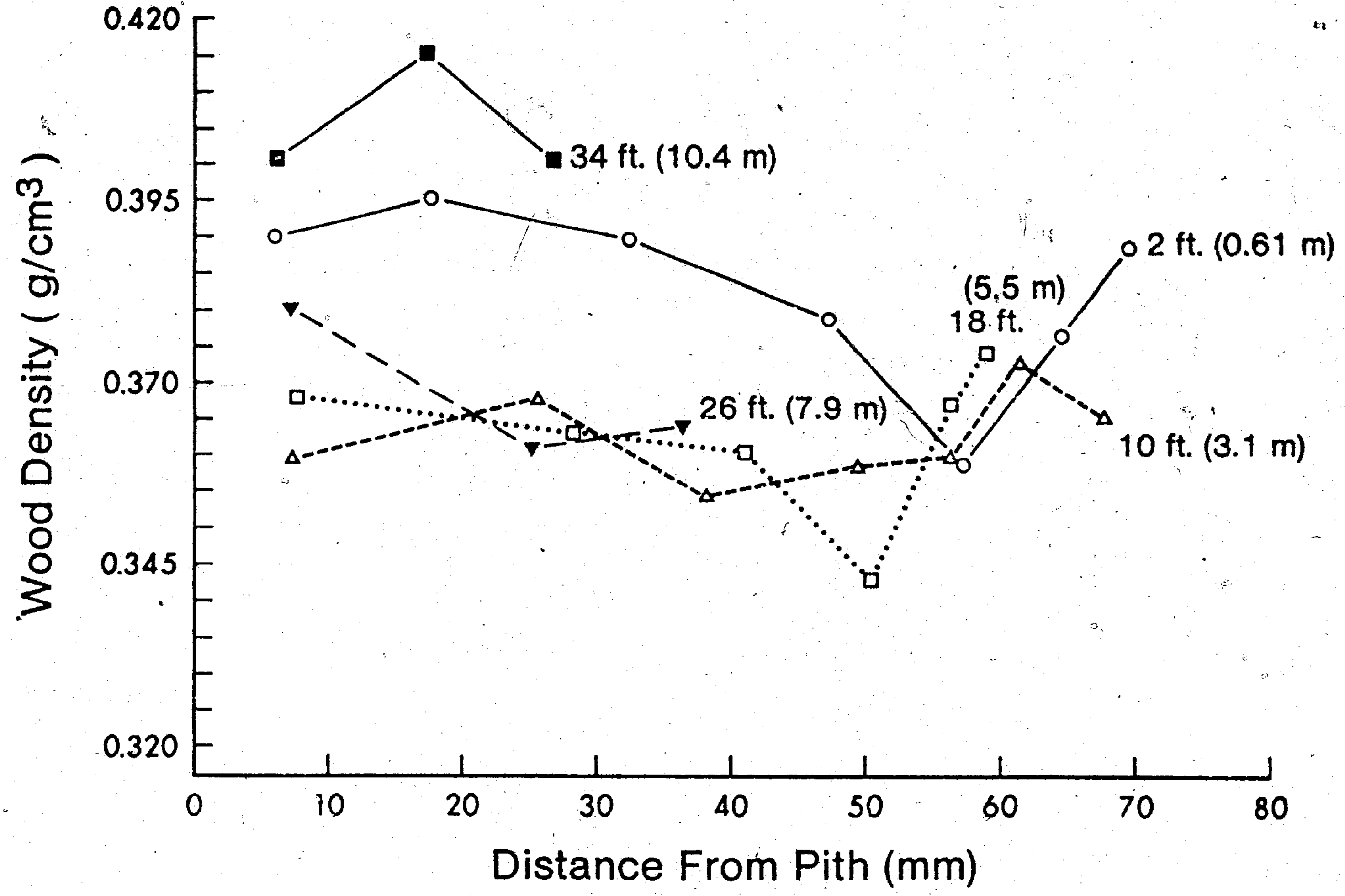

Figure 4 - Extracted wood density variation from four aspen trees from one clone (clone 1) at five different sampling heights with distance from the pith.

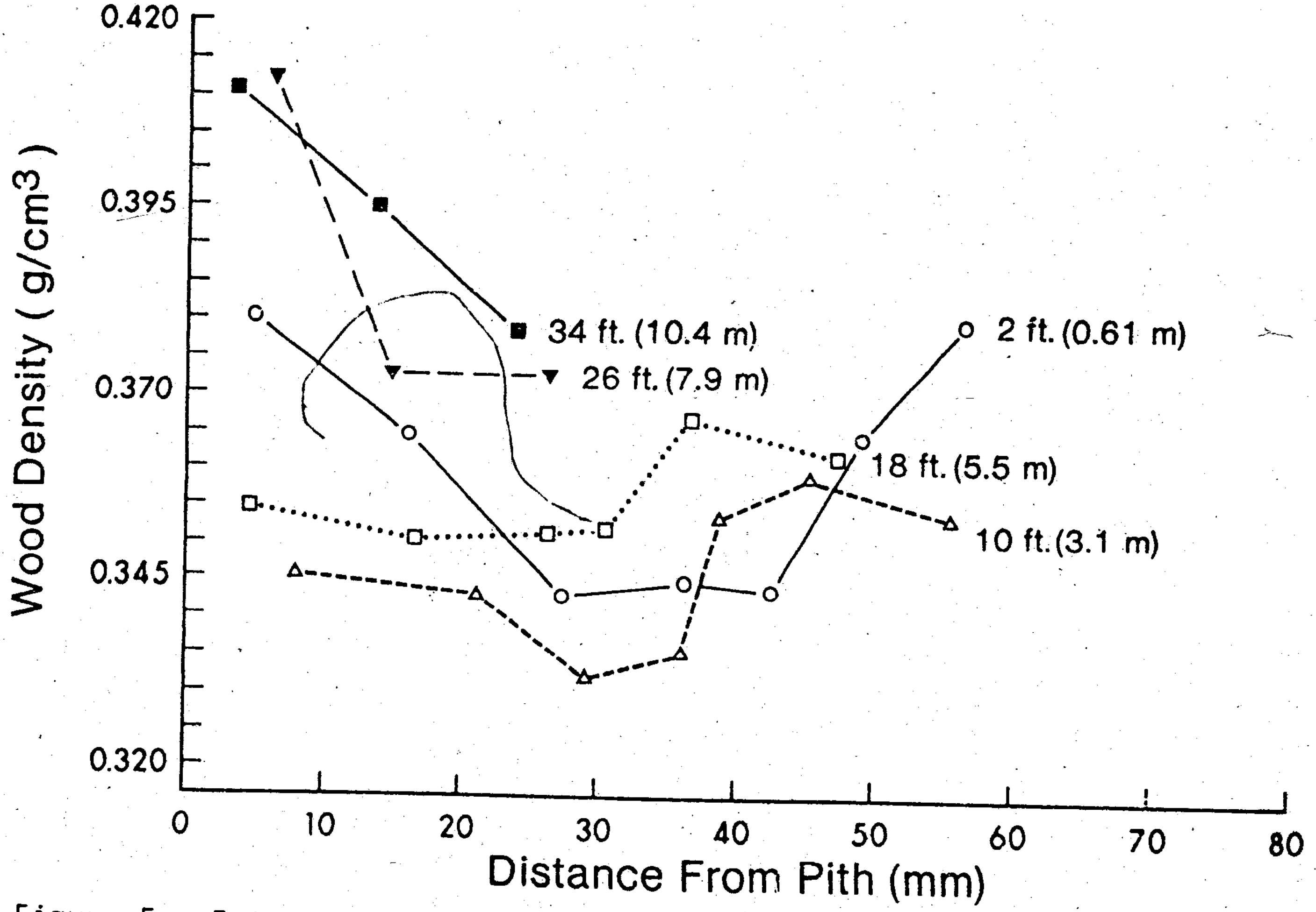

Figure 5 - Extracted wood density variation from four aspen trees from one clone (clone 2) at five different sampling heights with distance from the pith.

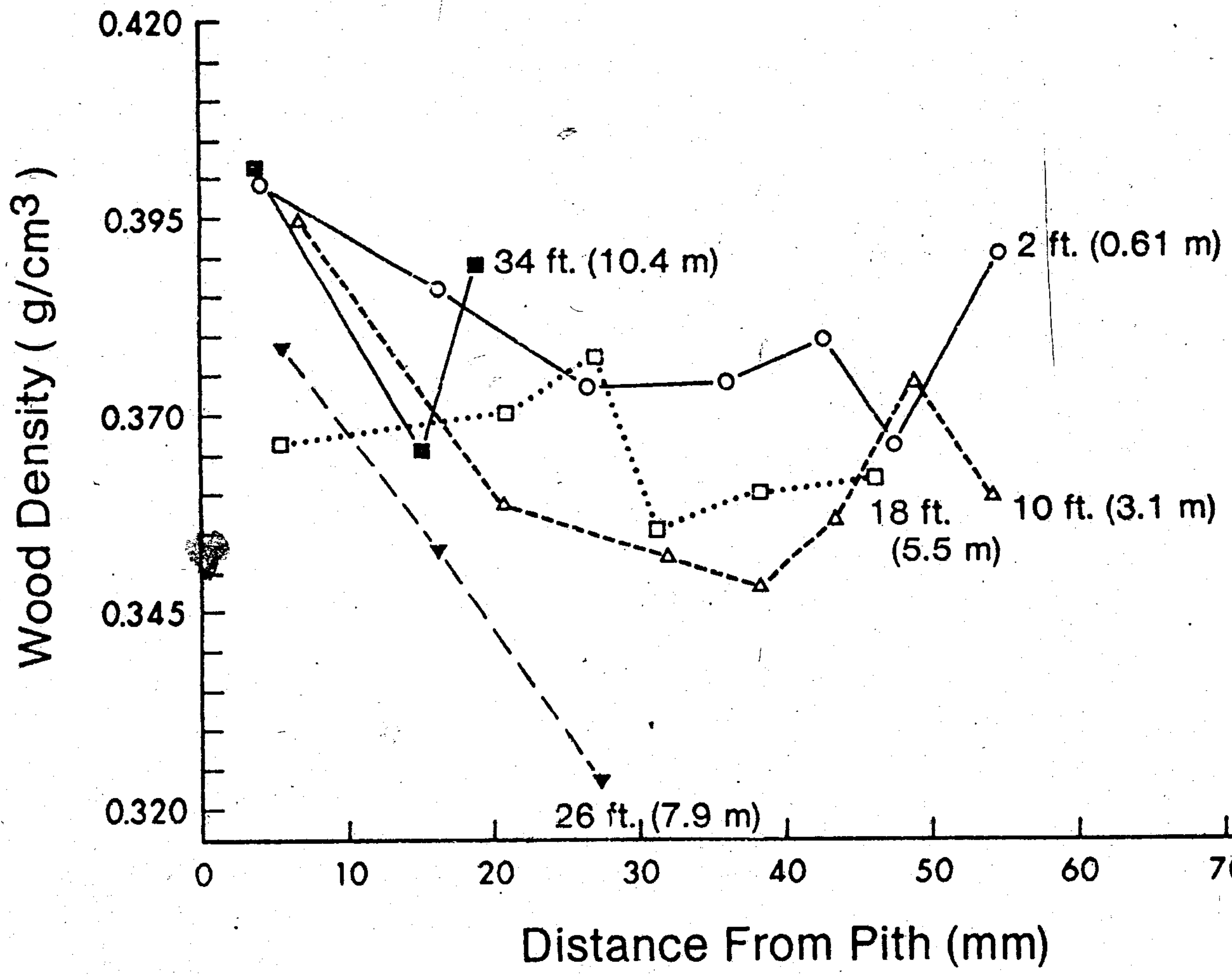

Figure 6 - Extracted wood density variation from four aspen trees from one clone (clone 3) at five different sampling heights with distance from the pith.

The presence of high wood density near the pith also has been found in other tree species. Panshin and DeZeeuw (1970) described this type of variation as typical of *Populus*. Isebrands (1972) found that wood produced by the juvenile crown of eastern cottonwood usually had a lower percentage of vessels than did the wood formed by a more mature crown. Further, he reported a noticable decrease in the percentage of fibres as distance from the pith increased and as tree height increased. If similar differences exist in aspen, the percentage and size of vessels and fibres may be the major underlying cause of wood density variation with height and diameter.

The analysis of variance model presented earlier had a regression added as a source of variation to explain variation across the radius (using the wood d[illegible]ity data obtained from the five-year sections from the southern radius). The covariate "distance from the pith", which accounts for the physical number of cell divisions from the pith irrespective of incremental age, was not significant in the model, indicating some non-linear relationship (Table 2); however, "clones" and "height" were significant. Brown and Valentine (1963) found that using "distance from the pith" did not increase the predictability of their linear model for wood density variation in aspen. This non-linear relationship is quite evident when examining wood density variation with distance from the pith (Figures 3, 4, 5 and 6).

Table 2 - Analysis of covariance of extracted wood density within aspen stems determined on five-year sections from the southern radius at five sample heights from four trees from each of three clones in north-central Alberta. The covariate "distance from the pith" accounted for variation across the radius.

SOURCE	DF	MEAN SQUARES	F
Clones	2	0.005363	6.965*
Trees/Clones	9	0.000770	1.433
Height	4	0.008801	16.37**
Regressions	1		
X2(distance from pith)	1	0.001925	3.581
Error	353	0.000538	

TOTAL SS = 0.231817

** significant at the 1% level.
* significant at the 5% level.

To better understand the variation across the radius, the five-year "sections" replaced the covariate "distance from the pith" in the model. In this analysis, "clones", "height" and "sections" were significant. This analysis, while explaining more of the variation within trees, also increased the *F* statistic among the three clones (Table 3). This is perhaps the reason why Van Buijtenen *et al.* (1959) may have suggested that a majority of the phenotypic variation present in wood density is among trees within clones. While this is true to some degree, the variation for trees within clones is still comparatively small. Accounting for within-tree variation, particularly variation across the radius, will undoubtedly make the model more appropriate (i.e., reduce the various error terms), and therefore increase inter-clonal differences.

The width of the five year sections (the covariate "section width" represented growth rate of the five-year sections) was significant, suggesting that as ring width increases wood density also increases (b=0.014698). This is in contrast to other reports, which generally indicate that a slight negative relationship exists between rate of growth and wood density in *Populus* (Kennedy and Smith 1959, Kennedy 1968). However, this positive regression coefficient may simply be due to the interaction of two variables. For example, the inherently wider rings and corresponding high wood densities near the pith are represented more than wood from other locations in the trees. This probably is the

Table 3 - Analysis of covariance of extracted wood density within stems of aspen determined on five-year sections from the southern radius at five sample heights from four trees from each of three clones in north-central Alberta. "Section" and "section width" accounted for wood density variation across the radius.

SOURCE	DF	MEAN SQUARES	F
Clones	2	0.003017	6.11*
Trees/Clones	9	0.000494	1.00
Height	4	0.010127	20.51**
Section	6	0.001615	3.27**
H x S	15	0.000694	1.41
Regression X1(section width)	1	0.005789	11.73**
Error	274	0.000494	

TOTAL SS = 0.209209

regression coefficient=b(X1)=0.014698

** significant at the 1% level.
* significant at the 5% level.

reason for the overall positive regression coefficient from the model in Table 2. The comparison of anatomically different wood (i.e., wood formed at different ages and heights) with an independent variable such as growth rate incorrectly may imply a relationship between these two traits. Although the regression coefficient may not accurately explain the growth rate relationship, it does indicate the overall average effect of differences in growth rate among the five-year samples within trees. Removing the covariate "section widths" from the analysis did not significantly change *F* ratios for "clones" and "sections" (Table 4).

The pattern of variation in wood density within stems of aspen probably is portrayed best schematically (Figure 7). The values in each cell represent the average wood density (adjusted for section width) for each five-year section at a particular sample height and increment period for all 12 stems examined. Large differences in wood density are present among the sampling positions, with a minimum average value of 0.348 g/cc at 3.1 m (rings 11-15) and a maximum average wood density of 0.402 g/cc at the top of the tree (rings 1-5) (Figure 7).

Similar wood densities exist in many places in the schematic drawing of the aspen stem. Because of the continually changing crown structure throughout a tree's life, it is unlikely that samples of similar density near the bottom and top of the tree are anatomically alike. As

Table 4 - Analysis of variance of extracted wood density within stems of aspen determined on five-year sections from the southern radius at five sample heights from four trees from each of three clones in north-central Alberta. "Sections" is the effect accounting for variation of wood density across the radius.

SOURCE	DF	MEAN SQUARES	F
Clones	2	0.003842	5.81*
Trees/Clones	9	0.000661	1.29
Height	4	0.008799	17.15**
Section	6	0.002793	5.44**
H x S	15	0.000686	1.34
Error	275	0.000513	

TOTAL SS = 0.209209

** significant at the 1% level.

* significant at the 5% level.

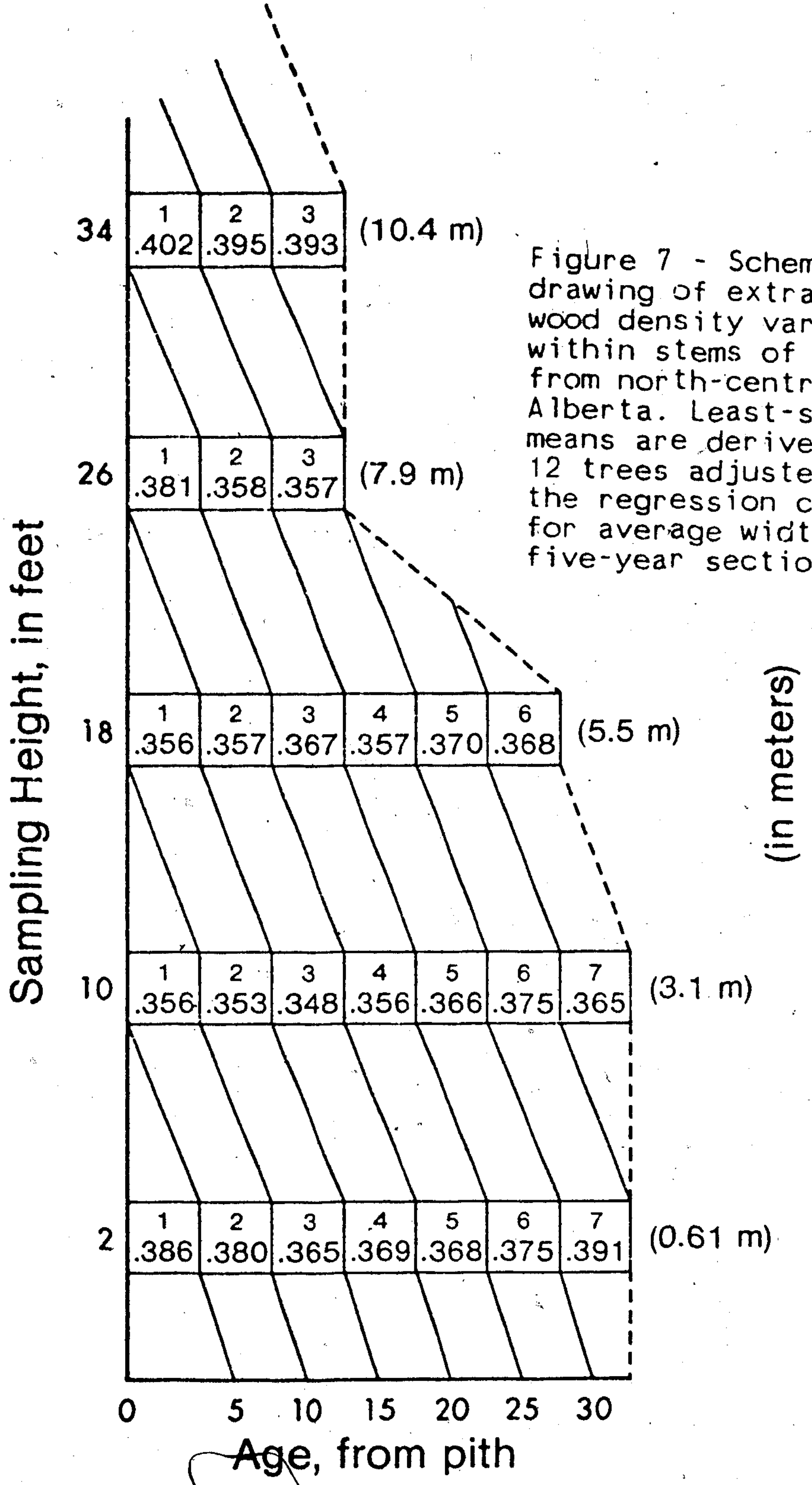

Figure 7 - Schematic drawing of extracted wood density variation within stems of aspen from north-central Alberta. Least-squares means are derived from 12 trees adjusted by the regression constant for average width of five-year sections.

mentioned earlier, Isebrands (1972) found large differences in percent cell composition at various heights and locations within stems of eastern cottonwood. Presumably, this difference is also present in aspen, and may be the major cause of this large within-stem wood density variation. Investigations specifically looking at cell compostion and its effect on wood density in proximity to the crown would be quite beneficial in clarifying within-tree variation of wood density in aspen.

III. Variation and Heritability of Wood Density and Fibre Length Among Clones

A. Materials and Methods

Sampling

Fifteen naturally occurring clones (located in the same general vicinity as the clones used in the first study) were delineated by the criteria outlined by Barnes (1969). The clones occurred in two stands located approximately five miles apart. Twelve clones were sampled in one area and three clones in the other. Since the effect of sample areas was not of concern, no attempt was made to sample more areas or discuss in detail the effects of areas.

Sample trees in each putative clone were at least 36 years of age at breast height and were selected for stem straightness and lack of decay. Ten trees initially were sampled in each clone. Due to an unusually high number of candidate trees containing some unacceptable amounts of rot, the number of acceptable trees in each clone varied from four to nine.

Whole cores from the pith to the bark were extracted from the southern radius at breast height of each tree using a large diameter (11 mm) increment borer. To account for the variation present in the radial direction, increment cores were segmented into four-year increments or sections (i.e., rings 1-4, 5-8, 9-12 etc.). The major assumption, therefore, was that one core taken at breast height gave an accurate estimate of wood properties for the whole stem. Ranking an individual tree's wood properties on the basis of one core taken at a particular sampling location has been commonly used in wood property studies (Gonzalez and Kellogg 1978, Maeglin and Wahlgren 1972).

Because aspen is a diffuse-porous species, ring counts are usually quite difficult to make. A razor was used to trim wood from one of the cross-sections of the core. The terminal axial parenchyma "band" (which is typically indicative of termination of annual growth) showed up quite well, and ring counts were made by examining the cores under low (10x) magnification.

The width (indicative of rate of growth over a four-year period) and physical distance from the pith (measured at the mid-point of each four-year section) of each section were measured using a dissecting microscope fitted with an eyepiece micrometer.

Because the actual size of the wood samples used in this study was relatively small (i.e., in the order of 0.5 to 2 cc), the Maximum Moisture Content (MMC) method of determining wood density was used (Smith 1955). Wood samples were submerged in distilled water for a period of two to four weeks depending on the relative size of the samples. During the period of saturation, samples were placed under vacuum to assist in attaining total saturation. The MMC method assumes that all intra- and inter-cellular space in the wood sample is filled with water. The formula used was;

$$\text{Wood Density(g/cc)} = \frac{1}{\dfrac{Mm - Mo}{Mo} + \dfrac{1}{1.53}} ,$$

where Mm is the wood sample weight plus the weight of bound and free water, and Mo is the oven-dry weight of the specimen. Oven-dry (Mo) and wet (Mm) weights were recorded to three decimal places. The basic density of wood substance (1.53 g/cc) remained constant in all calculations. This value has been shown to vary across the radius of aspen; however, its significance in changing the final wood density value is minimal (Brown 1961). A change of 0.01 only alters the wood density value of the sample by 0.001 g/cc. Brown (1961) found that that vari[illegible] of wood substance across a radius rarely varies more than 0.01; therefore, error due to a natural change in the constant across the radius would have a very small affect on the final wood density value obtained. This variation across the radius is caused primarily by a change in the ratio of cellulose to lignin in the wood cells from the pith outward (Panshin and DeZeeuw 1970).

Fibre length measurements were made on every second four-year section from the pith outward up to ring 36. Therefore, each tree is represented by five fibre length values (i.e., rings 1-4, 9-12, 17-20, 25-28 and 33-36). The four-year sections were macerated in a 50:50 mixture of glacial acetic acid and hydrogen peroxide (30%) for a 24 hour period at 60 degrees (C). The pulping solution then was removed from the vials, and the samples were washed with water. Vigorous shaking separated the wood cells and also provided a means for randomizing fibres within the vials. Small samples of fibres were removed from each vial with forceps, and the cells were stained with a two percent solution of Acridine Orange.

To obtain an unbiased estimate of fiber length from a representative sample, glass slides with etched "sampling zones" were used (Taylor 1975b). The stained fibres were placed on the sampling slides, distributed across the sampling boundries using a dissecting needle, and made into temporary slides. Fifty whole fibres in each four-year sample were measured using a micro-computer digitizer apparatus (Micko *et al.* 1982). The prepared sample slides were projected through a light microscope onto the digitizer screen (25x). Since fibres were traced with a hand-held cursor, bent or distorted fibres posed no problem in measurement. The average length of 50 fibres was used to represent each four-year composite sample.

Statistical Analyses

The sources of variation in the split-plot least-squares analysis of covariance (ANCOVA) model were "areas", "clones within areas", "trees within clones within areas" and "sections". The linear model in this study was therefore:

$$Y(ijklm)= u + A_i + C_{j(i)} + T_{k(ij)} + S_l + e_{m(ijkl)} ,$$

where A = areas(fixed)
C = clones/areas(random)
T = trees/clones/areas(random)
S = sections(fixed)
e = error

The split between the whole-plot and the split-plot is between "trees/c/a" and "sections". The two ANCOVA's used are the models which best accounted for the within-tree variation for wood density and fibre length. As in the within-tree study, the covariate "distance from pith" was not used in the model, because the pattern of variation across the radius is not linear. To obtain a statistically balanced design (using "sections" as a source of variation), only the first 36 increments (counting from the pith outward) in each core were used. Using rings from the pith outward allowed for the comparison of wood formed by the cambium at similar physiological ages.

The natural clonal growth habit of aspens facilitates the estimation of the amount of genetic control of various morphological and anatomical characters. All broad-sense heritabilities (which is the ratio of the genotypic variance over the phenotypic variance) were calculated from variance components derived from Harvey's program. Standard errors of heritabilities were also obtained from Harvey's program. [2] Broad-sense heritabilities were calculated as described by Zsuffa (1975) as follows:

$$h^2 = \frac{V(g)}{V(p)} = \frac{V(c)}{V(c) + V(t) + V(e)},$$

where V(g)= genotypic variance
V(p)= phenotypic variance

V(c)= variance among clones
V(t)= variance among trees within clones
V(e)= error variance

"Areas" was considered a fixed effect and "clones within areas (nested)" and "trees within clones" (nested) were considered random effects. The latter two effects in the model (i.e.,"clones within areas" and "trees within clones") were considered random because they were

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[2] Harvey(1977) indicated that these standard errors should be considered as minimum estimates of true standard errors. Because Harvey's program calculated heritabilities as paternal half-sibs[i.e., 4V(c)/V(p)], the heritability from Harvey's program was four times the "true" broad-sense heritability. Therefore the standard error of the heritability also was assumed to be multiplyed by four, and standard errors presented here were derived by dividing the paternal half-sib standard error by four.

representative of trees and clones in the area and there is no interest in the specific differences among the 15 clones. Since error is always considered random, with a mean of 0 and a variance (σ_e^2)(Searle 1971a), clones and trees within clones also had the same distribution.

For graphical purposes only, least-squares means used in Figures 8 and 10 were obtained by considering clones as fixed effects. Plots presented in Figures 9 and 11 were derived by calculating simple means at various age intervals from the pith. Significance was determined at $P<0.05$. Expected mean squares used for deriving variance components for random effects in Tables 5, 6 and 8 are given in Appendix (Table A1).

B. Results and Discussion

Because rate of growth data were recorded in the investigation, variation among clones for growth rate also was analyzed. The overall average annual increment at breast height for the 103 trees examined (only using the first 36 rings) was 1.86 mm. Average growth rates among the nine four-year sections varied from 1.3 mm/year to 2.55 mm/year. Therefore the average DBH for the 100 stems at 36 years of age was approximately 14.0 cm. Although the average growth rate exhibited by 15 clones seems relatively low, a few clones showed superior growth. For example, clones 1 and 15 had average annual increments of 2.5 mm/year, whereas clones 2 and 6 averaged increments of 1.3 mm/year. Since rate of growth was shown to vary among clones and its effect on both wood properties was uncertain, it was necessary in the analyses of the wood property data to adjust for growth rate using covariance analysis.

There were significant differences in rate of growth among clones (Table 5). The broad-sense heritability obtained for rate of growth was only 0.23, indicating that substantial within-clone variation is present. Van Buijtenen *et al.* (1959), Farmer (1970) and others also have found that diameter growth in *Populus* is under relatively low genetic control.

Wood Density

Mean wood density varied from 0.32 g/cc to over 0.40 g/cc among the fifteen clones (Figure 8). In addition to the large differences observed for average clone wood density, there were substantial differences among clones in the range of average wood densities for trees within clones. For example, the highest wood density tree measured in clone 4 was 0.36 g/cc, whereas the lowest wood density tree in clone 13 averaged 0.39 g/cc. Most clones exhibited narrow ranges similar to clones 4 and 13, however, large variation was present in a few cases (i.e., clones 2, 3 and 6). The cause of such large variation may be due to the presence of tension wood or fungal bacterial infections, which is often quite difficult to detect. Therefore a more informative approach in looking at intra-clonal variation may be to consider the standard error of the wood character, in this

Table 5 - Analysis of variance of growth rate for 15 aspen clones from north-central Alberta. Rate of growth was measured on four-year increments from the pith outward up to age 36.

SOURCE	DF	MEAN SQUARES	F	VARIANCE COMPONENTS
Areas	1	13.390700	0.09	
Clones/A	13	144.772191	9.15**	2.08709588
Trees/C/A	88	15.823663	2.73**	1.11522433
Section	8	160.926221	27.81**	
S x A	8	65.419209	2.39**	
Error	808	5.786644		5.78664427

TOTAL SS = 9375.7777

** significant at the 1% level.
* significant at the 5% level.

Broad Sense Heritability = 0.232. S.e. of h^2 = 0.08

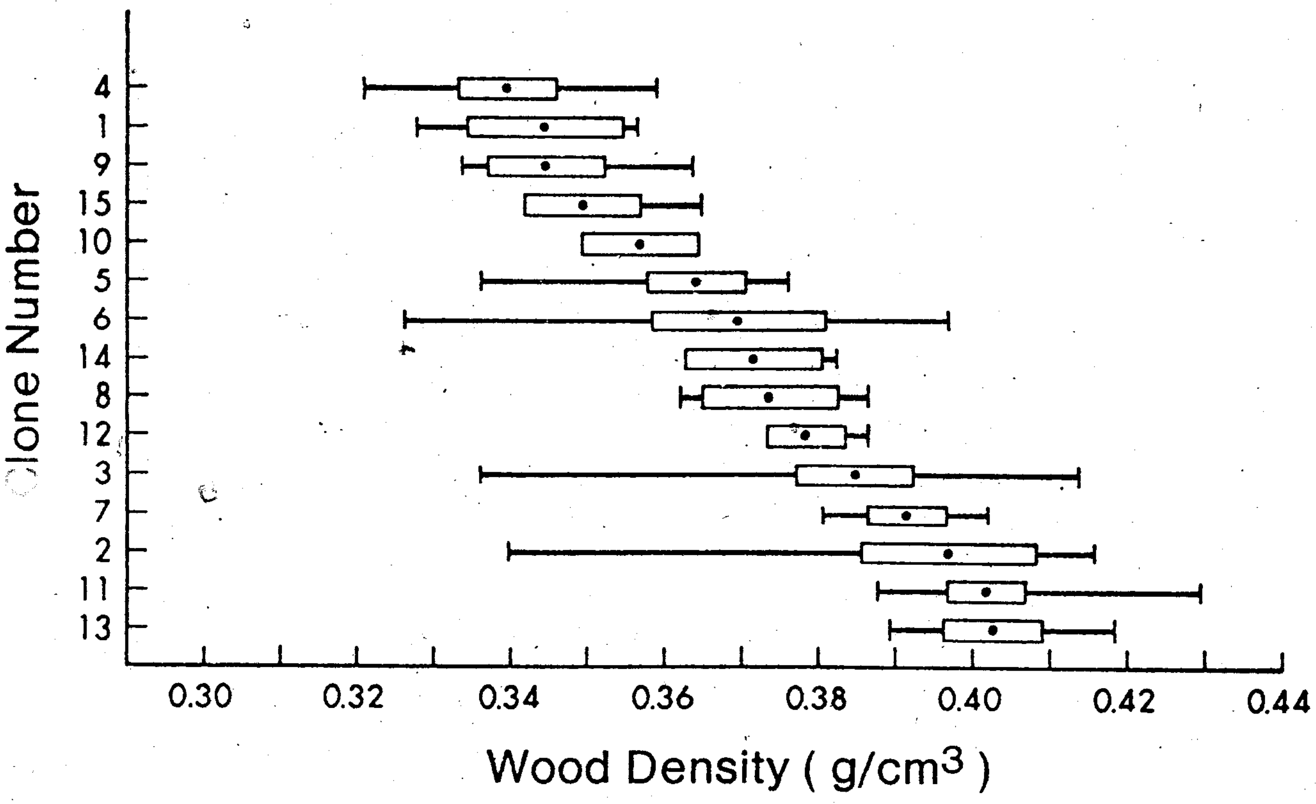

Figure 8 - Ranking of 15 aspen clones from north-central Alberta for mean unextracted wood density. Solid dots, open bars and solid lines represent least-squares means, one standard error and range within each clone, respectively.

case wood density, for each clone. The standard errors indicated that intra-clonal variation was relatively small compared to inter-clonal variation (Figure 8).

There were significant inter-clonal differences in wood density (Table 6). The estimated variance components suggest that the effect of clones accounted for approximately 35 percent of the variation in wood density. This is similar to the values reported for wood density elsewhere (Van Buijtenen *et al.* 1959, Einsphar *et al.* 1963), confirming that heritabilities for wood density are moderate to low in trembling aspen.

As expected from results of the within-stem study, the effect of the four-year sections in the model also was significant, indicating that large variation is present in the radial direction at breast height (Table 6). Clones 11 and 4 represent clones of high and low wood density, respectively, while clones 2 and 5 represent clones of intermediate density (Figure 9). Except for the large, erratic variation exhibited by clone 2 (which was very atypical and probably due to a combination of incipient decay and small numbers of trees in a clone), wood density near the pith was always high, then decreased to a minimum at 30-40 mm from the pith and increased in the "mature wood" zone.

The magnitude of this decrease in wood density over the transition from juvenile to mature wood would seem to be the major factor contributing to average wood density for a

Table 6 - Analysis of covariance for unextracted wood density for 15 aspen clones from north-central Alberta. Model includes the covariate "section width" and "sections" to account for within-tree variation of wood density.

SOURCE	DF	MEAN SQUARES	F	VARIANCE COMPONENTS
Areas	1	0.017646	0.68	
Clones/A	13	0.025946	10.46**	.00038767
Trees/C/A	88	0.002480	4.93**	.00022022
Section	8	0.004205	8.34**	
S x A	8	0.001821	3.61**	
Regression X1(section width)	1	0.002492	4.95*	
Error	807	0.000503		.00050324

TOTAL SS = 0.510789

** significant at the 1% level.
* significant at the 5% level.

regression coefficient = b(x1)= 0.00073009
Broad Sense Heritability = 0.35 S.e. of h^2 = 0.09

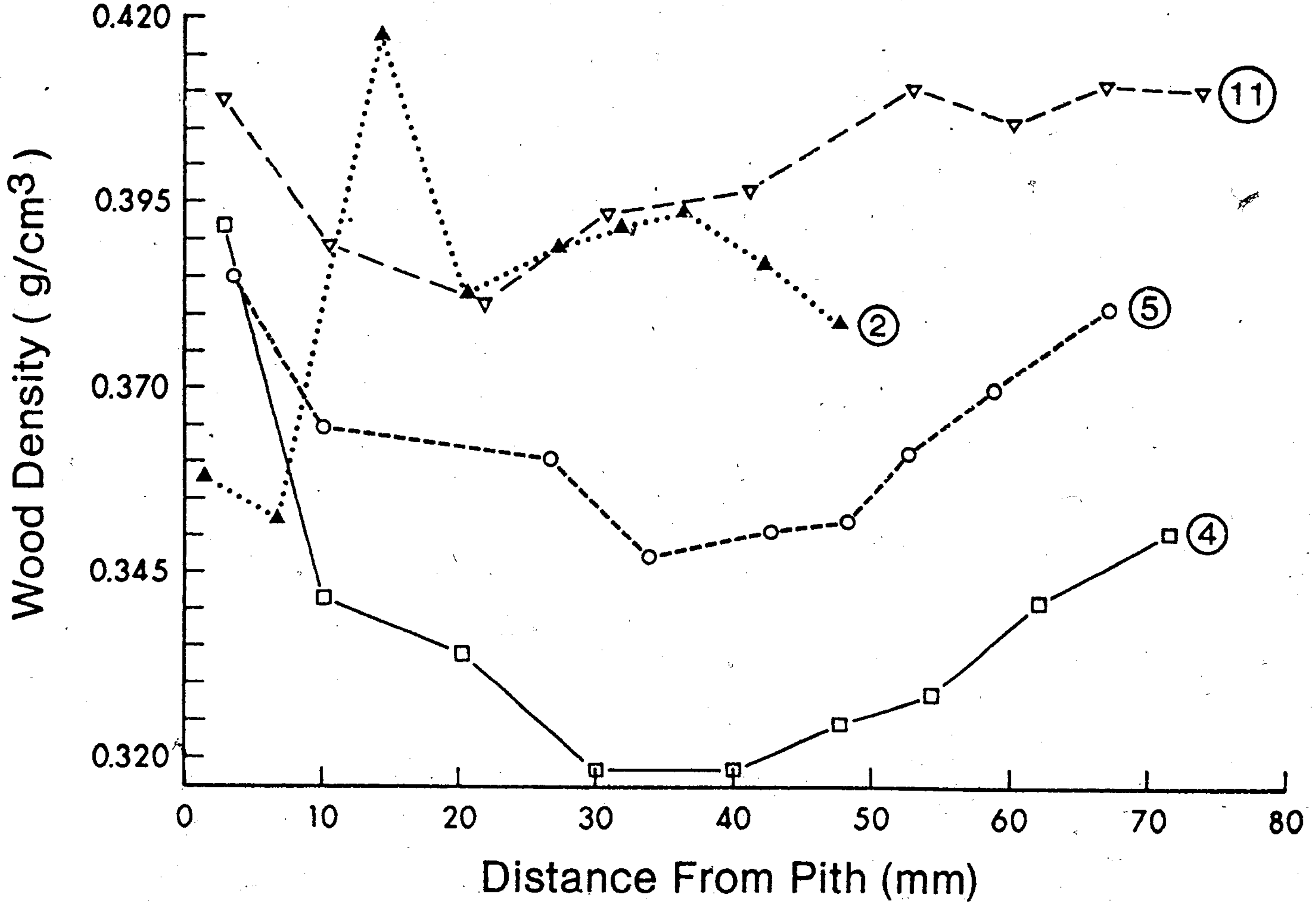

Figure 9 - Variation of unextracted wood density with distance from pith for four aspen clones from north-central Alberta. The four clones represent a high, two intermediate and a low wood density clone from the 15 sampled.

clone. The high wood density near the pith of most of the clones may indicate that some type of inherent growth pattern may consistently influence the types of wood cells produced at breast height near the pith. This inherent growth factor, however, may be substantially influenced be environmental variables, since clonal wood density values near the pith did not exhibit the variation that was evident at later stages (i.e., farther across the radius). As mentioned previously, possible anatomical reasons for this high wood density, such as cell composition and tension wood distribution, can only be clarified by detailed anatomical study similar to that done by Isebrands (1972) for eastern cottonwood.

The covariate "section width" (X1-in Table 6) accounted for the variation in growth rate among the four-year sections, suggesting that a weak positive correlation exists for rate of growth and wood density. However, the overall regression coefficient (b=.000730), does not account for the known differences exhibited between juvenile and mature wood. Statistical comparisons between growth rate and wood density from different locations in a tree may lead to incorrect conclusions about the actual relationship. Therefore each four-year section, which represents a specific increment period in each tree, was analyzed separately. Averaging the specific increment periods over a large number of trees from 15 different putative genotypes should give a good indication of what the actual relationship might be. All but two of the sections from 100 trees showed slight negative correlations between wood density and rate of growth (Table 7). These correlations correspond to those reported earlier for *Populus* (Kennedy 1968, Kennedy and Smith 1959, Smith and Rumma 1971). While the statistical significance of the correlations is relatively weak in most cases, the overall trend of a negative relationship between rate of growth and wood density is evident (Table 7).

Fibre Length

Mean fibre lengths for the 15 clones also showed a large range of variation (Figure 10). Clone 1 had a mean fibre length of 0.97 mm, whereas clone 6 had a mean fibre length of 0.67 mm. Relative to wood density, a comparatively large amount of within-clone variation was present for fibre length. However, this was not unexpected because fibre length differences between juvenile and mature wood exhibit much more variation. Even though the variation present within clones for fibre length is large, the range of variation in each clone is relatively similar (the open bars in Figure 10 represent one standard error on each side of the mean.

As was the case for wood density, there were significant differences among clones for fibre length (Table 8). The effect of clones accounted for 43 percent of the phenotypic variation (as calculated from the variance components given in Table 8). This heritability for fibre

Table 7 - Simple correlations for rate of growth (of four-year increment samples) on wood density and fibre length. Section number represents a four-year increment from the pith outward for 100 aspen trees from 15 clones in north-central Alberta.

Section number	years (rings) represented	fibre length (r)	wood density (r)
1	1-4	.404**	-.143
2	5-8		-.093
3	9-12	.196*	-.128
4	13-16		-.197*
5	17-20	.207*	.007
6	21-24		.272**
7	25-28	.401**	-.166
8	29-32		-.041
9	33-36	.288**	-.266**

** significant at the 1% level
* significant at the 5% level

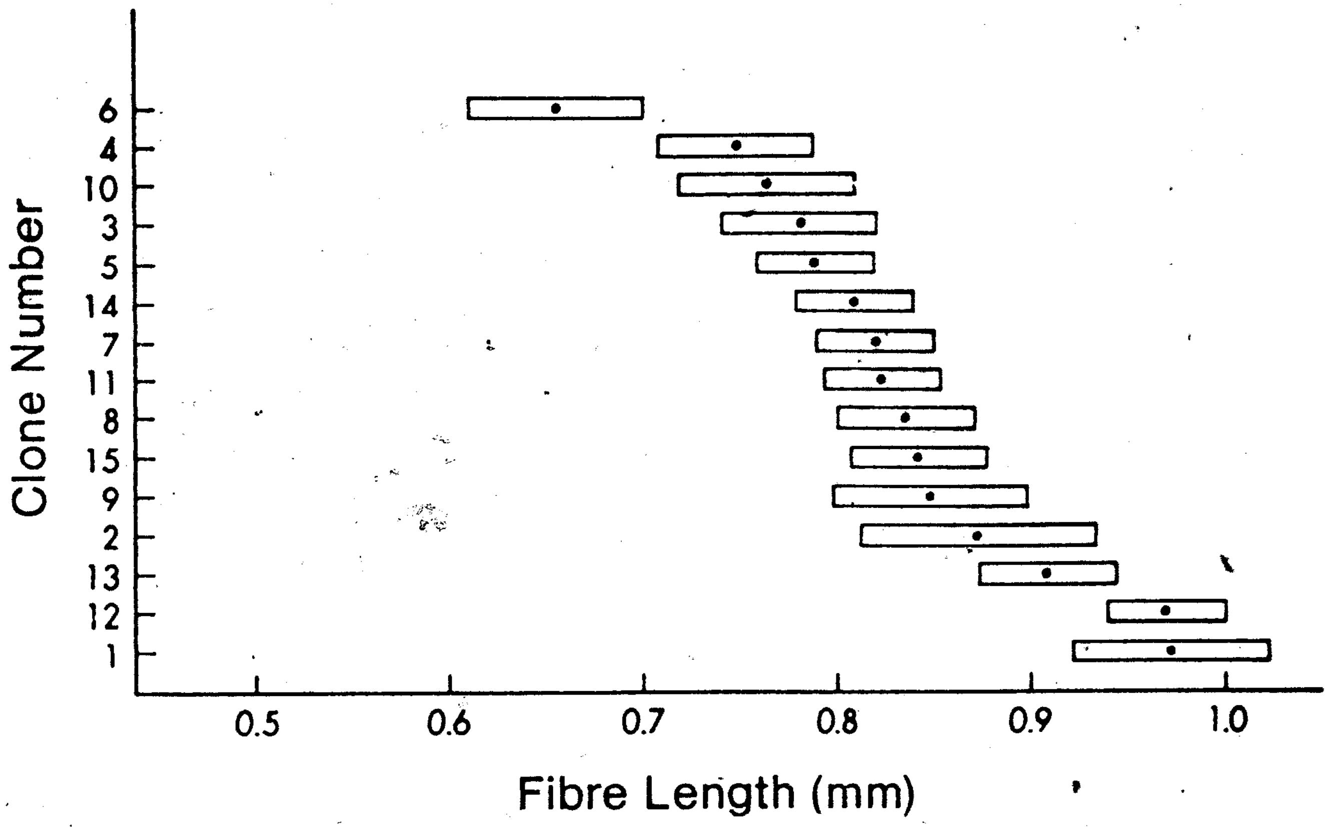

Figure 10 - Ranking of 15 aspen clones from north-central Alberta for libriform fibre length. Solid dots and open bars represent least-squares means and one standard error within each clone, respectively.

Table 8 - Analysis of covariance for libriform fibre length for 15 aspen clones from north-central Alberta. "Sections" and the covariate "section width" is in the model to account for within-tree variation .

SOURCE	DF	MEAN SQUARES	F	VARIANCE COMPONENTS
Areas	1	0.306795	2.22	
Clones/A	13	0.138217	13.41**	.00442823
Trees/C/A	73	0.010311	2.23**	.00114078
Section	4	1.475830	318.55**	
Section x Areas	4	0.013564	2.93*	
Regression X1(section width)	1	0.081551	17.60**	
Error	343	0.004633		.00463301

TOTAL SS = 12.36447

** significant at the 1% level.
*,significant at the 5% level.

regression coefficient=b(x1)=0.0063183
Broad Sense Heritability = 0.43 S.e. of h^2 = 0.11

length is within the range of heritabilities reported earlier for fibre length in trembling aspen (Einsphar *et al.* 1963, Van Buijtenen *et al.* 1959).

The source of variation, "section[illegible], was very significant in the analysis (Table 8), indicating that there were large differences in fibre length across the radius. Fibre length is initially quite short near the pith, steadily increases, and then levels off near 40-50 mm from the pith (Figure 11). The clones used in Figure 11 represent a high, intermediate and low range of variation in mean clone fibre length. Clones which had long fibres in the first four years also had long fibres later. This may have practical applications, since it would permit selection of clones with long fibres at an early age.

For the five four-year sections, there was a slight positive correlation between fibre length and rate of growth (Table 7). This positive relationship between rate of growth and fibre length corresponds to that generally reported for *Populus* (Kennedy 1957, Spurr and Hyvarinen 1954). The strength of the correlations between rate of growth and fibre length are somewhat stronger than those between growth rate and wood density.

Because the stems were of varying age, it is unlikely that similar four-year increments originated under similar environmental conditions. This undoubtedly would have increased both variances in the denominator of the heritability calculation. Assuming that a majority of

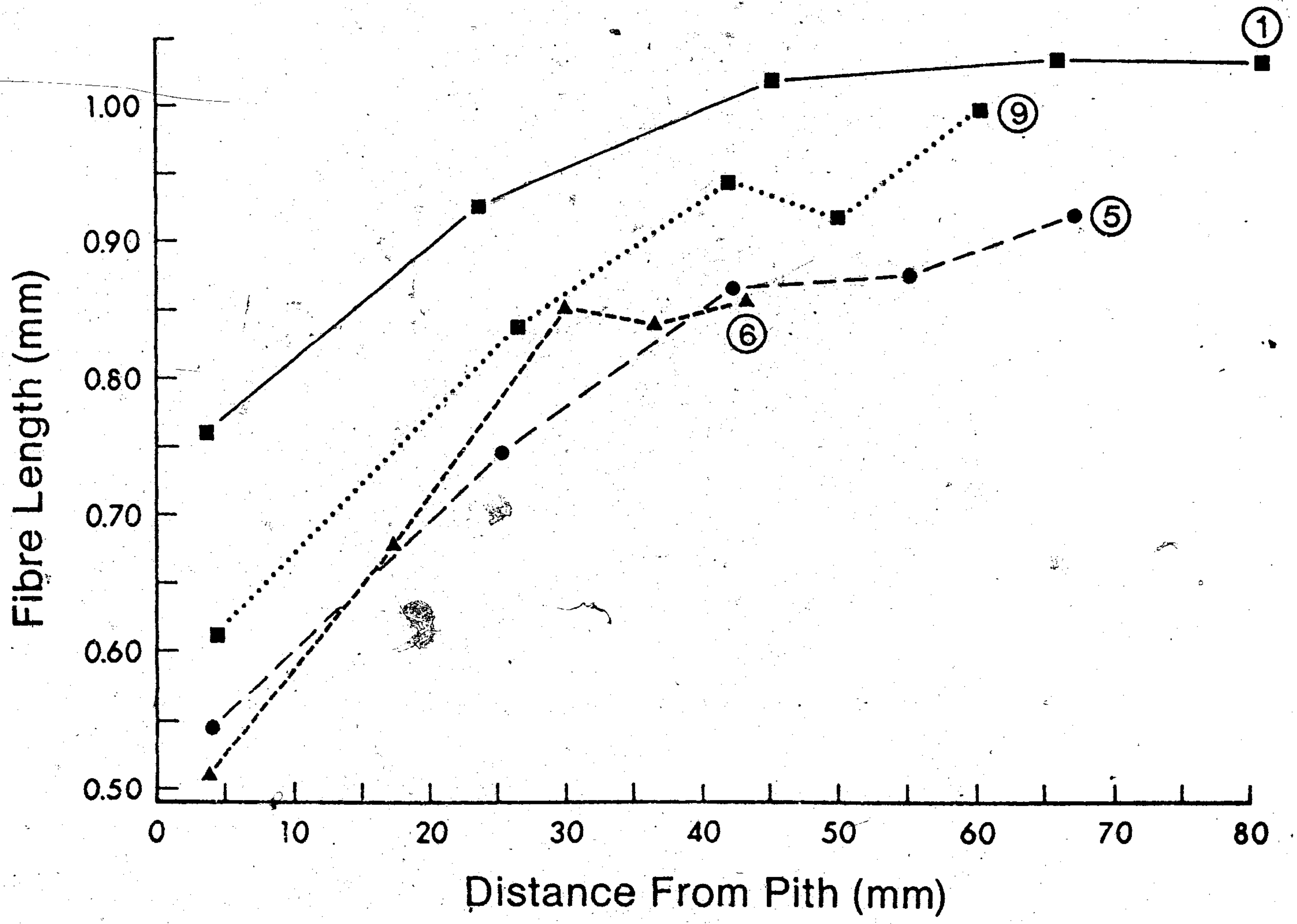

Figure 11 - Variation of libriform fibre length with distance from the pith for four aspen clones in north-central Alberta. The four clones represent a long, two intermediate and a short fibre length clone from the 15 sampled.

similar four-year sections did arise under different environmental conditions, it may be reasonable to suggest that the heritabilities reported may be conservative estimates for aspen.

The inclusion of the four-year sections as a source of variation (for both wood density and fibre length) also substantially reduced the error variance [V(e)], thereby decreasing the overall phenotypic variance component [V(p)]. This would increase the heritability value obtained; however, the variance component for "trees within clones" [V(t)] was separated and added to the total phenotypic variance [V(p)]. Although this may not change the final heritability value a great deal, it should increase the reliablity of the heritability because within-clone and among-clone variances have been separated.

Namkoong and Squillace (1970) indicated that estimating heritabilities from clonal material in this manner may force the inclusion of special genetic and non-genetic effects which make each experiment quite separate and site specific. These special effects are probably due to lack of replication among clones and unequal growing spaces and age for all ramets in a clone (Barnes 1966). Therefore, the heritabilities estimated here may only be applicable to the two stands sampled; however, it is likely that these results could be repeated if carried out in other stands or areas.

IV. Discussion of Aspen Wood Property Variation Study

A. Sampling for Wood Properties in Aspen

The measurement of characters which affect wood quality is involved and time consuming compared to measurement of a trait such as growth rate. Therefore, it is important that studies investigating variation of wood properties be designed so that valid conclusions can be drawn from the results. In this study the main effect, "areas", was not significant in the analyses for rate of growth, wood density and fibre length (Tables 5, 6 and 8). Since this study was not designed to make any implications about variation between stands or areas, "areas" was left in only to account for variation caused by sampling error between areas (i.e., only three clones in one area). If geographic differences in wood properties are to be ascertained properly, a large number of "areas" (with a large number of clones within each area) need to be sampled. Einsphar and Benson (1966) reported that wood density appeared to decrease in a northerly direction, and fibre length exhibited an increase from west to east for aspen in Wisconsin. Their sampling scheme, however, only included four sample areas, so that these geographic differences could be due to chance and may not demonstrate any clinal pattern.

Even if geographic patterns of phenotypic variation are present for these wood properties of aspen, without common garden or similar tests one could not conclude that they have a genetic basis. The geographic variation observed in wood density of slash pine by Larson (1957) and Goddard and Strickland (1962) was found to be closely associated with regional precipitation patterns at critical periods of the growing season. Such environmental influences may result in: 1) direct phenotypic plasticity of the trait, or 2) changes in gene frequencies which result in a genetic and phenotypic response. However, selective pressure exerted by environmental differences over a large geographic range will not have an important role in changes in gene frequencies of a trait that is neutral in its effects on fitness (Falconer 1960). The question then becomes how important, or how neutral, is the effect of wood density on fitness? Intuitively, it would seem unlikely that traits such as fibre length or wood density are closely related to fitness in forest trees. Traits that have low heritabilities typically are closely related to fitness; however, it is not heritability that is relevant, but the proportion of genetic variance that is additive (Falconer 1960). Therefore, heritabilities reported here do not give an indication of how wood properties would be related to fitness, because they were calculated using the total genotypic variance. However, previous wood property studies in softwoods (Squillace *et al.* 1962 and others), indicate that additive genetic variance in wood density is relatively large. Therefore, it is likely either that wood density affects fitness to some degree or is linked to a trait that affects fitness. Hence, clines observed in the field possibly have some genetic basis, although that genetic basis cannot be determined without further study. Since studies such as Larson's (1957), only deal with phenotypic variation, nothing can be concluded about genetic differences. The only practical method of ascertaining what proportion of the phenotypic variation in wood properties is due to genetic variation in geographic surveys is through common garden experiments. The observation of phenotypic clines, however, does provide a basis for pursuing the genetic causes of the clinal variation patterns.

Related to the intra-clonal study, the patterns of wood property variation within stems indicated that sampling intensity could be reduced and among-tree differences still adequately detected. For example, the high wood density noted for the first few growth rings near the pith largely could be ignored since its occurrence is variable and does not represent much volume in the stem. It also appears feasible to reduce the sampling intensity from nine four-year sections to perhaps three or four four-year sections and still detect the large variation across the radius. Therefore, more stems or clones could be studied with the same amount of laboratory work.

Although a precise relationship between the size of the crown and its effect on wood density variation was not identified here, the general pattern of wood density variation with height remained rather constant. This relatively consistent pattern of variation for a wood property within stems is one of the assumptions behind the use of small wood samples at a fixed stem location to represent the trait for the entire tree. While this technique of ranking individuals from small samples is subject to large error (because of the variable nature of within-stem wood properties), sampling a large number of individuals should minimize the effect of this type of error. Conversion equations usually have been developed between core sample and whole tree wood properties (Maeglin and Wahlgren 1972). However, they only change the value associated with each tree; final ranking among all individuals probably changes very little. Also, weighting wood property values by the proportion of volume they represent in the stem is quite common, but its effect on the ranking of a particular individual is again probably quite small. Therefore, on the basis of the results of this study, the values obtained from one core at a fixed location in a stem is quite suitable for detecting among-individual or clonal differences in wood density or fibre length.

B. The Statistical Models for Wood Properties in Aspen

The aspen stems in the clonal study were chosen so that inferences about clonal variation for the two wood properties in north-central Alberta could be made. Therefore, clones and trees-within-clones had to be considered random effects (except when least-squares means in Figures 9 and 11 were calculated for each clone). However, clones and trees-within-clones were not selected in a typically random manner. Because the selected trees had to meet certain criteria for the wood property measurements, a true random selection procedure was not possible. Searle (1971b) indicated that one of the primary concerns of an effect which is considered random is to estimate variance components and make inferences about the population mean. Therefore the assumptions of randomness, although not following a strict random selection process, are valid.

Broad-sense heritabilities (which are calculated similar to repeatibility and intra-class correlation estimates [Falconer 1960]) for growth, wood density and fibre length had standard errors of 0.08, 0.09 and 0.11, respectively. These values indicate that from the population sampled, heritability estimates are subject to an approximate flucuation of 25 percent.

The basic linear models used in the within-tree and clonal study (from pages 19 and 42) are repeated here for the readers convenience:

$$Y(ijkl) = u + C_i + T_j(i) + H_k + e_l(ijk) , \qquad [\ 1\ ]$$

where C = clones(random)
T = trees/clones(random)
H = height(fixed)
e = error

and

$$Y(ijkl) = u + A_i + C_{j(i)} + T_{k(ij)} + e_{l(ijk)} , \qquad [\ 2\ ]$$

where A = areas(fixed)
C = clones/areas(random)
T = trees/clones/areas(random)
e = error

In models 1 and 2, the error term accounted for all of the variation within trees [except for "height" in (1)], this variation primarily being variation across the radius. The covariates "distance from the pith" and "section width" were included in both analyses initially to reduce the size of the error term. "Distance from the pith" was not significant when used in model 1 with "section width" (Table A2). In model 2, which was used strictly to examine variation at breast height in the trees (to detect clonal differences), "distance from the pith" was significant for wood density and fibre length (Table A3, A4), but since variation across the radius is typically non-linear (Figures 3, 4, 5, 6 and 9), it was not included. Furthermore, it did not reduce the error mean square term very much when compared to the analysis with "sections" as a source of variation (Table 6). Also, the two effects "distance from the pith" and "sections" account for the same variation.

Therefore, in the analyses of both wood characters, "sections" (fixed) was used as a main effect since it was not fitting a straight line in a non-linear relationship.

As discussed earlier for both wood density and fibre length in the clonal study, the regression coefficient for "section width", while adjusting all means for the average effect of growth rate differences, did not accurately explain the relationship between both wood properties and growth rate. Since clonal differences were noted for growth rate, it was thought that some type of adjustment should be made for differences in rate of growth among trees for the two wood properties. However, rate of growth did not have a large effect on wood density or fibre length when differences due to the juvenile or mature wood effect were considered separately (Table 7). Therefore, the appropriate model for analyzing these wood property data in aspen need not include an adjustment for variation in growth rate. The final analyses presented in Tables 6 and 8, therefore, were only slight modifications of (1) and (2). The alterations included the addition of "sections" and the covariate "section width" in the split-plot of both (1) and (2), and an interaction term "sections x areas" in (2). All other interactions were assumed to be unimportant and were pooled in the error term.

C. Some Considerations for Selection and Breeding

As stated earlier, wood density and fibre length are under moderate genetic control. The remainder of the unexplained variation, therefore, must be due to environmental influences. These influences may be caused by factors such as soil, micro-site, water availability, stocking, and competition; however, these should only be considered as indirect effects. Larson (1962) emphasized the importance of indirect effects altering growth, resulting in variability in wood properties. Factors of the environment tend to modify crown structure, which in turn affects growth and hence wood formation. A few studies have indicated an association between various soil characteristics and wood density in aspen, but no strong relationships have been found (Van Buijtenen *et al*. 1959, Wilde and Paul 1959). Considering the report of Larson (1962), such results are not unexpected. It is doubtful that soil differences could directly affect wood density or fibre length, simply because they first must influence growth. The interaction between such indirect effects and wood properties is probably too complex to be explained by studying phenotypes in natural stands. Therefore, the remainder of the phenotypic variation that could not be explained by the effect of clones is probably due to a combination of those environmental factors which affect crown formation, crown structure and the tree's ability to maximize growth. Some of these factors possibly could be separated out by a replicated and regularly spaced field trial using clonal material.

The actual relationship between wood density and wood quality in aspen probably is not as good as the association in softwoods. Softwoods have a much more uniform cell composition (i.e., primarily longitudinal tracheids) than hardwoods, and an increase in wood density in conifers indicates an almost direct increase in cell wall thickening. However, in hardwoods high wood density may be due to variations in cell composition as well as cell wall thicknes. Consideration of the proportion and size of cell types is probably as important as wood density in hardwoods.

Although relatively high wood densities were found in the first few growth rings, Einsphar *et al.* (1972) showed that fibres are extremely short in the juvenile portions of aspen stems. This may suggest that young aspen may be unsuitable for many uses, particularly those involving pulping. However, a number of reports suggest that although juvenile poplar does exhibit low wood quality (i.e., low wood density, short fibres and a high proportion of bark [Anderson and Zsuffa 1975]), most concern about the use of juvenile wood for kraft pulps is unfounded (Bella and Hunt 1973, Cech *et al.* 1960, Hunt and Keays 1973). These studies suggest that aspen can be managed on a short rotation, but discussion and analysis of various alternatives to improve future crops is needed.

The occurrence of tension wood, as described earlier, is quite prevalent in *Populus* and usually is associated with leaning stems. However, it has also been found in many vertical stems and also has been associated with fast-growing stems of *Populus* (Isebrands and Bensend 1972). Parham *et al.* (1977) emphasized the inferior strength of tension wood pulp was due primarily to fibre morphology. Furthermore, clonal variation in tension wood content has been shown to vary from zero to 45 percent in hybrid cottonwood (Anderson and Zsuffa 1975). It would be expected, therefore, that substantial gains could be obtained over natural populations of aspen by selection for growth, wood density, cell composition, fibre length and tension wood.

While it is easy to suggest and speculate that these characters should all be considered, it may be uneconomical to invest the money and time on such intensive screening for wood quality. Whether or not it is economically sound or viable to include characters like wood density or fibre length in genetic improvement programs can only be determined by some type of cost-benefit analysis. Derivation of a good selection index equation including some of these wood quality characters without information on their economic value would be difficult.

Conclusions

Large inter-clonal variation has been found for wood density and fibre length of trembling aspen in north-central Alberta. The broad-sense heritabilities reported here generally confirm those reported for aspen elsewhere. As expected, rate of growth exhibited a lower heritability than did the two wood characters.

Rate of growth does not have an important effect on either wood density or fibre length. Generally it may be concluded that a slight negative and a slight positive relationship exists between rate of growth and wood density or fibre length, respectively.

There were no significant differences between stands or areas for either wood density or fibre length; however, sampling in this study was not intended to clarify these potential differences. Other reports suggest geographic variation of these traits of aspen is quite large, but it is likely that inter-clonal variation will exceed inter-population differences.

Variation of wood density within stems is quite large. Even though patterns of wood density variation have been examined here, an understanding of the factors causing such variation need to be investigated. The causes of such variation are important for determining the utility of aspen stems at various ages.

Implications and Future Research

There are two fundamental and practical implications of this study. First, clonal differences and the extent of within-clone variation indicate that selection of superior phenotypes in the field for the three traits examined is feasible. From the correlations between growth rate and the two wood properties, it seems that any negative effect rate of growth may have on wood density can be largely ignored. The slight positive relationship between fibre length and growth rate indicates that selection for fast growth also may be beneficial to the quality of fibre obtained. Realistically, what needs to be considered are the products for which aspen is going to be used for, and what are the growth and wood quality characters that will be selected. Clearly, rate of growth, branching patterns, stem form and rot are the characters that need to be considered before wood properties. However, it should be possible to select clones exhibiting better than average attributes for the desired characters.

Secondly, the results of the within-tree study indicate that a substantial amount of low density wood is formed in all trees at certain ages. The proportion of this low density wood is strongly influenced by genotype and position in the stem. This may have practical implications, as it suggests growth and wood quality may be manipulated by silvicultural practises.

This study provided some basic information of how wood density and fibre length vary within stems and among naturally occurring clones. Practical research extending from findings presented here should deal with the causes of wood density variation within stems. A quantitative investigation into the proportion of cells and cell types, cell lengths and tension wood occurrence within stems and branches would be beneficial in understanding some of the causes of wood density variation within stems. These studies should also include or account for the effect of crown size and structure on percent cell composition.

Future studies dealing with phenotypic variation should be directed at geographic or clinal variation of these wood properties in aspen clones. Replicated field studies, or controlled crosses among genotypes will give a much better indication of the genetic control of growth, wood density and fibre length. These tests will remove some of the non-genetic effects that are included in this study by lack of replication and unequal growing space among trees.

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APPENDIX

Table A1 - Expected means squares for random effects in Tables 5, 6 and 8 for rate of growth, wood density and fibre length, respectively. Variance components presented for Clones/A, Trees/C/A and error were obtained by equating the mean squares to the expected mean squares.
Coefficients(k values) for unequal data were obtained from Harvey's program.

Means Squares for...	Table 5 (rate of growth)	Table 6 (wood density)	Table 8 (fibre length)
Clones within areas $(\hat{\sigma}^2_{c/a})$	$\sigma^2_e + 9.0\,\sigma^2_{t/c/a} + 61.788\,\sigma^2_{c/a}$	$\sigma^2_e + 8.874\,\sigma^2_{t/c/a} + 60.589\sigma^2_{c/a}$	$\sigma^2_e + 4.944\,\sigma^2_{t/c/a} + 28.893\sigma^2_{c/a}$
Trees within clones $(\hat{\sigma}^2_{t/c/a})$	$\sigma^2_e + 9.0\,\sigma^2_{t/c/a}$	$\sigma^2_e + 4.9774\,\sigma^2_{t/c/a}$	$\sigma^2_e + 4.9774\,\sigma^2_{t/c/a}$
Error $(\hat{\sigma}^2_e)$	σ^2_e	σ^2_e	σ^2_e

Table A2 - Analysis of covariance of extracted wood density from four trees from each of three clonesin north-central Alberta. The two covariates X1(ring width) and X2(distance from the pith) are accounting for within-stem variation.

SOURCE	DF	MEAN SQUARES	F
Clones	2	0.002315	4.84*
Trees/Clones	9	0.000478	0.95
Height	4	0.010367	20.53**
Regressions	2		
X1(ring width)	1	0.012295	24.39**
X2(distance from pith)	1	0.000534	1.06
Error	352	0.000504	

TOTAL SS = 0.231817

** significant at the 1% level.
* significant at the 5% level.

regression coefficient=b(x1)=0.00158807
regression coefficient=b(x2)=0.00008864
r(x1)=0.2264
r(x2)=-0.1721

Table A3 - Analysis of covariance for unextracted wood density for 15 aspen clones from north-central Alberta. X2(Distance from the pith) accounting for within-stem variation.

SOURCE	DF	MEAN SQUARES	F	VARIANCE COMPONENTS
Areas	1	0.013493	0.45	
Clones/A	13	0.030126	11.05**	.00039588
Trees/C/A	90	0.002727	4.38**	.00020746
Regressions	1			
X2(distance from pith)	1	0.006071	9.76**	
Error	962	0.000622		.00062214

TOTAL SS = 0.604564

** significant at the 1% level.
* significant at the 5% level.

Broad Sense Heritability =0.323, S.e. of h^2=.089
regression coefficient=b(x2)=0.00010173
r(x2)=0.1002

Table A4 - Analysis of covariance of libriform fibre length for 15 aspen clones from north-central Alberta. X1(ring width) and X2(distance from the pith) are accounting for within-stem variation at breast height.

SOURCE	DF	MEAN SQUARES	F	VARIANCE COMPONENTS
Areas	1	0.489236	5.11*	
Clones/A	13	0.095695	5.96**	.00275921
Trees/C/A	73	0.016052	2.00**	.00161691
Regressions	2			
X1(ring width)	1	0.253643	31.69**	
X2(distance from pith)	1	9.303240	1162.45**	
Error	350	0.008003		.00800316

TOTAL SS = 12.36447

** significant at the 1% level.
* significant at the 5% level.

Broad Sense Heritability = 0.223, S.e. of h^2=.08
regression coeficient=b(x1)=.00862930
regression coeficient=b(x2)=.00679287
r(x1)=-.1450
r(x2)=.8677