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By

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ABSTRACT

COMPARATIVE PHYSIOLOGY AND DEVELOPMENT OF TREMBLING ASPEN (POPULUS TREMULOIDES MICHX.) AND BIGTOOTH ASPEN (POPULUS GRANDIDENTATA MICHX.) FROM MICHIGAN POPULATIONS

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Trembling and bigtooth aspens are taxonomically very closely related and morphologically similar species of the genus Populus. However, they differ significantly in their ecological requirements which probably partially accounts for trembling aspen having a far greater natural range than bigtooth aspen. Studies of the comparative physiology of both species were undertaken in order to determine further possible reasons for their differences in distribution.

The ability to produce adventitious shoots (suckers) from excised root segments by trembling and bigtooth aspens was studied over two successive years. Growth patterns of shoots and roots of container-grown seedlings were examined for both species under greenhouse conditions. A study of comparative development of container-grown seedlings and sucker-derived vegetative propagules in the greenhouse was conducted. Rates of photosynthesis and respiration in a

controlled environment were also compared for both species.

Juvenile shoot development showed very similar patterns for both species; cumulative height growth, dry matter accumulation and leaf area were similar in spite of significant differences in the number of leaves. Trembling aspen developed many more leaves than bigtooth aspen but the latter compensated by producing much larger leaves. Trembling aspen also significantly outgrew bigtooth aspen in height.

Root development was very similar for both species. Excised root segments of either species suckered equally well. Trembling aspen was consistent in its sprouting ability between the two years of study, but bigtooth aspen varied significantly. Seedlings of both species produced lateral roots at the same rate, the roots showed similar growth rates, and their total dry weights were similar.

Developmental comparisons of seedlings and sucker-derived cuttings revealed that seedlings grew at least three times as fast as cuttings during the 15 week observation period. Seedlings were superior in all the developmental measurements made, except in leaf number, which was similar in both propagule types, and net assimilation rate, in which values for cuttings were higher for both species.

Signifcant geographic variation in height growth was observed in both species between clones from different areas of Michigan. The results also showed that seedlings of northern Michigan origin are superior in height growth to southern Michigan sources in this early stage of evaluation.

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Rates of photosynthesis and respiration were determined in the laboratory with an infra-red gas analyzer in a closed system. Seedlings of both aspen species showed similar rates of photosynthesis and respiration. However, under light-saturating conditions, leaves of trembling aspen had significantly higher photosynthetic and respiration rates, but their CO_2 compensation points were similar.

Distinct differences were observed in the survival and first growing season performance between outplanted containerized and bare-rooted seedlings. Containerized planting stock survived and grew better than bare-rooted seedlings by the end of the first growing season after transplanting.

ACKNOWLEDGMENTS

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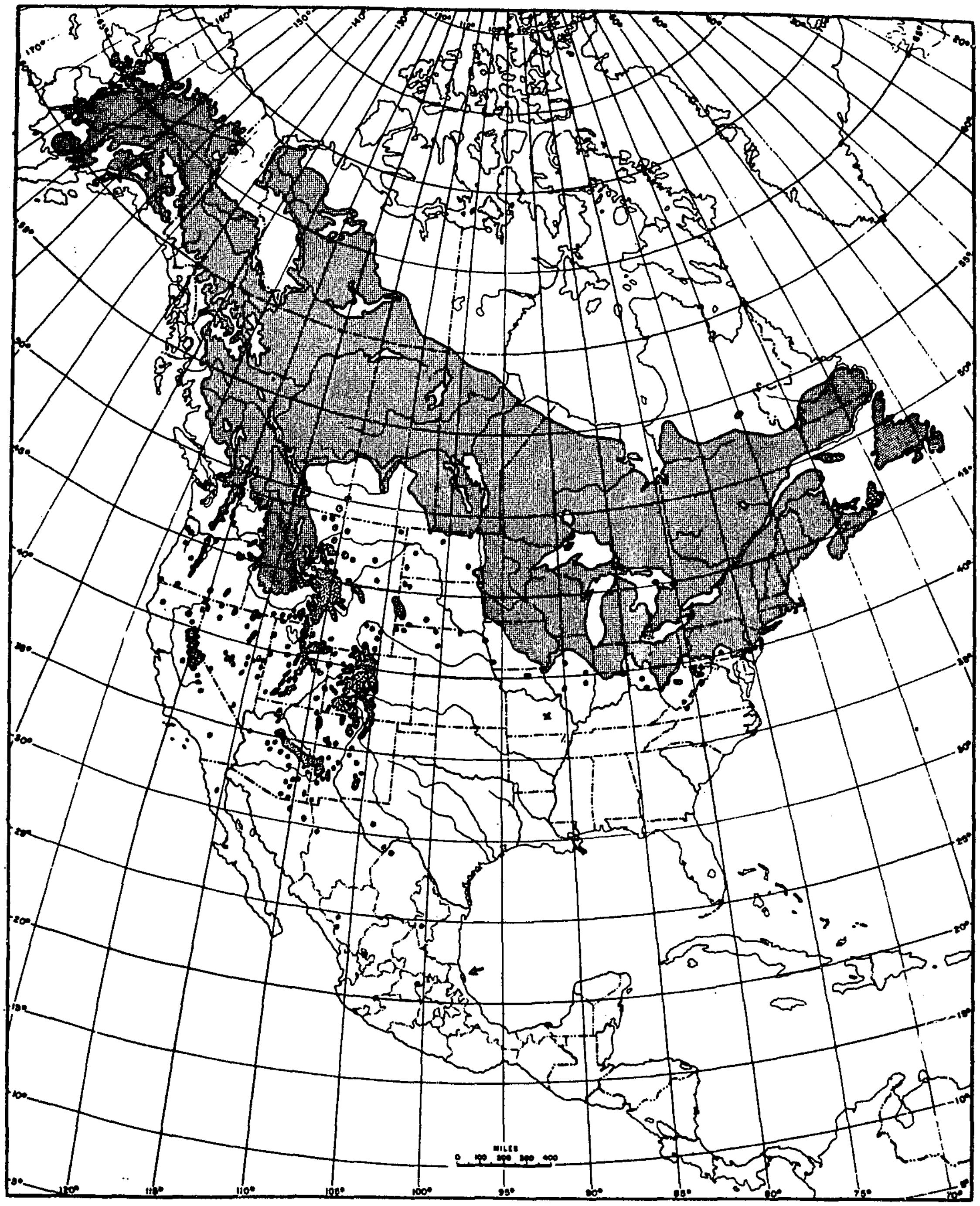
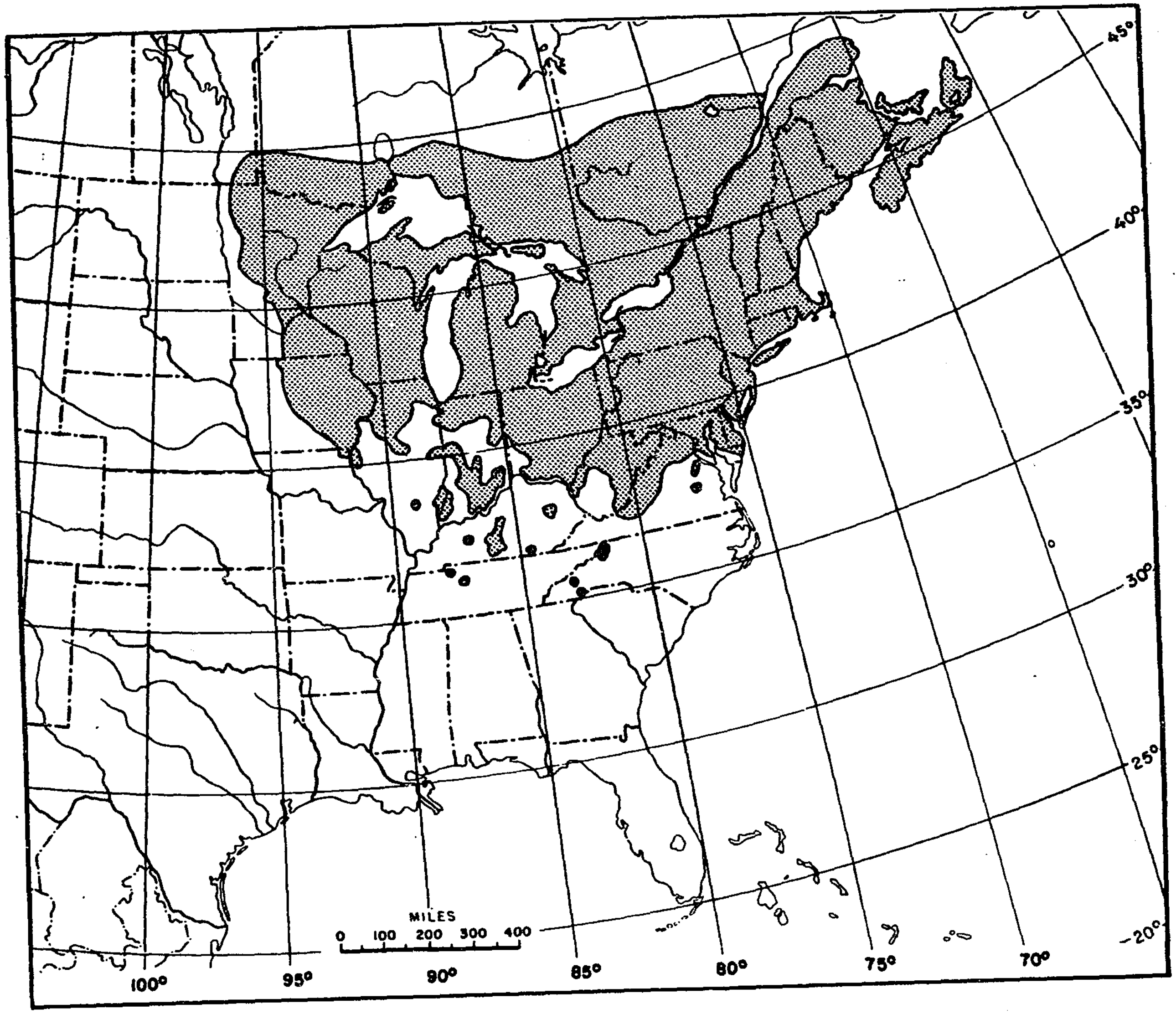
INTRODUCTION

The American aspens, trembling aspen (*Populus tremuloides* Michaux), and bigtooth aspen (*Populus grandidentata* Michaux), belong to the section Leuce of a genus comprising 30 species spread throughout the world. Trembling aspen is the most widely distributed native tree species in North America (Barnes, 1975). Its range is transcontinental, stretching from the tundra of Alaska down to Mexico through the high elevations in the Rocky Mountains. It is found across the entire breadth of Canada, does exceedingly well in the Great Lakes region, and is also present in most Midwestern States. A belt along the Appalachian Mountains to Georgia marks the southern limits of this expansive range in the United States (Graham et al., 1963).

Bigtooth aspen on the other hand, has a relatively smaller distribution. It is restricted to a range extending from Maine and southern Canada to Tennessee and North Carolina, with the lower peninsula of Michigan near its center of distribution (Graham et al., 1963). Both species flourish in the Great Lakes region, where an estimated third or more of the forested land (20 million acres) is occupied by the aspens. In essence the two species are sympatric in the area of distribution of bigtooth aspen. Although the American aspens have been found to hybridize



The range of quaking aspen.



The range of bigtooth aspen.

in nature, they have been effectively kept distinct by a difference of about two weeks between their flowering times early in the spring (Barnes, 1961).

Until recently aspen was regarded as a weed tree. In fact, its major exploitation in the post-World War II period has a history of less than 30 years. In the Lake States where aspen finds most of its present day use, less than 100,000 cords were harvested in 1936 (Graham et al., 1963). In 1970 however, 2 million cords of aspen pulpwood were cut in this region (Leuschner, 1972).

Pulpwood accounts for 60% of all aspen used in Canada, and a much higher percentage in the Lake States (Keays, 1972). In fact, aspen represents 40-50% of all pulpwood used in the Lake States region, and 85% of pulpmills in this area use some aspen (Auchter, 1972).

Although their wood properties are very similar, the two aspen species differ in their botanical and silvical characteristics. Either species may grow up to 80 feet in 35 years under ideal site conditions (Graham et al., 1963). However, trembling aspen is by far more adaptable than bigtooth aspen. The former can grow on soil types ranging from very poor sandy outwash plains to fertile loamy soils where it may attain 100 feet in 35 years. Trembling aspen predominates along margins of seepages, streams or bogs where bigtooth aspen is conspicuously absent. The latter is usually able to grow on well-drained uplands of medium to good quality (Graham et al., 1963).

Both aspen species rely heavily on root suckers for stand reproduction and spread. The hazards of nature such as fire, pests, windthrow and even logging promote suckering and thus the spread of both species (Farmer, 1962; Perala, 1972). Because of very short term seed viability and high susceptibility of seedlings to pests, environmental stress and herbaceous competition, seedlings play a minor role in local stand spread of aspens, but are significant in the extension of their ranges.

In spite of their close taxonomic relationship and great similarity the reasons for the wide disparity in the relative ranges of these aspen species are not clear. It is not certain when either species diverged. However, fossil aspen records show that trembling aspen was widespread in Pliocene times (Barnes, 1975). Unless it evolved in the recent past, bigtooth aspen would seem to have had enough time to extend far beyond its present day range. Nevertheless, it does appear that, apart from other ecological factors, differences between both species in developmental and physiological features would partially account for their relative spread. Hence the present study sought in part to investigate some of these adaptive features at the seedling stages, namely,

1. pattern of cumulative shoot growth
2. pattern of relative shoot to root development and dry matter accumulation
3. photosynthetic and respiration rates.

The relative performance of seedlings to cuttings of sprout origin was also studied to find out which propagule type produced faster growing material to be used in further genetic studies. Because a provenance test is a necessary prerequisite in any forest genetic project aimed at producing superior genotypes (Wright, 1976), a study was conducted on the variation in growth rates of materials from different geographic areas in Michigan. The field outplanting method best suited to young aspen trees was also investigated.

CHAPTER I

VARIATION IN SUCKERING ABILITY OF ASPENS IN MICHIGAN

North American aspens are characterized by the vigorous production of adventitious shoots (suckers) on roots when the stems are suddenly cut or killed (Pauley, 1949). This type of vegetative reproduction is generally believed to be the most common mode of aspen stand reproduction and spread (Baker, 1925; Maini, 1972).

Clones and species of aspen differ in their genetic ability to produce suckers (Zasada and Schier, 1973). Non-genetic environmental factors have also been shown to influence sucker production. Initiation of sucker initials (primordia) in the phellogen results as a response to an environmental disturbance or injury to the tree, upsetting the hormonal balance of the tree (Eliasson, 1971; Schier 1973a). Further development of these initials will depend to a large extent on the severity of such a disturbance (Schier, 1973a). It would thus appear that differences in clonal response to the degree of any environmental disturbance will largely account for clonal variation in sprouting ability.

Auxin may be involved in the suckering process by an apical control mechanism as described by Farmer (1962) and Eliasson (1961, 1971). Schier (1973b) and Wolter (1968) showed that other growth regulators including gibberelins, cytokinins, and abscisic acid may also be involved. Nutritional status of the roots (Tew 1970) as well as temperature, light, and moisture play an indirect role in sucker formation and development (Farmer, 1962).

However, in spite of the fact that both aspen species rely almost exclusively on adventitious shoot formation for reproduction and spread, it is significant that whereas trembling aspen has the widest range of all major tree species in North America, bigtooth aspen is relatively restricted to the Lake States. The following study was carried out to determine (1) if differences in suckering ability are related to this striking disparity in the species ranges; (2) the amount and pattern of clonal variation in sprouting ability within the state of Michigan.

Materials and Methods

In Spring 1974 aspen root segments were collected from clones located in 12 areas, 6 in each of the upper and lower peninsulas of Michigan. All major climatic divisions except the South East Lower climatic division of Michigan were represented. Where possible, root segments were collected from one tree in each clone to assure identity of the genotypes. The root segments, which varied from .95cm to 2.5cm mid-diameter, were cut to about 23 cm long.

The segments were stored in perforated plastic bags containing wet sphagnum moss to keep them moist. Collections were made from May 9 through May 31. Length of collection trips varied from one to three days, at the end of which the root bags were placed in a refrigerated room at 5°C until planted. Roots were collected from 93 clones of trembling aspen (52 in Lower Peninsula (LP), and 41 in Upper Peninsula (UP)), and 51 clones of bigtooth aspen (31 from LP and 20 from UP).

On July 5, four root segments were randomly chosen from each selection, and cut to 20cm length to expose fresh tissue. The root segments were sown 3.8cm deep in a greenhouse bed filled with heat-sterilized river sand. The beds were watered as required. When sprouting started 2 to 3 weeks later, suckers with four expanded leaves or more were cut from their point of attachment to the root segment, and planted in paper plant bands filled with peat-vermiculite soil mix. The cuttings were intermittently misted. Sprouts were transplanted daily until suckering stopped. At that time all root segments were excavated and the number of sprouts 5mm or longer remaining on each root were recorded.

Prior to the beginning of this experiment, 23 clones of each species had been randomly selected to investigate the relationship between sprouting ability and root size. The mid-diameter of each of the four root segments belonging to each clone was determined. Each root segment was cut to 20 cm in length, trimmed of all lateral roots similar to those in the other experiments. The root segments of each clone were then randomly assigned to each of the four greenhouse beds described above. Suckers produced from these root segments were transplanted at the 5-leaf stage, and the total number of sprouts recorded for each root segment. Height was measured on all transplants.

In Spring 1975, a similar experiment was carried out with 39 clones of trembling aspen and 62 clones of bigtooth aspen. All the climatic divisions of Michigan were represented in this second study. Sowing of roots was done in greenhouse beds containing sandy-loam top soil. Ground level temperatures in the greenhouse varied from 78°-87°F, a range considered by Maini and Horton (1966) to be very good for sucker production.

The data were analyzed statistically to determine the significance of observed differences in sprouting between species and clones during the two years, and to determine relationships between sprouting ability and (i) length of storage period; (ii) mid-diameter (size) of root segment; (iii) height growth of sprout cuttings nine weeks after transplanting.

Results and Discussion

No significant correlation was observed between the length of storage period and the number of suckers produced by root segments from the clone. This shows that roots may be collected and stored at least three weeks before sprouting without affecting sprouting ability.

Suckering ability and mid-diameter (size) of root were unrelated in both species. This seems to agree with the conclusions of Tew (1970) and Schier et. al. (1973) who showed that production of suckers was not significantly correlated with excised root carbohydrate reserves. However, while the former demonstrated suckering ability to be more related to growth rate of the clone, the latter workers showed that the dry weight of suckers produced by each root segment was strongly related to the carbohydrate reserve of the root segment as well as the number of suckers produced by the root segment. In the present study, there was no significant relationship between the total number of suckers produced by root segments from each clone and average growth put on by cuttings made from such sprouts nine weeks after transplanting. No record was kept of growth of transplants from specific root segments, hence, growth of transplants from each root segment could neither be correlated with number of sprouts produced by the segment nor with size of the segment.

A t-test (Table 1-1) showed that in both years the difference in ability to produce suckers between species was not significant (at 5% level). In successive years of testing, root collections of trembling aspen showed no difference in suckering ability, whereas bigtooth aspen collected in 1974 significantly outsprouted root collections made in 1975. Most suckers that sprout from excised roots

Table 1-1. Comparison of suckering ability of bigtooth and trembling aspens in two successive years.

Species	Number of sprouts per meter of root segment 1974	1975
Trembling aspen	16	15
Bigfoot aspen	21	12*

*Difference between values for the two years significant at 5 percent level.

originate from primordia in an advanced stage of development, but whose further development and outgrowth had been inhibited by the flow of auxin from the shoots of the parent tree (Schier, 1973a). The fall in auxin level in root segments after excision (Eliasson, 1971) probably permits the stimulation of further development and outgrowth of primordia by gibberelins which continue to inhibit the further development of primordia in early stages of development (Schier, 1973b). Root primordia are initiated in response to environmental disturbance or stress, and only primordia in advanced stage usually form suckers on excised roots (Eliasson, 1961; Schier, 1973a). It would appear that most suckers observed in the present study were initiated during a previous growing season, but further development beyond a particular stage was prevented by auxin inhibition. The relative degree of seasonal accumulation of these primordia by any species could probably be regarded as a manifestation of the mode of reaction of the species to stress factors in its environment.

The figures thus suggest that bigtooth aspen may tend to react more to stresses in the environment than would trembling aspen.

The strong difference between clones (Table 1-2) in both species is perhaps a reflection of the inherent ability of clones to react differently to changes in their environment.

Table 1-2. Analysis of variance in suckering ability between clones and collection areas for trembling and bigtooth aspens.

Source	1974			1975		
	d.f.	M.S.	F-value	d.f.	M.S.	F-value
Trembling aspen						
Between clones	90	45.10	5.52**	38	111.31	.90
Between counties	9	86.19	1.91	7	59.72	.52
Between peninsulas	1	15.51	.18	1	94.82	1.59
Bigtooth aspen						
Between clones	46	34.62	2.37**	61	116.49	1.23
Between counties	7	44.30	1.28	11	213.29	1.83
Between peninsulas	1	9.75	.22	1	105.98	.50

**Means significant at 1 percent level.

The nonsignificant difference between geographic areas observed for both species in 1974 and again in 1975 should perhaps be expected. Granted that these differences might be related to adaptive features; nevertheless, the sporadic occurrence of such hazards as fire, insect and disease attacks, browsing by animals and logging, all of which are known to stimulate suckering, may not happen often enough in the same areas to bring about responses in the adaptive strategies of the species. It seems doubtful whether such observed differences between areas will be of any genetic value.

Selection for suckering ability _per se_ is perhaps of little importance to the genetic improvement of the species, unless it is correlated with some other more desirable trait. However, the value of sprouting ability in fixing any observed genetic gains in aspen breeding must be emphasized.

Clones collected from the upper and lower peninsulas did not differ significantly in the number of suckers produced. This suggests that the relatively colder temperature and shorter growing seasons of upper Michigan did not significantly affect the suckering ability.

Summary and Conclusions

On the basis of studies done in two consecutive years, trembling and bigtooth aspens in Michigan did not differ in their suckering ability in the greenhouse. However, bigtooth aspen showed significant variation in its suckering over the two years whereas trembling aspen was consistent. This might suggest a greater phenotypic flexibility of trembling than bigtooth aspen. Whereas the strong clonal variation in suckering might indicate inherent differences in genotype x environment interaction, variations between areas might be less meaningful, since factors which affect adventitious shoot initiation, namely, fire, logging, browsing, and pest hazards, are not consistent in their pattern of occurrence. Sprouting ability thus seems to have shed little light on the reasons that underlie the striking difference in the ranges of the two aspen species.

CHAPTER II

GROWTH PATTERNS OF ASPEN SEEDLINGS UNDER GREENHOUSE CONDITIONS

Introduction

Crucial to the problems that confront a forest biologist is the need for thorough understanding and adequate explanation of the nature and patterns of tree and stand growth. Upon this information hinges the basis for better predictions and improvement in yield (Gordon 1974). Plant growth and development are very complex phenomena, a product of multifarious factors, but certainly basic to the study of the physiology of any given species. Maini (1966a) has explained that among other factors, the interaction of their genetic potential, environment, and nutrition, is very important in determining the growth patterns of individuals. The phenology of height growth of deciduous hardwoods, with respect to preformed or determinate, and indeterminate shoot growth habits is also an important consideration (Kozlowski and Ward, 1957).

The American aspens, like all other members of the genus *Populus*, are characteristically heterophyllus (Critchfield 1960). The preformed, early appearing leaves satisfy the photosynthetic demand of the tree early in the vegetative season, while the late leaves, which arise from a season-long functional indeterminate meristem, affect internodal elongation (Larson, et. al., 1972). Although some growth related studies have been done on aspen and related species (Larson and Gordon, 1969; Larson and Isebrands, 1972), information on juvenile growth and developmental patterns is hitherto very fragmentary.

My study of the two aspen species is essentially one of comparison. The seedling stage is widely believed to be the most crucial in the development of a plant (Clark, 1961; Cleary and Waring, 1969). While aspens are known to spread predominantly by root suckers, dispersal by seedling occurs occasionally (Day, 1944). Seedlings provide the necessary genetic variation needed to drive the evolution of the species. For any tree species, fast juvenile growth rate is an essential element in overcoming herbaceous competition, which along with deer browsing is the most important factor limiting successful aspen seedling field establishment in the first two years (Benson, 1972). It seems accordingly appropriate that a comparative study of the juvenile growth patterns of these two aspen species be made.

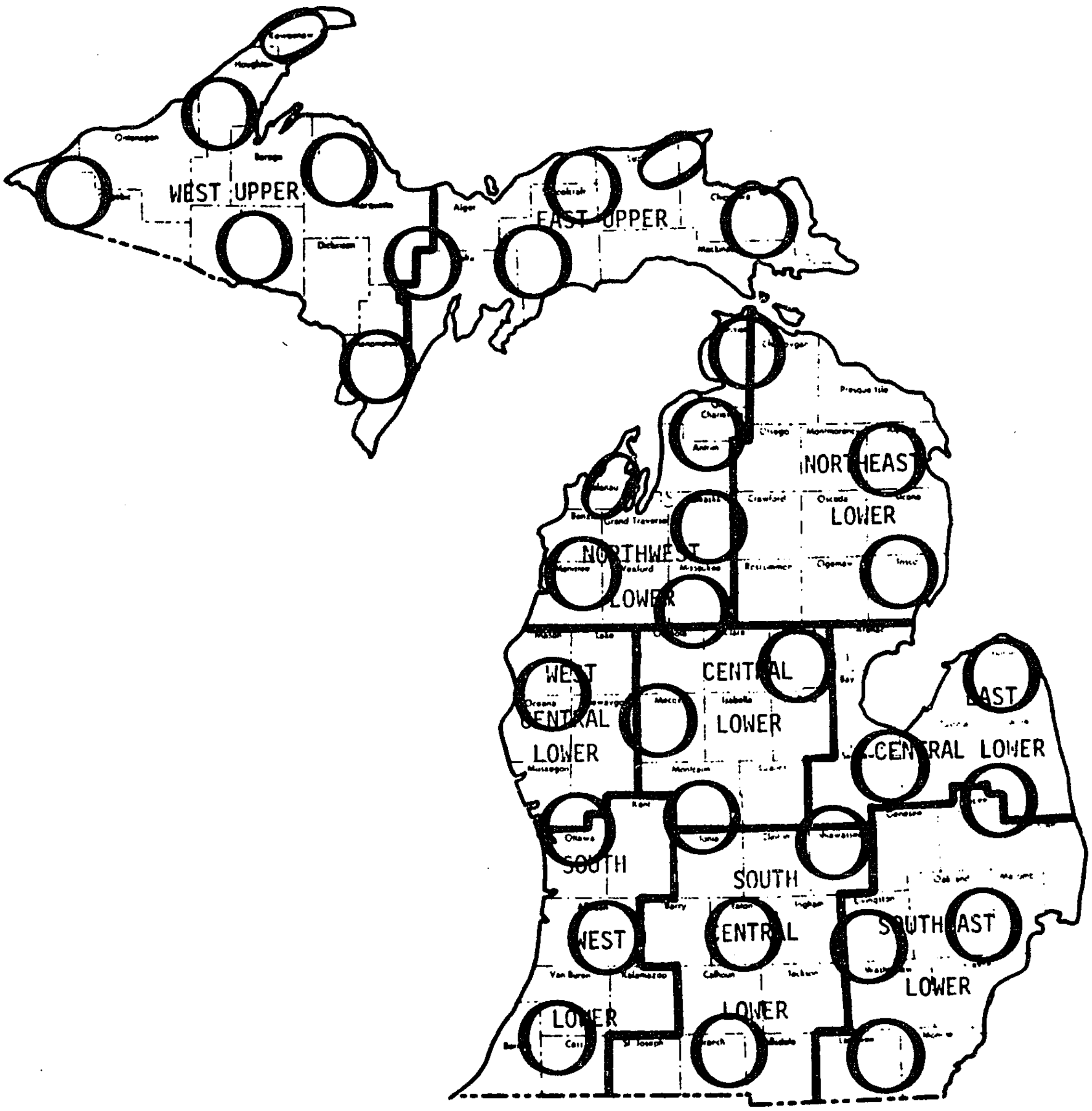
The objective of this study was thus to establish the relative height growth pattern, leaf accretion, and dry matter distribution during the first vegetative season of seedlings of both species under greenhouse conditions.

Materials and Methods

During the last week of April and the entire month of May 1975, a state-wide collection of fruiting branches of bigtooth (Populus grandidentata) and trembling (P. tremuloides) aspens was made. Collection areas were uniformly distributed over the entire state so as to fully represent all the climatic divisions of Michigan (Figure 2-1). Trembling aspen is thought to flower one to two weeks before bigtooth aspen (Pauley,1956; Heimberger, 1936). Yet, an overlap in flowering and fruiting periods does occur (Barnes, 1961), enabling collections of both species to occur simultaneously. Moreover, the two-week lag in the phenology of aspens in upper Michigan behind that of populations in warmer lower Michigan, made collection over the whole state possible.

In each area, fruiting twigs 60 to 90cm long were collected from a single tree in a clone. Samples of root segments were simultaneously taken, as described in Chapter I. The twigs were firmly tied at the base to hold the branches together, and labeled with masking tape. The base of the fruiting bunch was then immersed in a water-filled plastic bag, its loose end tied around the bunch to minimize spilling, and the water bag put in empty coffee cans (1 lb. size). This way, the different fruiting bunches were stably placed in the vehicle, and necessary continuous topping of the water level made easier. Fruits were collected from at

Figure 2-1. Location of areas from which collections of bigtooth and trembling aspen materials were made.


WEST UPPER
EAST UPPER
NORTHEAST LOWER
NORTHWEST LOWER
WEST CENTRAL LOWER
CENTRAL LOWER
EAST CENTRAL LOWER
SOUTH WEST LOWER
SOUTH CENTRAL LOWER
SOUTHEAST LOWER

five different clones for each species in each area.

The fruiting bunches were brought back to the greenhouse where they completed development and shed seeds. It was necessary to change the water in the containers to ensure adequate aeration, and each twig was continuously cut back every two days or so, to expose fresh stem surface. Thus, damage caused by decay fungi was minimized. The period spent in the greenhouse prior to shedding of cotton varied with the developmental stage of the catkins. Because samples were sufficiently separated spatially, cotton was easily hand-picked from the twigs as they were shed, put in labeled storage jars containing drierite, and kept in cold storage (4°C) until extracted.

The aspen seeds were extracted by passing a jet of air over aspen cotton which has been placed in a 1190 micron mesh sieve (U.S. Standard Sieve Series No. 16) below which a finer 53 micron mesh sieve (No. 270) has been added as a receiver for the seeds. Seeds were kept in coin envelopes, put in drierite-containing jars, and stored in the cooler.

For the present study on the growth and development of both species, four areas were randomly chosen, two from each of the two peninsulas of Michigan. From each of these areas, a seedlot was randomly chosen for each species for study. The seeds were sown on June 12, placed in poly-coated paper board containers (milk carton stock) each 5cm x 5cm x 28cm, and packed in groups of 16 in plastic milk cases. Each case contained seedlings belonging to one seed lot only. The growth medium was Terra-Lite brand, Redi-Earth, a peat-vermiculite mix of pH 5.6. Ten seeds were broadcast on top of each band, and a light layer of washed river sand put on top. Peters 20-20-20 liquid fertilizer was applied as recommended for greenhouse use throughout the study period.

The seeds germinated two days later, and were thinned down to three most vigorous seedlings after seven days of growth. After 2 weeks, they were finally thinned to the most vigorous seedling in each band. At the same time, the biggest and most vigorous five seedlings of each seedlot were selected and tagged for weekly measurements. The number of expanded leaves (excluding the cotyledons) borne on each tagged seedling as well as its height were taken on a weekly basis until the seedlings were 12 weeks old.

The five tallest seedlings in each seedlot at the end of 12 weeks were measured, and the band and growth medium carefully washed free of the roots. Leaf area of each seedling was determined with Lambda Portable Leaf Area Meter Model LI-3000. The leaves, stems, and roots were separately packed for oven drying and subsequent weighing. The t-test was used to determine the similarity between the two species in the various growth parameters.

Results and Discussion

Data on all the measured growth parameters are presented in Table 2-1. Figure 2-2 shows the cumulative height growth patterns for both species as observed over the 12 week study period. Curves for both species are typically logistic, similar in shape, but not in magnitude. A graph of weekly height growth increment (Figure 2-3) reveals that both species put on their fastest height growth between the seventh and tenth weeks from seed, with a culminating point in the eighth week.

Table 2-1. Comparison of developmental parameters of trembling and bigtooth aspens 12 weeks from seed.[1]

Trait	Aspen species		Significance level
	Trembling	Bigtooth	of difference
Leaves per seedling	21	13	**
Total leaf area (cm^2)	404.12	393.09	n.s.
Height (cm)	49.9	33.5	**
Dry Weight (gms)	3.288	2.946	n.s.
Net Assimilation Rate ($mg\ dm^{-2}\ wk^{-1}$)	67.65	63.21	n.s.
Leaf Area Ratio ($cm^2\ gm^{-1}$)	123.32	121.20	n.s.
Leaf Weight Ratio ($gm\ gm^{-1}$)	.43	.50	**
Specific Leaf Area ($cm^2\ gm^{-1}$)	286.38	268.08	n.s.
Relative Leaf Growth Rate ($cm^2\ gm^{-1}\ wk^{-1}$)	10.28	10.10	n.s.
Shoot/Root Ratio	3.66	3.07	n.s.

** = significant at the 1 percent level.

[1]Each value is based on measruements of 20 seedlings.

Figure 2-2. Cumulative height growth of trembling and bigtooth aspen seedlings.

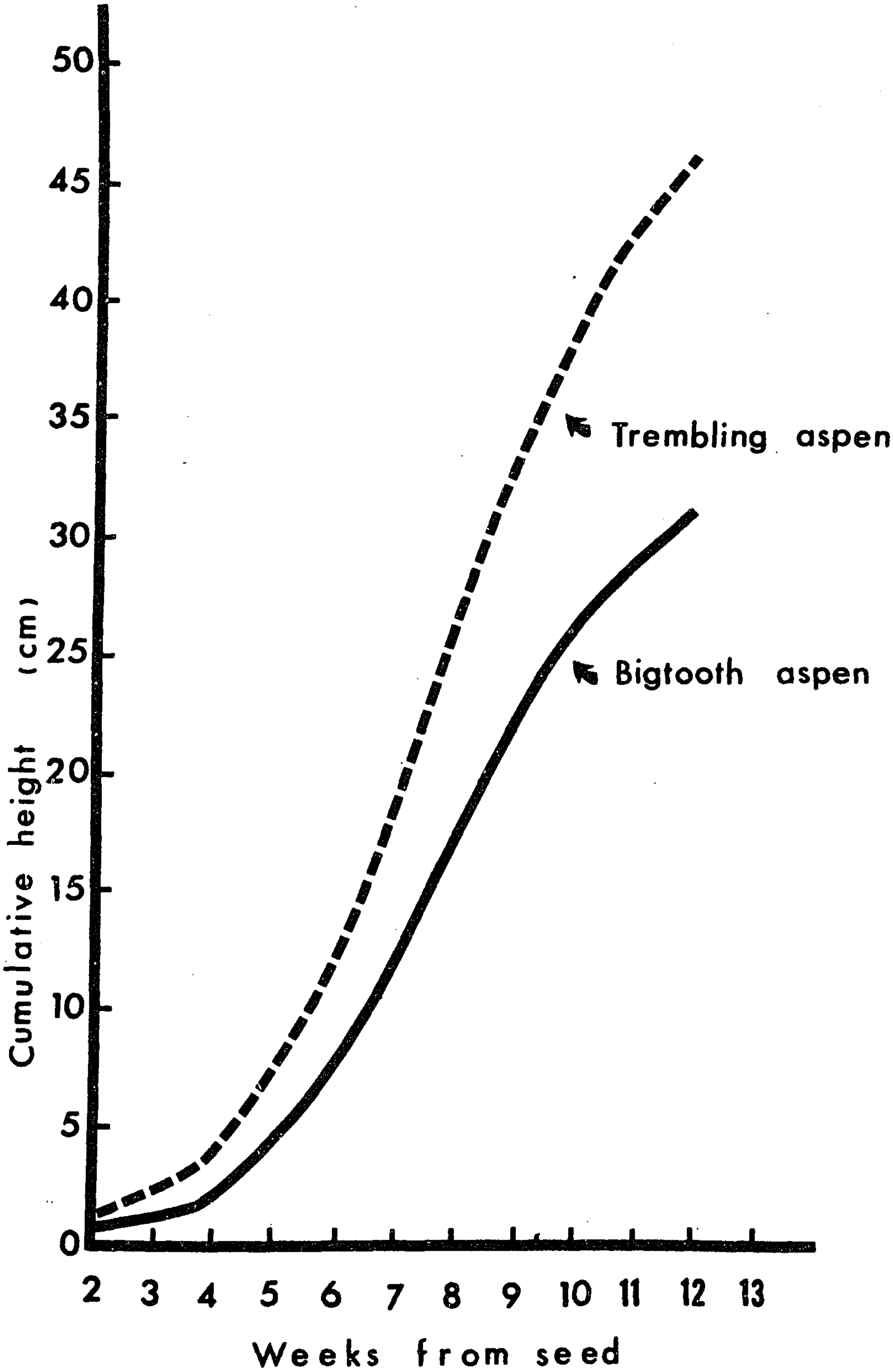
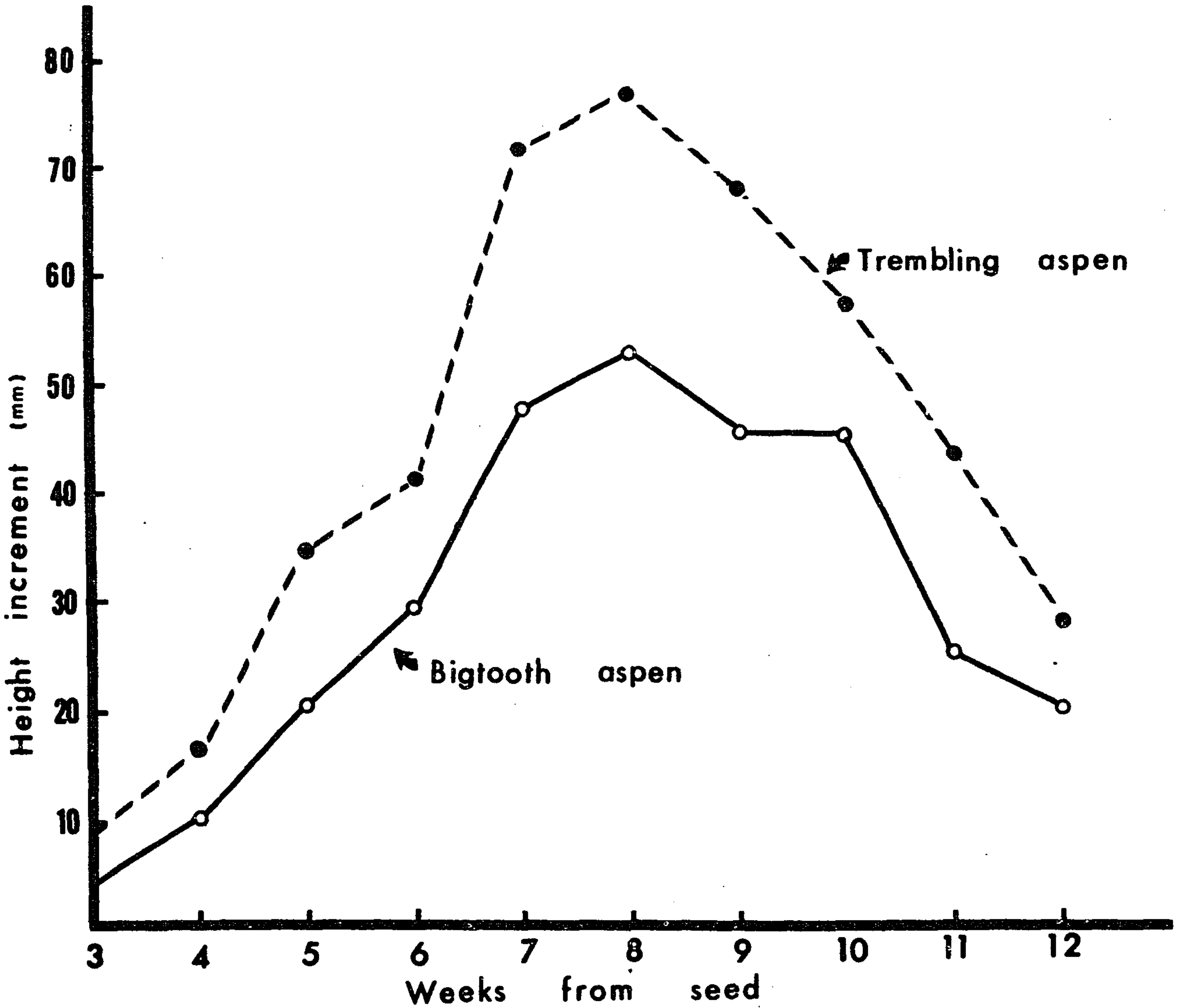

Cumulative height (cm)
0
5
10
15
20
25
30
35
40
45
50
Trembling aspen
Bigtooth aspen
2
3
4
5
6
7
8
9
10
11
12
13
Weeks from seed

Figure 2-3. Periodic height increment of trembling and bigtooth aspen seedlings.


Height increment (mm)
80
70
60
50
40
30
20
10
3
4
5
6
7
8
9
10
11
12
Weeks from seed
Trembling aspen
Bigtooth aspen

It is perhaps significant that at an early age of two weeks from seed, trembling aspen had already established its height growth superiority over bigtooth aspen. Height between the two species at this age was highly statistically significant. This difference in height growth was maintained over the entire observation period. It is noteworthy, however, that one of the bigtooth aspen seedlots outgrew two trembling aspen seedlots over the entire period. On the average, nevertheless, bigtooth aspen grew only 65% as fast as trembling aspen.

Benson (1972) stated that trembling aspen seeds (c. 7,500/gm) are on the average larger than those of bigtooth aspen (c. 10,700/gm). If seed size is a reflection of the amount of food reserve available to the germinating embryo and subsequent early seedling stage, trembling aspen seedlings would appear to have an advantage over seedlings of bigtooth aspen in this respect. Wright (personal communication) noted that early height growth advantages resulting from relative seed size have been observed to last up to 15 years in several coniferous species. However, size of the embryo relative to the size of its food reserve could be more important than total seed weight in determining relative advantages germinating embryos possess over one another. The use of electron microscopy in investigating aspen seed structures will shed more light on this aspect of growth for both aspen species.

The pattern of leaf accretion for both species is compared in Figure 2-4 and 2-5. Trembling aspen once again

Figure 2-4. Cumulative increase in leaf number for trembling and bigtooth aspen seedlings.

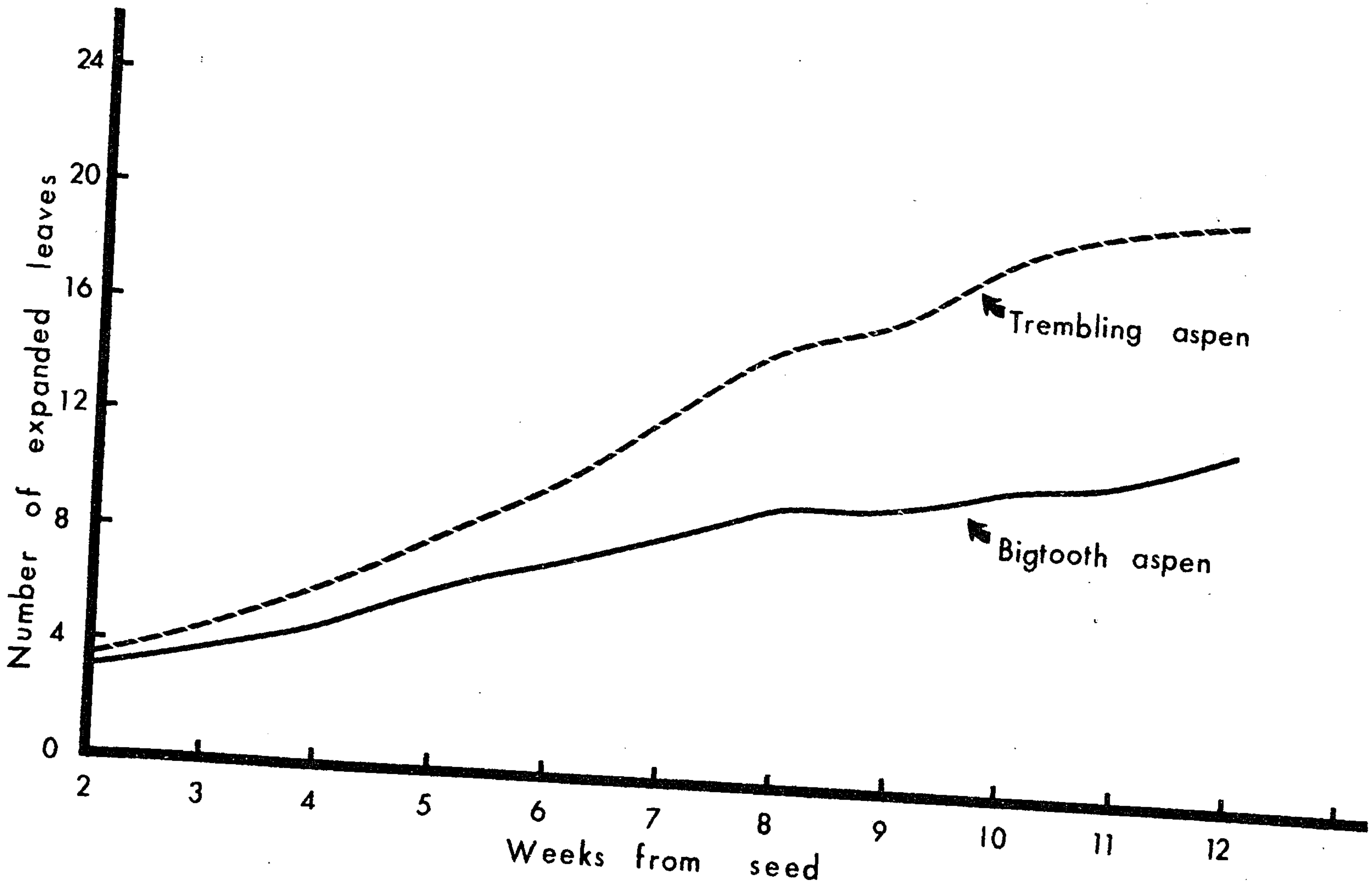
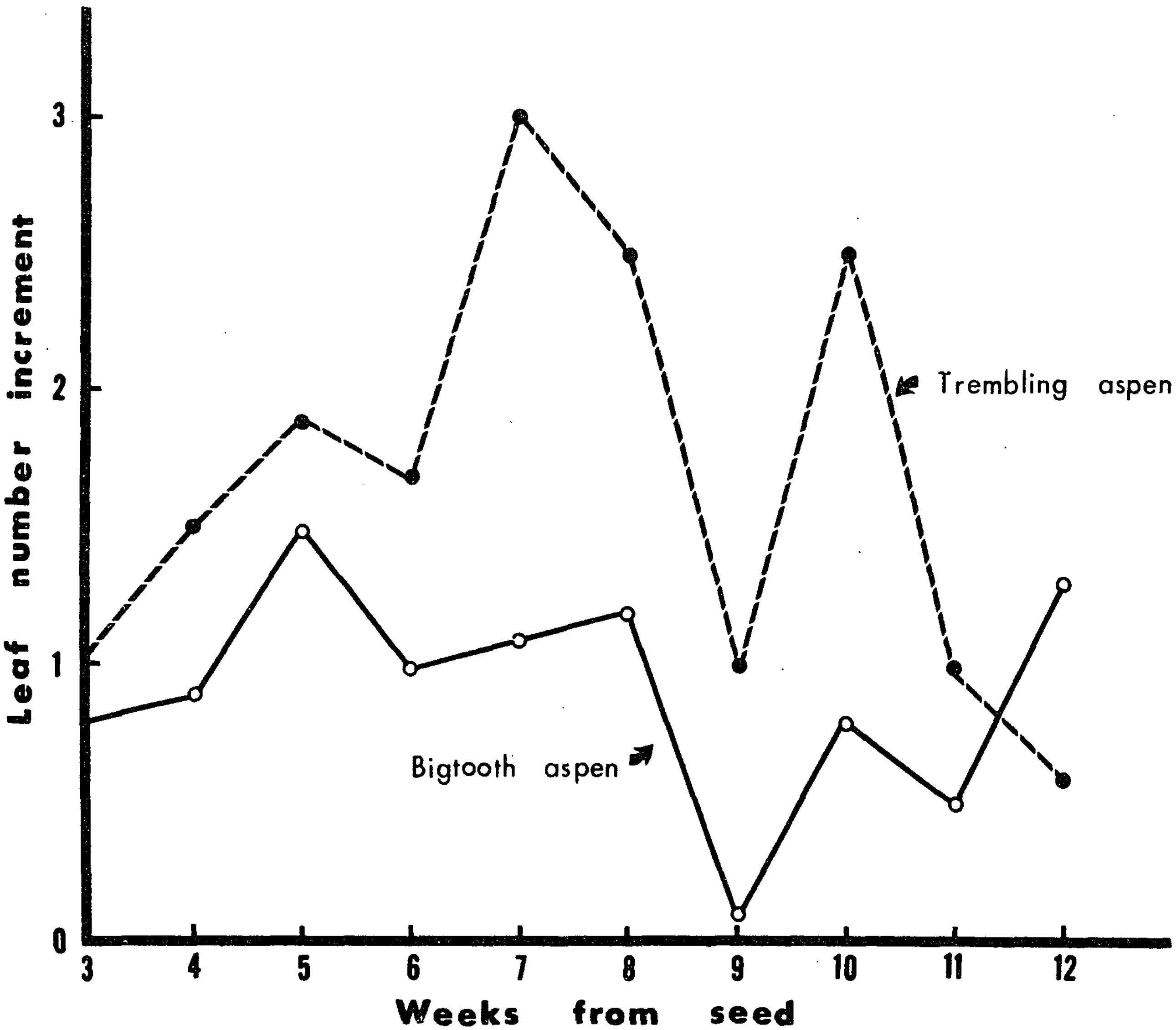

24
20
16
12
8
4
0
Number of expanded leaves
2
3
4
5
6
7
8
9
10
11
12
Weeks from seed
Trembling aspen
Bigtooth aspen

Figure 2-5. Periodic increase in leaf number for trembling and bigtooth aspen seedlings.


Leaf number increment
0
1
2
3
3
4
5
6
7
8
9
10
11
12
Weeks from seed
Trembling aspen
Bigtooth aspen

outproduced bigtooth aspen in number of leaves. It should be noted that only the leaves still retained on the plant were counted. Leaf scars of abscised leaves were not taken into account, nor was the physiological state of the leaf a major factor. It will be observed from Figure 2-4 that the period between the fifth and eighth weeks showed the smoothest and most rapid accretion of leaves. Within this period, trembling aspen produced 2 to 3 expanded leaves for each leaf that was produced by bigtooth aspen. However, because trembling aspen produced much smaller leaves (Table 2-1), there was no significant difference in the total leaf area per seedling displayed by both species. Thus, while trembling aspen produced more numerous but smaller leaves, bigtooth aspen expanded to larger sizes the fewer leaves it produced--a reflection of different strategies in compensatory growth. It is conceivable that bigtooth aspen faces a disadvantage in this connection, because any accident of nature that results in mechanical excision of a whole leaf will do proportionately more damage to the photosynthetic machinery of bigtooth aspen than trembling aspen.

Mention has already been made of trembling aspen being significantly taller than bigtooth aspen. However, dry weight measurements reveal that there was no significant difference in the dry matter accumulated by both species during the study period. Trembling aspen seedlings were tall, rather thin, and relatively flexible, whereas bigtooth seedlings were shorter, stouter, and relatively brittle.

Could these properties be related to their relative ability to grow above herbaceous competition in nature?

Net assimilation rates (NAR) were similar for the two aspens, since similarities were found to exist in the leaf area expanded during the growth period as well as the dry matter accumulated. NAR is thought to be an index of conversion and conservation of photo-assimilated carbon over the observation period (Ledig 1974; Pollard 1972). Whereas the leaf area ratio (LAR), an index of leafiness (Ledig 1974), is similar for both species, leaf weight ratio (LWR) was highly statistically different. The latter parameter indicates the relative distribution of dry weight growth between the photosynthetic and primarily non-photosynthetic tissue. It would appear that bigtooth aspen invests half of the total amount of carbon assimilated into production of photosynthetic machinery, while trembling aspen puts in relatively less.

The similarity in specific leaf area (SLA) suggests that both species spatially expand their leaf dry weight (Ledig 1974) in a similar fashion. Furthermore, both species were found to increase in leaf area per unit time per unit growing plant material (relative leaf growth rate, RLGR) similarly over the study period. The shoot-root ratio was also not statistically significant between the two aspen species. However, it is worth noting that about three-fourths of the total dry matter of the aspen seedlings was tied up in the aerial portions of the plant. This aspect of growth is further discussed in a more elaborate study dealing with correlative and allometric growth between the aerial and subterranean portions of the plant. It is not known what restricting effect the plant bands had on root growth. However, the negative role of air pruning was avoided by terminating the study at the first sign of root tips observed from underneath the milk case.

Summary and Conclusion

This study appears to have revealed some pertinent differences in the strategies adopted by aspen species at the very crucial seedling stage of their development. If these observations made in the greenhouse are indicative of the actual situation in the wild, it would suggest that trembling aspen seedlings stand a better chance of establishment in nature. Their superior height growth is better suited for overcoming the very critical herbaceous competition, since aspens are very strongly light demanding. The investment of relatively higher proportion of its dry matter into the production of much fewer leaves by bigtooth aspen, would seem to be the less advantageous strategy, given the hazards, notably wildlife browsing, that face aspen seedlings in the wild. Moreover, at the end of the growing season, bigtooth aspen stands to lose proportionately more of its dry matter production through leaf abscission.

CHAPTER III

GEOGRAPHIC VARIATION IN GROWTH CHARACTERISTICS OF ASPEN SEEDLINGS AND VEGETATIVE PROPAGULES

Introduction

Trembling and bigtooth aspens are capable of reproducing both from seed and vegetatively by means of root suckers. Both forms of stand reproduction occur in nature, but sucker stands generally predominate (Shirley 1941, Graham et. a. 1963, Perala 1972). The limited natural regeneration through seeding may be attributable to exacting requirements of mineral soil, and adequate light and moisture by aspen seeds for germination (Benson 1972). Other important factors include short seed viability, the presence of a water-soluble germination and growth inhibitor in seed hair, the susceptibility of seedlings to high temperatures of fire-blackened surfaces, as well as fungal damping-off, deer browsing, and herbaceous competition (Maini 1972). Nevertheless, it would appear that many of the sucker stands originally were established by seed blown into favorable seed beds of ash-covering provided by freshly burned lands, or into areas where mineral soil had been exposed (Shirley 1941). The relative frequency of seedling stands is evident from several examples of their presence in Michigan cited by Graham et. al. (1963).

Both seedlings and vegetative propagules are useful and important in genetic studies aimed at breeding and improving forest trees. Several growth comparisons between these two propagule types have been done in the past, and the results obtained seem to vary with the species used. Whereas Sweet (1973) and Tufuor (1973) observed that seedlings of radiata pine outperformed cuttings by 38-44% in height and diameter growth after 3 years and 5½ years in the field, respectively, Garrett (1975) observed no significant difference in height and diameter between cuttings and seedlings of sycamore after one season's growth in the field. Day (1944) and Graham et al. (1963) have stated that in natural stands, suckers of either aspen species, which depend entirely on the root system of the parent trees may reach 1.2m to 2.4m in the first growing season, as opposed to the 15cm to 60cm grown by the independent seedlings.

The present study was initiated to compare the growth rates of both propagule types in order to find which would provide the faster growing material for further genetic studies. The developmental and physiological basis for any observed differences was also investigated.

The preponderance of geographic variation in various traits of different aspen populations has been emphasized, but has not been systematically studied (Barnes 1959; Brown and Valentine 1963; Einspahr et al. 1963; Valentine 1961; Van Buijtenen et al. 1959). Information on geographic variation in growth rate and other desirable traits would, therefore, appear to be a necessary first step in any improvement work on Michigan aspens. Hence, the present study also investigated the nature of juvenile growth rate variation among chosen Michigan aspen populations.

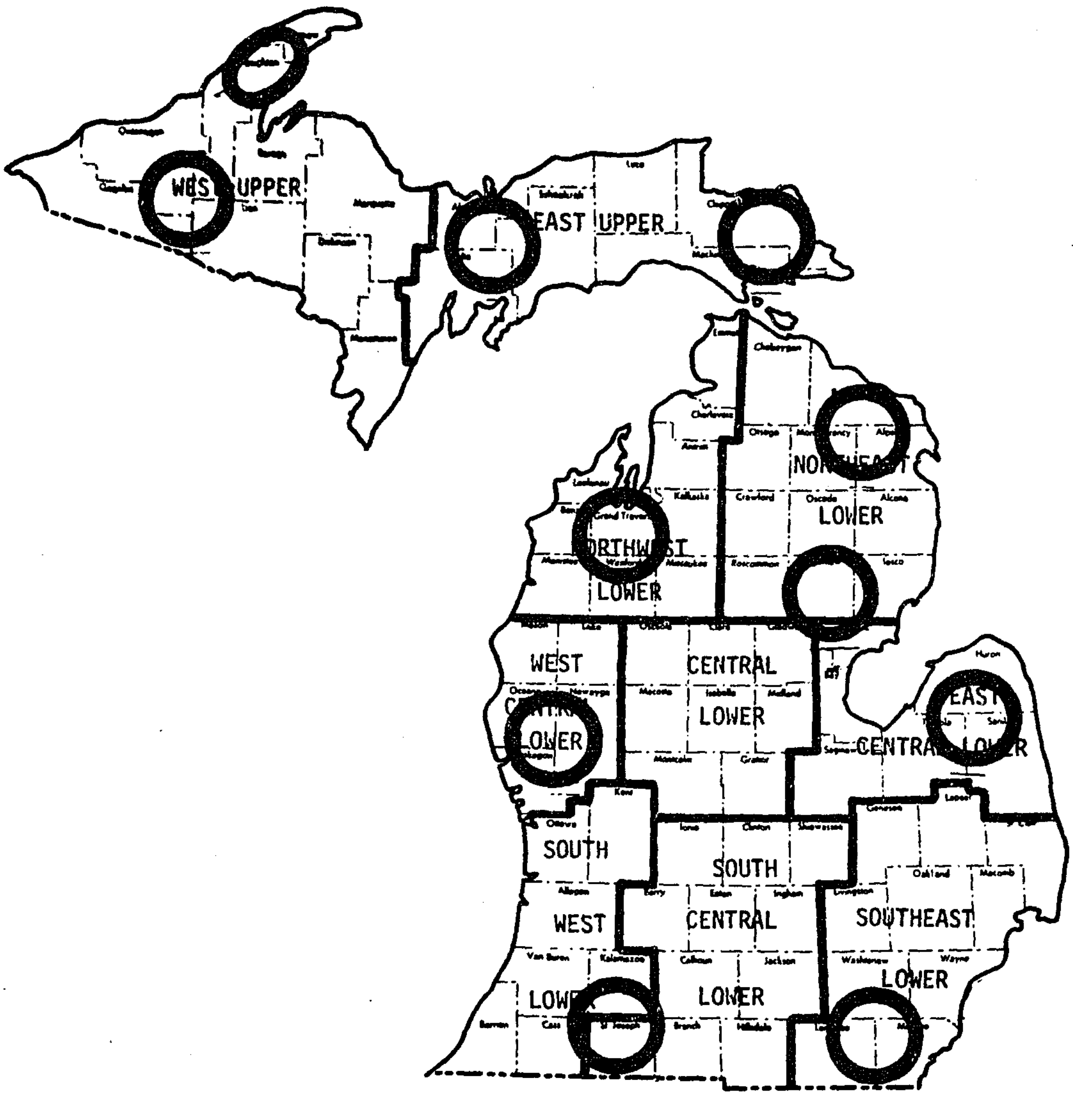
Materials and Methods

The materials used in this study originated from the state-wide collection of root segments with corresponding seeds of same clones made in April and May 1975. Details of the method of collections were described in Chapter II. The distribution of eleven of the collection areas chosen for this study is shown in Figure 3-1.

On July 29, 1975, at least 5 clones of each species from each study area were selected for propagation. Four root segments were randomly selected from each clone. Each segment was cut off on both ends to expose fresh tissue and to ensure that the root was healthy, and trimmed of all lateral roots. The root lengths were measured prior to randomly planting them horizontally 1-2 cm deep and 25 cm apart in roto-tilled greenhouse beds filled with top soil. Each root segment was properly identified with a plastic peg.

Young sprouts 1-3 mm long had already broken through the root surface on some of the segments and care was taken to minimize any injuries to them during planting. Later the same day, seeds corresponding to the same clones were

Figure 3-1. Location of the areas from which bigtooth and trembling aspen study materials were collected.


WEST UPPER
EAST UPPER
NORTHEAST LOWER
NORTHWEST LOWER
WEST CENTRAL LOWER
CENTRAL LOWER
EAST CENTRAL LOWER
SOUTH WEST LOWER
SOUTH CENTRAL LOWER
SOUTHEAST LOWER

sown on peat-vermiculite soil mixture (Redi-Earth by Terra-Lite) very evenly settled in polycoated paper plant bands 5cm x 5cm and 28cm deep. They were packed in milk cases, each case containing 36 bands. Each case contained only seeds from one clone. Ten seeds were sown per band, and clone assignment to cases was random. A fine layer of washed river sand was sprayed over the seeds and watered down with a fine mist spray. Both the root beds and seed cases were watered adequately throughout the study. Young trees that subsequently arose from both propagation methods were fertilized with Peters 20-20-20 liquid fertilizer throughout the observation period.

Sprouting of suckers started on the seventh day, and continued over the following three to four weeks. As the suckers reached the five-leaf stage (about 8cm tall) they were surgically transplanted (Larsen 1946; Pauley 1949; Farmer 1963; and Zufa 1971) into the plant bands as described for the seedlings. Sucker stem cuttings belonging to one clone were similarly planted in one case. The cases were arranged in two columns of 16 rows with 4 cases forming each row, adjacent to similar columns containing the developing seedlings. However, intermittent mist systems were activated over the sucker stem cuttings until they established root systems of their own. Dates of transplanting were recorded, and a survival score was made four weeks after transplanting.

Seedlings were thinned to the most vigorous three per plant band after two weeks growth and finally to the biggest tree at the end of four weeks. Height measurement of the tallest five trees in each clone, both of seedlings and cuttings were made 10 and 15 weeks from planting date.

Two collection areas, one from each of the peninsulas, were randomly chosen for dry matter comparisons of young trees that have been raised by both propagation methods. From each area, three clones were randomly chosen for each species; hence, six clones represented each species. Four of the best developed plants were selected from the seedling group and sucker-derived group of each clone, the leaves collected from each tree and the roots gently washed free of the soil and plant band. The stem and roots were collected separately for oven-dry weight determinations. The leaves were also dried and weighed after their areas had been determined with a Lamda Model LI-3000 portable area meter.

Analysis of variance was used to determine the significance of height variability observed among the cuttings and seedling of clones of both species. The significance of height differences between seedlings and cuttings, as well as between both species in each propagule category, was calculated by the t-test. The t-test was also employed to determine the significance of difference in survival ability of cuttings, and differences in dry matter and other developmental parameters. The correlation between the height growth of cuttings and seedlings was also calculated.

Results and Discussion

The relationship between the performance of clonal cuttings and their seedlings was not significant for either species after fifteen weeks of growth (Table 3-1).

Table 3-1. Comparison of survival and height growth of trembling and bigtooth aspens.

	Trembling aspen	Bigtooth aspen	Significance
Survival (%) cuttings	78.2	54.9	**
Height (cm) cuttings	30[1]	23[1]	n.s.
Height (cm) seedlings	85	68	**
Correlation between seedlings and cuttings in height	-0.07	0.20	n.s.

[1]Means difference in height between cuttings and seedlings of same species significant at .001 probability level.

** = P<.01

However, there was a conspicuous difference in height growth between the cuttings and the seedlings. In both species, seedlings grew about three times as fast as cuttings. A major reason for this great disparity in growth could be the interruption of sprout development caused by the surgical separation of cuttings from the parent root segments prior to transplanting. The consequent transplant shock, and adjustment to the production of its own root system, conceivably would be highly energy-consuming, and could cause delay in shoot growth of a cutting. Preliminary studies showed that with root hormone treatment, this rooting period lasted 7-10 days. Because hormonal treatment was not applied to cuttings used in this study, roots were not formed until the third or fourth week after transplanting. With such a handicap imposed on the growth of cuttings in the greenhouse, comparisons based on juvenile growth would not appear to be relevant.

Neither is there a basis for judging the growth of suckers relative to those of seedlings in nature. Depending entirely on the root systems of the parent tree, an aspen sucker of either species in the wild may reach 1.2 to 2.4m the first full growing season, and 3.7m by the end of the second (Graham et al. 1963). On the other hand, if successfully established, an aspen seedling only grows up to 15cm to 60cm the first growing season (Day 1944; Graham et al. 1963). Perhaps it might be fairer to compare seedling growth with the growth of suckers left growing on excised root segments. However, Schier et al. (1973) showed that the dry weight of suckers is a function of excised root carbohydrate reserve, which in turn varies with the size of root segment. It would accordingly be very difficult to determine the exact size of root food reserve for the developing shoot primordia in an amount comparable to the food reserve in aspen seeds for the young embryo. Indeed, fairness of judgment may only be achieved by culturing excised embryos from seeds and excised shoot primordia from roots in similar growth media, and comparing their rates of growth. Alternatively, seedlings and cuttings could be raised in the greenhouse, established in field plantings, and after several years, current year's performance evaluated.

Trembling aspen seedlings significantly outgrew bigtooth aspen seedlings. The apparent superior growth of trembling aspen cuttings over those of bigtooth was not significant (Table 3-1).

Analysis of variance revealed that variations in growth of cuttings between clones and geographic areas were not significant, and perhaps because of the relatively slower development of cuttings discussed earlier. However, seedlings of each species showed significant difference in growth between areas of collection (Table 3-2).

Table 3-2. Analysis of variance on seedling and cutting height growth of trembling and bigtooth aspens 15 weeks from seed.

Source	Trembling aspen					
	Seedlings			Cuttings		
	D.f.	M.S.	F-Value	D.f.	M.S.	F-Value
Between clones	30	1774.3	1.601	37	75.01	.944
Between areas	6	4451.39	2.508*	6	52.10	.695
Between peninsulas	1	8061.62	1.811	1	66.51	1.277
	Bigtooth aspen					
	Seedlings			Cuttings		
	D.f.	M.S.	F-Value	D.f.	M.S.	F-Value
Between clones	24	1606.86	1.599	44	47.03	1.10
Between areas	5	4865.33	3.028*	9	64.12	1.36
Between peninsulas	1	3583.17	0.736	1	0.94	0.02

* = P<0.05

Furthermore, growth differences between Lower and Uper Peninsula sources were substantial, but not significant for either species.

Table 3-3 shows the relative heights of seedlings from different areas.

Table 3-3. Relative height of trembling and bigtooth aspen seedlings from different areas in Michigan

Area	Species	
	Trembling aspen	Bigtooth aspen
	Percent of total mean height[1]	
Lower Peninsula		
Lenawee-Washtenaw	87	
Cass-Branch	105	99
Muskegon-Oceana	100	93
Kalkaska		122
Huron-Sanilac		124
Gladwin		56
Presque Isle	55	
Upper Peninsula		
Chippewa	80	
Schoolcraft-Alger	116	
Houghton-Gogebic-Iron	121	118
Upper Peninsula, combined	111	118
Lower Peninsula, combined	89	94

[1]Means calculated percentage based on mean of at least 4 clones.

The apparent superior height growth of aspen seedlings from northern Michigan, seems to agree with trends observed for black cherry (Wright 1976) in which sources from northern latitudes outgrew southern sources. However, studies with eastern white pine from Michigan sources, and from sources over its entire range, show the opposite trend, with southern sources having a faster height growth (Wright 1970). In fact, experience with several coniferous and hardwood tree species of North American continent demonstrate a general pattern of growth rate decreasing with increase in latitude (Wright 1976). Among others, differences in phenology, length of growing season, temperature, and photoperiod seem to be most significant in explaining the faster growth of southern sources. A range-wide provenance test for both aspen species is needed to confirm the exact trend exhibited by American aspens.

Data on developmental parameters are shown in Table 3-4. It will be noted that for each species there is no significant difference between seedlings and cuttings in the number of leaves produced, but their leaf areas differ greatly. This obviously stems from the much smaller leaves produced by suckers. Interesting, however, is the fact that cuttings of both species had a significantly superior net assimilation rate. The leaves of suckers are physiologically mature, having been derived from old and mature root tissue of the parents. Seedling leaves on the other hand are strictly juvenile and are different in texture from sucker leaves, though much larger. This physiological age difference probably partly accounts for the observed differences in net assimilation rates. It is also conceivable that greater self-shading resulting from bigger

Table 3-4. Comparison of developmental parameters between 15-week old seedlings and cuttings of trembling and bigtooth aspen

	Trembling aspen			Bigtooth aspen		
	Seedling	Cutting	Sig. Level	Seedling	Cutting	Sig. Level
Number of leaves per plant	29	31	n.s.	16	15	n.s.
Leaf area [L.A.] (cm^2)	1423	252	**	1707	267	**
Leaf area ratio [L.A.R.] ($cm^2 gm^{-1}$)	144	120	**	171	134	**
Dry Weight (gm)	10.11	2.15	**	10.32	1.98	**
Net Assimilation Rate [N.A.R.] (mg $dm^{-2} wk^{-1}$)	47	56	**	40	53	**
Leaf Weight Ratio [L.W.R.][2]	.47	.54	**	.51	.64	**
Shoot-Root Ratio	5.85	3.58	**	4.86	4.84	n.s.
Root Weight Ratio [R.W.R.][3]	.15	.23	**	.18	.18	n.s.

[1] L.A.R. = Leaf Area/Total Plant Weight

[2] L.W.R. = Leaf Weight/Total Plant Weight

[3] R.W.R. = Root Weight/Total Plant Weight

leaves of the seedlings will contribute in lowering the values of their N.A.R. The investment of a significantly higher proportion of their dry matter into leaf growth by cuttings (L.W.R.) also helps to explain their apparently higher N.A.R. even though their slower rate of development resulted in less dry matter accumulation than was observed in the seedlings.

Trembling aspen seedlings have a significantly higher shoot/root ratio than the cuttings, but in bigtooth aspen, the difference was not significant.

Summary and Conclusions

The relatively slower development of cuttings during the study period seems to have obscured any information on geographic variation in growth. However, differences observed among the faster developing seedlings showed significant growth superiority of northern Michigan sources over southern Michigan sources. This observation could serve as a useful guide in seed collection for further improvement work on Michigan aspen, if this trend holds true to sexual maturity. Without doubt, patterns observed in subsequent field test, will provide the ultimate clue and guide to further genetic improvement of the aspens.

The apparent faster growth of seedlings over cuttings under greenhouse conditions agrees with observations of Tufour (1973) and Libby (1974); although the magnitude of this difference appears to have been exaggerated by the interruption of developing root suckers during their propagation. Nevertheless, the potential usefulness of cuttings in fixing any hybrid vigor obtained in subsequent work, in establishing seed orchards and clone banks, and as a means of estimating the success of environmental manipulations to growth and development (Libby 1974), must not be underestimated.

CHAPTER IV

SEEDLING ROOT DEVELOPMENT OF TREMBLING AND BIGTOOTH ASPENS IN CONTAINERS

Introduction

Tree roots have received less investigative attention than have the aerial organs. Some of the reasons given for this relative neglect include:

(a) rarely of direct use to man

(b) difficult to study in their natural state owing to their extensive size and weight, as well as their perennial and anastomotic habit (after Kuntz 1973).

Apart from their normal functions of mechanical support, mineral solution absorption, food storage, synthesis of organic compounds, especially amino acids (Kuntz 1973), the root systems of aspen are the most important and effective means of stand reproduction (Graham et al. 1963; Maini 1972). In fact, Day (1944) observed that second year seedlings in the wild may start reproducing vegetatively by root suckers. He further observed that laterals of the more commonly found fibrous root system of trembling aspen, rarely exceed 15cm in length the first year, but could grow to 30 to 40cm the second year. Mature trees, however, have root systems that may extend 12 to 24 meters from the base, and are usually fibrous and shallow in nature (Graham et al. 1963; Byle 1964; Maini 1972). They form an anasmotic network which may involve few to several trees (Day 1944; Byle 1964). Maini (1972) observed that while trembling aspen suckers emerge from lateral roots 0.5 to 5.0cm thick and occur in the top 5cm of the soil, those of bigtooth aspen are borne on roots 0.5 to 11cm thick and may occur in soil depth exceeding 7.5cm. He further observed that lateral roots of bigtooth aspen are less profusely branched, possess fewer adventitious roots and are more deeply located in the soil than those of trembling aspen.

The objectives of the present study were (1) to monitor the development of the root systems of both aspen species, especially with regard to formation and growth of lateral roots, and (2) to observe the relationship between root and shoot system development at the seedling stage of bigtooth and trembling aspens.

Materials and Methods

Seeds used for this study were a part of the statewide seed and root collection project that took place from April-June 1975, and has been described in detail in Chapter II.

For each of the aspen species, four seedlots were randomly chosen from the collection, two each from the upper and lower peninsulas of Michigan. The seeds were germinated in poly-coated, paper board containers, 5cm x 5cm x 28cm (milk carton stock) which had been filled with a peat-vermiculite soil mixture (Redi-Earth brand by Terra-Lite), and then settled by watering to field capacity. Thirty-six such compartments were held together in a plastic milk case, which contained only seedlings from one seedlot. Thus, eight cases for the eight seedlots were used in this experiment. About ten seeds were sown in each of the 36 cells within a case, by lightly broadcasting them on the surface of the growth mixture. After applying a thin layer of washed river sand over the seeds, they were wetted to field capacity with a fine spray mist. The seeds germinated within four days. Throughout the study, the plants were kept adequately watered and fertilized with Peters 20-20-20 liquid fertilizer.

The seedlings were thinned to the most vigorous three at the end of two weeks, and finally to the largest seedling after three weeks from seeding.

Seedling growth of root and shoot systems are logarithmic in many plants; the ratio of their relative growth rates is a constant which can be approximated by the regression coefficient of the relationship between the logarithm of the dry weight of the shoot, and the logarithm of the dry weight of the root (Ledig 1970). With uniform treatment to the seedlings of both species, comparison of the slopes of the allometric relationships indicate differences in the relative development of the aerial and underground plant parts between the two species being studied.

However, preliminary studies had indicated that differences in the dry weight accumulated in the respective plant organs could not be accurately determined until about their fourth week of growth. Hence, measurements made in this study did not start until the fifth week, and continued until the roots began to emerge from the container bottom.

Starting from week five and on a weekly basis, six seedlings were randomly chosen from each case (i.e. each seedlot). Any damaged or unhealthy tree was discarded. The seedlings with their containers were carefully pulled out of the case, and the roots were gently washed free of soil. The length of the longest root was recorded, as was the number of primary lateral roots arising from the taproot when present. In absence of a taproot system, the number of primary or major lateral roots was recorded for each seedling, which was then separated into its respective organs, and packed in envelopes for oven-drying and subsequent weighing. A photograph was taken of each weekly group of seedlings to show the degree of development of their exposed root systems.

The t-test was used to determine the significance of differences in root length, number of lateral roots, and root weight, each on a weekly basis. The nature of the relationship between shoot growth and root growth was examined by regressing $\log_{10}$ of shoot dry weight on $\log_{10}$ of root dry weight (Ledig 1970).

Results and Discussion

The trend of elongation of major roots of both species is shown in Figure 4-1. Except in the ninth week, no significant difference was observed in the root lengths of the two species on any week during the study period.

The difference in number of primary lateral roots was also not significant, until the ninth week when trembling aspen had significantly more lateral roots than did bigtooth aspen (Figure 4-2). Nevertheless, total root dry weight differences were not significant throughout the observation period (Figure 4-3). Significant differences observed in seedling samples of the ninth week may be attributed to errors of sampling.

The shoot-root ratio did not differ significantly between species in any week of the observation period. However, the ratio changed with the growth of the plant. Figure 4-5 shows the decrease of the shoot-root ratio for both species over the observation period; while in Figure 4-6 change in shoot-root ratio is shown as a function of growth in total plant dry weight. Similar downward trends in shoot-root ratio have been observed for Scots pine (Ovington 1957; Wareing 1950), white spruce (Mullin 1963), and loblolly pine (Ledig et al. 1965, 1970). This is the result of a more rapid growth of roots than tops as the seedling develops (Ledig and Perry 1965). The steeper downward trend shown by the shoot-root ratio of trembling aspen

Figure 4-1. Comparison of increase in root length between trembling and bigtooth aspens.

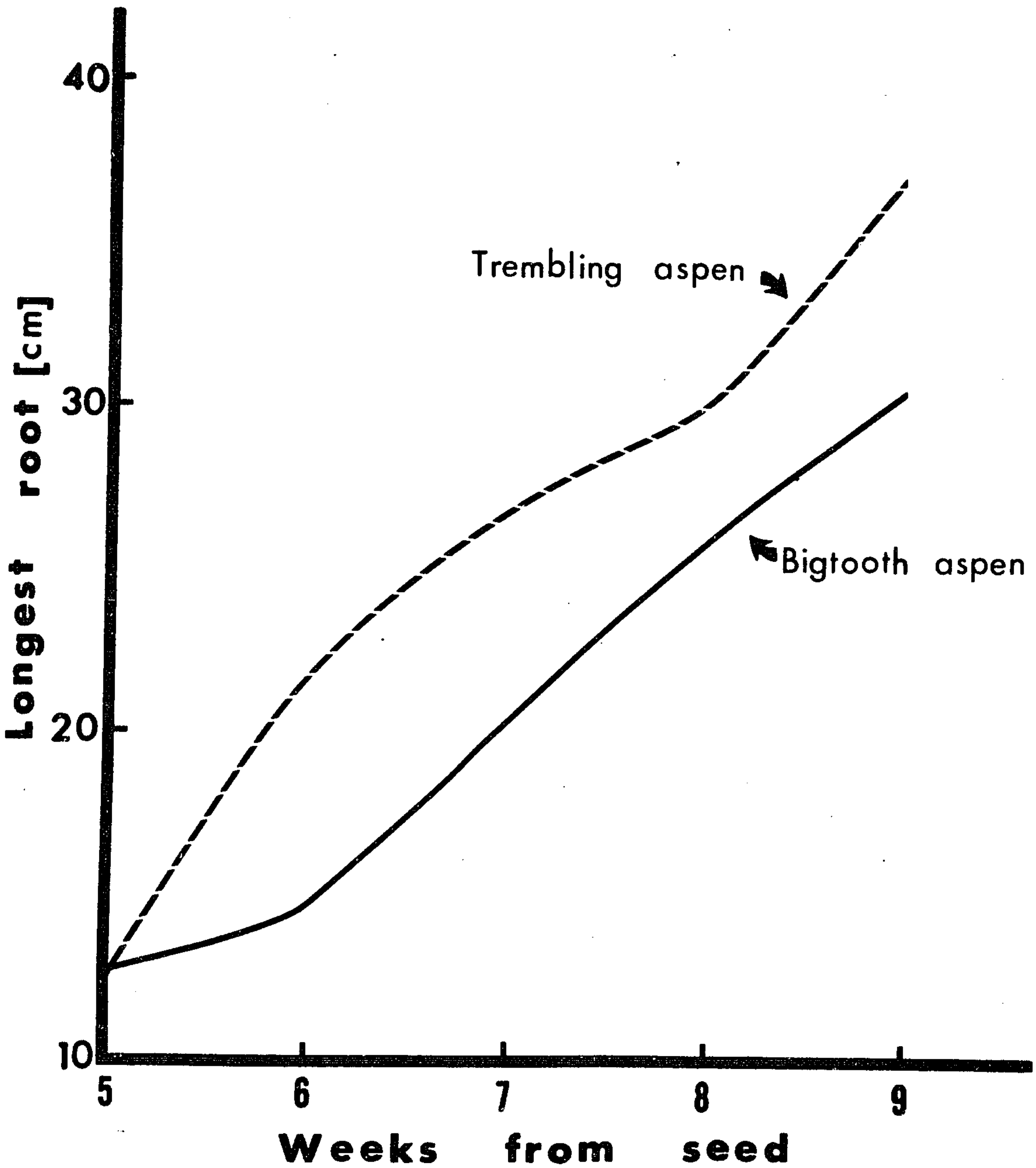

Trembling aspen
Bigtooth aspen
Longest root [cm]
40
30
20
10
5
6
7
8
9
Weeks from seed

Figure 4-2. Comparison of increase in lateral roots between trembling and bigtooth aspens.

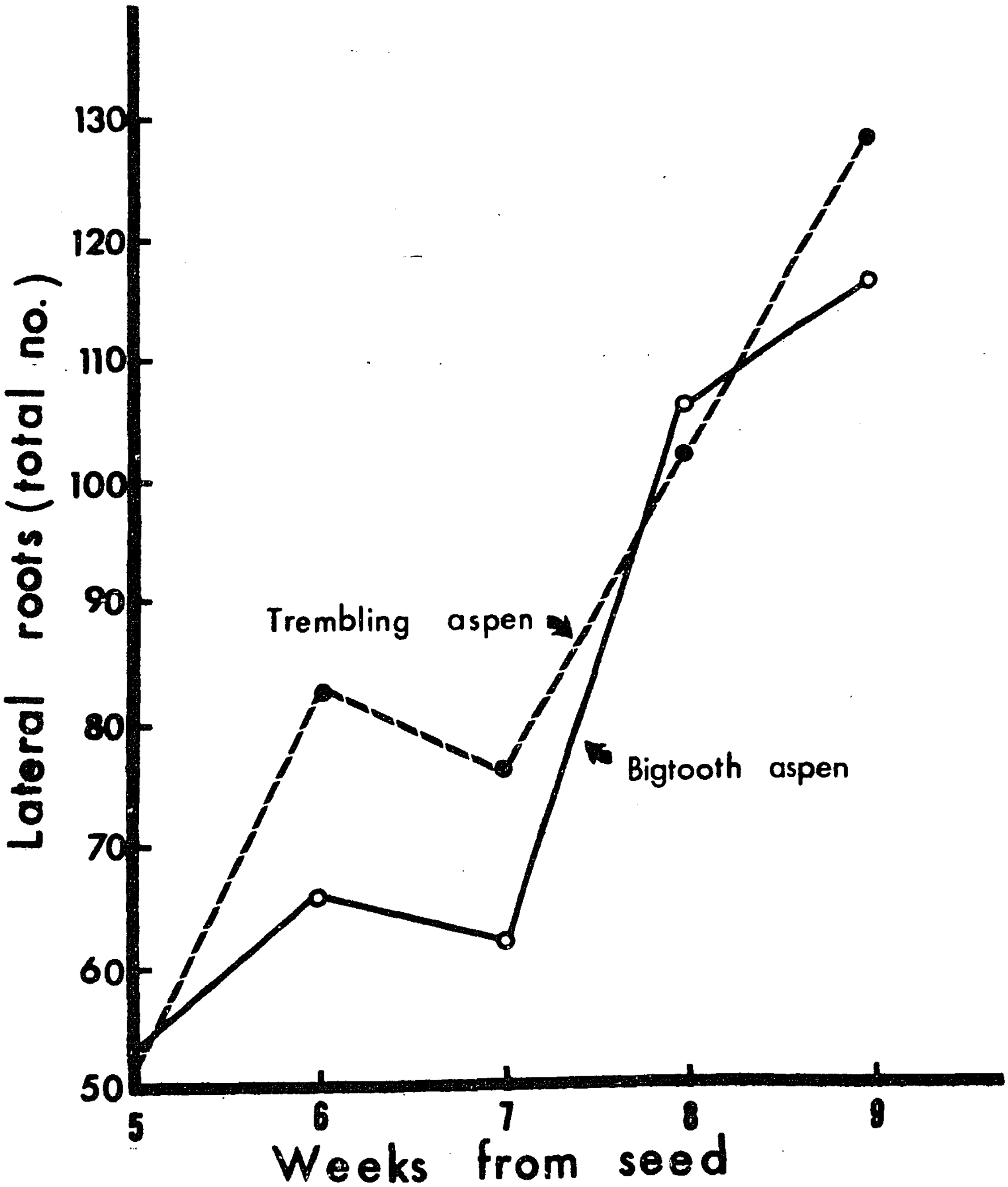
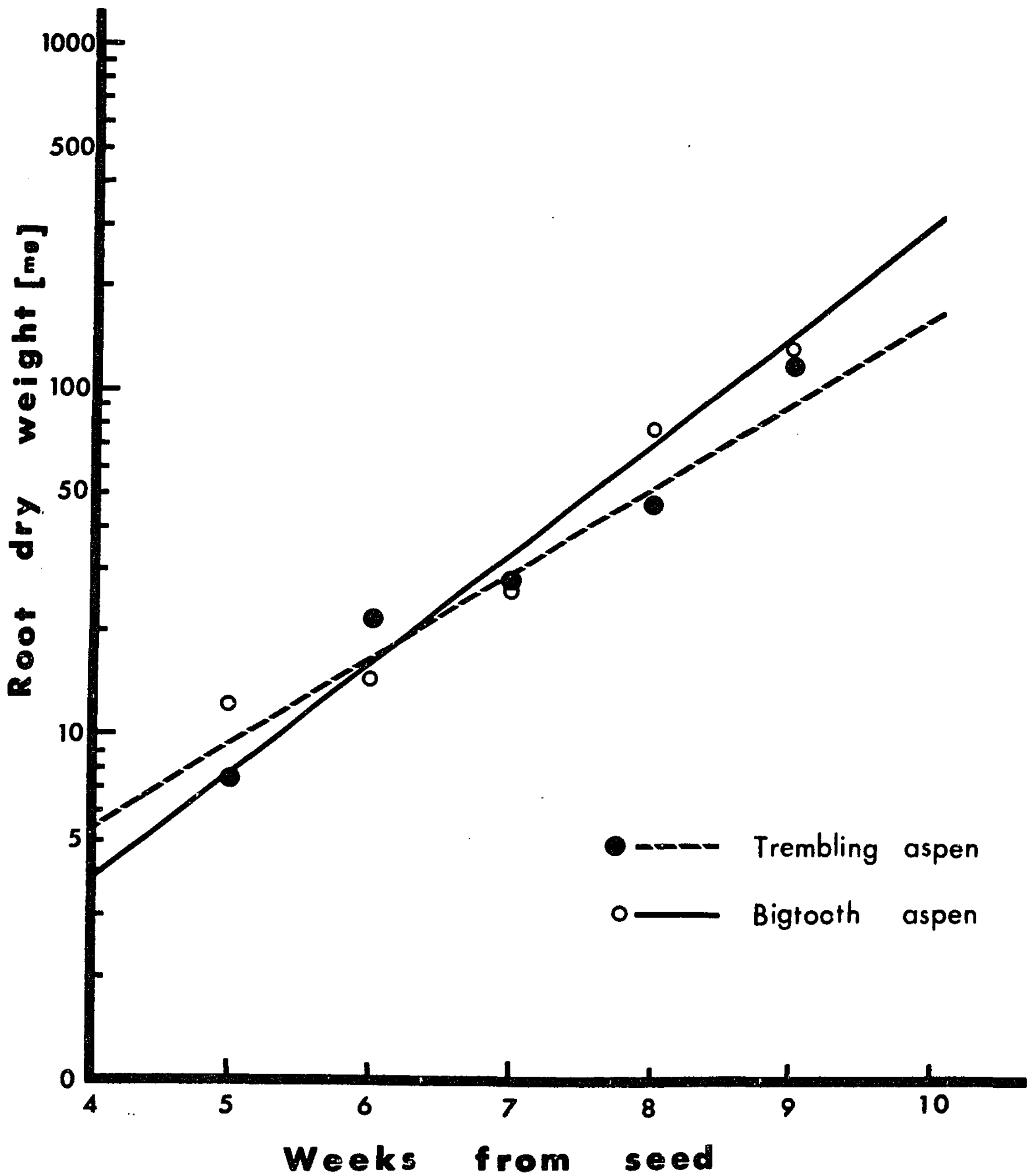

Lateral roots (total no.)
130
120
110
100
90
80
70
60
50
Trembling aspen
Bigtooth aspen
5
6
7
8
9
Weeks from seed

Figure 4-3. Comparison of increase in root dry weight between trembling and bigtooth aspens.



Root dry weight [mg]
1000
500
100
50
10
5
0
4
5
6
7
8
9
10
Weeks from seed
Trembling aspen
Bigtooth aspen

Figure 4-4. Comparison of increase in shoot dry weight between trembling and bigtooth aspens.

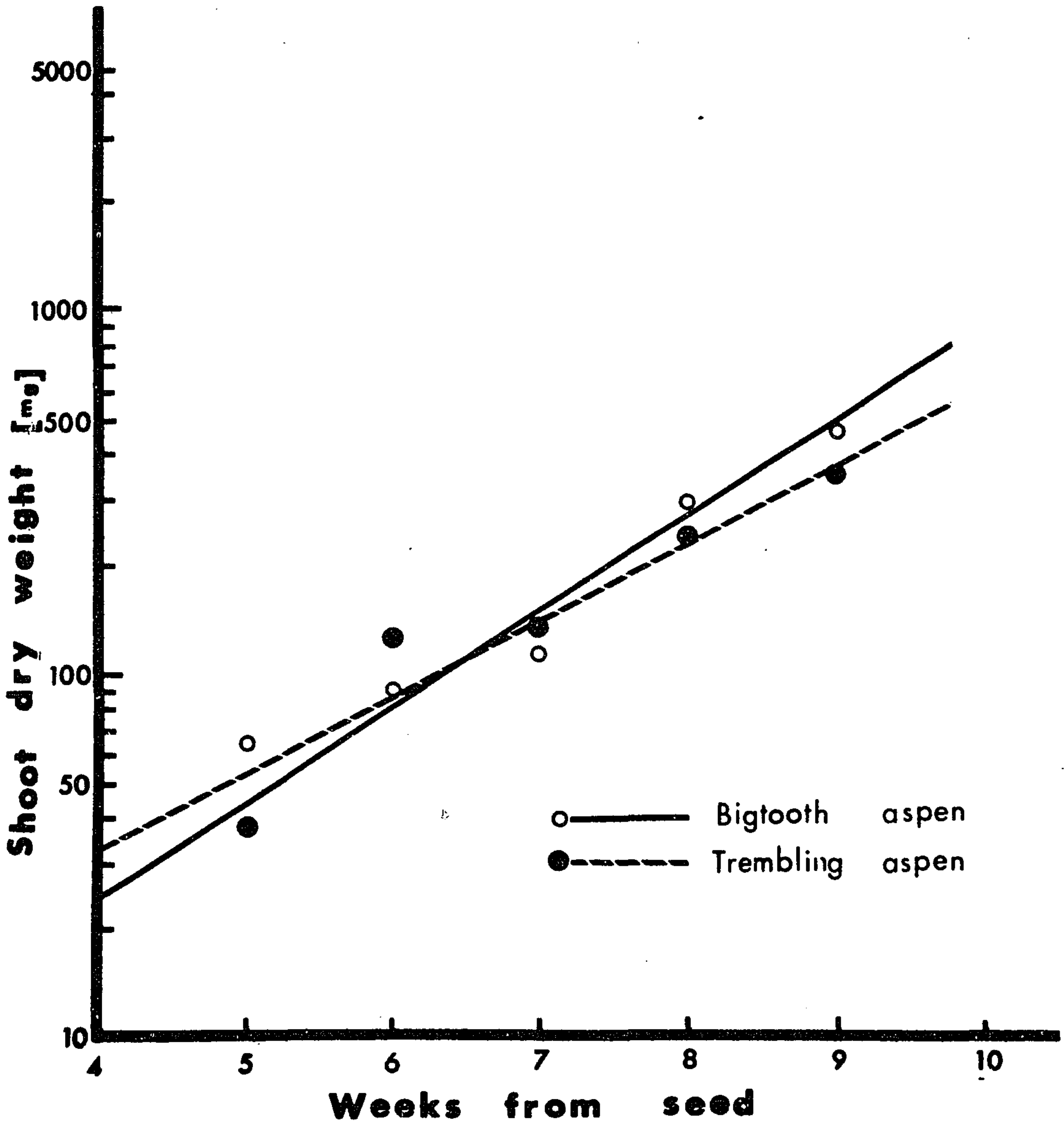

5000
1000
500
100
50
10
Shoot dry weight [mg]
4
5
6
7
8
9
10
Weeks from seed
Bigtooth aspen
Trembling aspen

Figure 4-5. Comparison of periodic change in shoot-root ratio between trembling and bigtooth aspens.

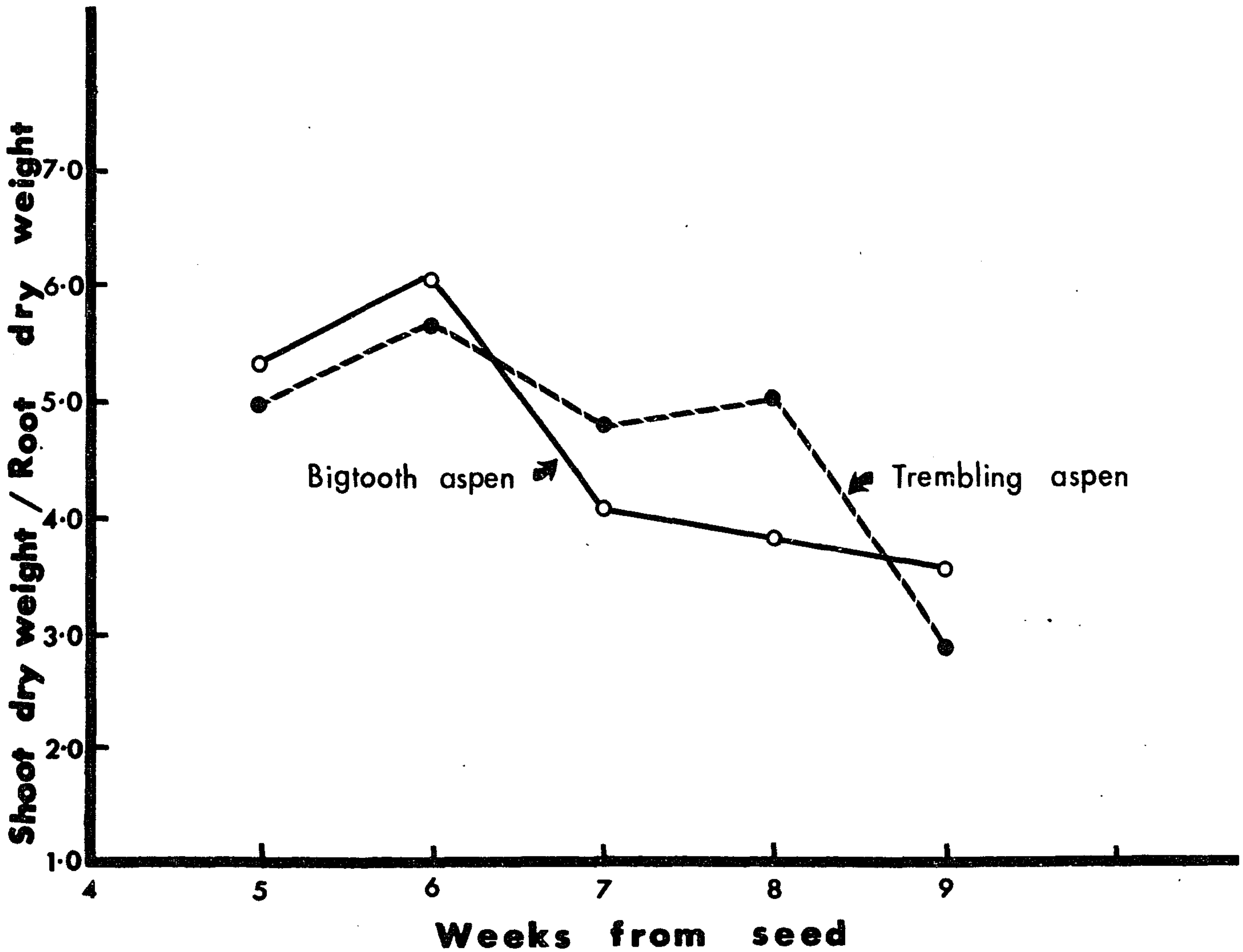
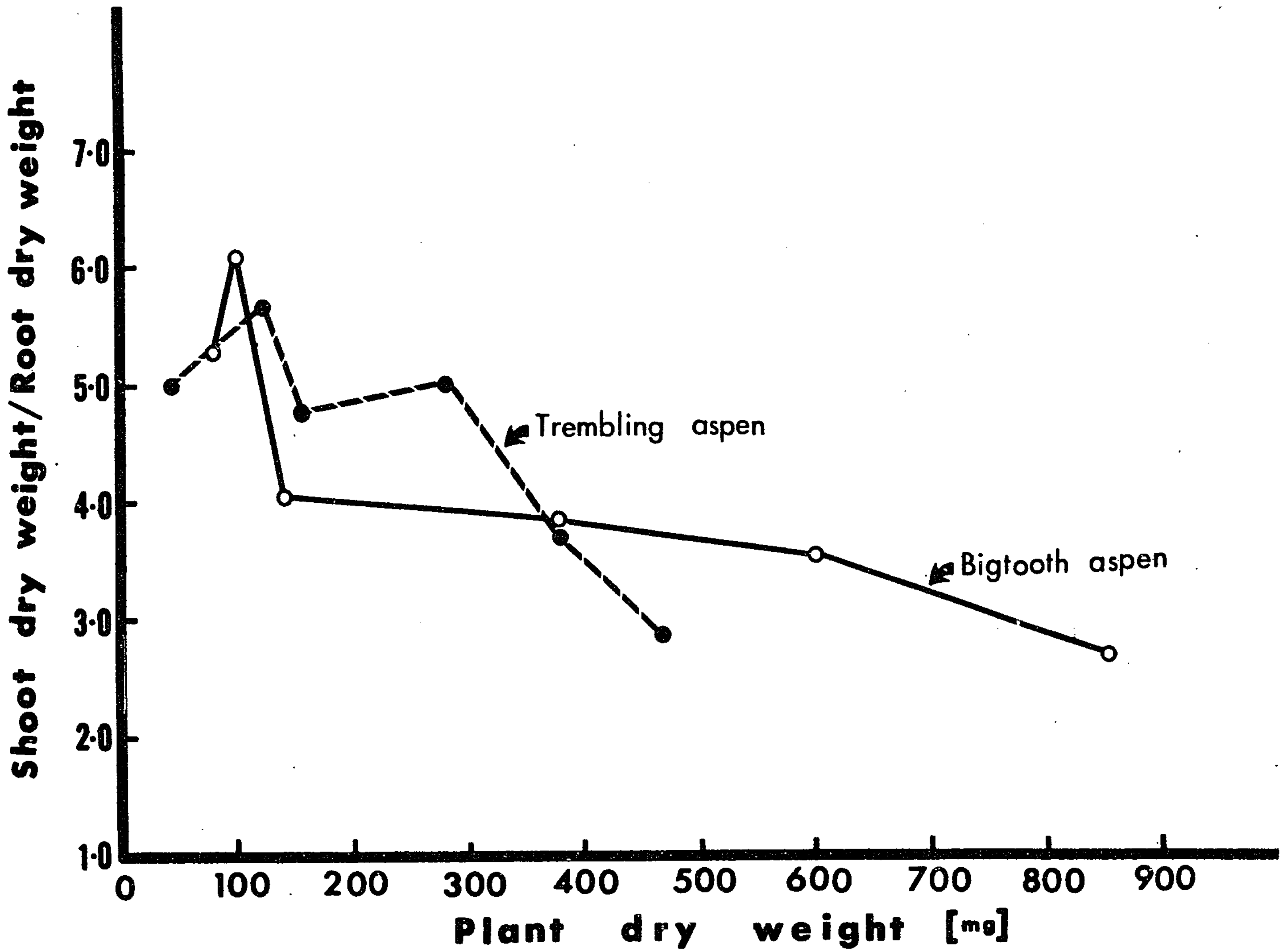

Shoot dry weight / Root dry weight
7·0
6·0
5·0
4·0
3·0
2·0
1·0
4
5
6
7
8
9
Weeks from seed
Bigtooth aspen
Trembling aspen

Figure 4-6. Comparison of changes in shoot-root ratio associated with increase in total plant dry weight of trembling and bigtooth aspens.


Shoot dry weight/Root dry weight
7·0
6·0
5·0
4·0
3·0
2·0
1·0
0
100
200
300
400
500
600
700
800
900
Plant dry weight [mg]
Trembling aspen
Bigtooth aspen

(Figure 4-6) suggests that this faster relative growth of roots is more pronounced in this species than in bigtooth aspen.

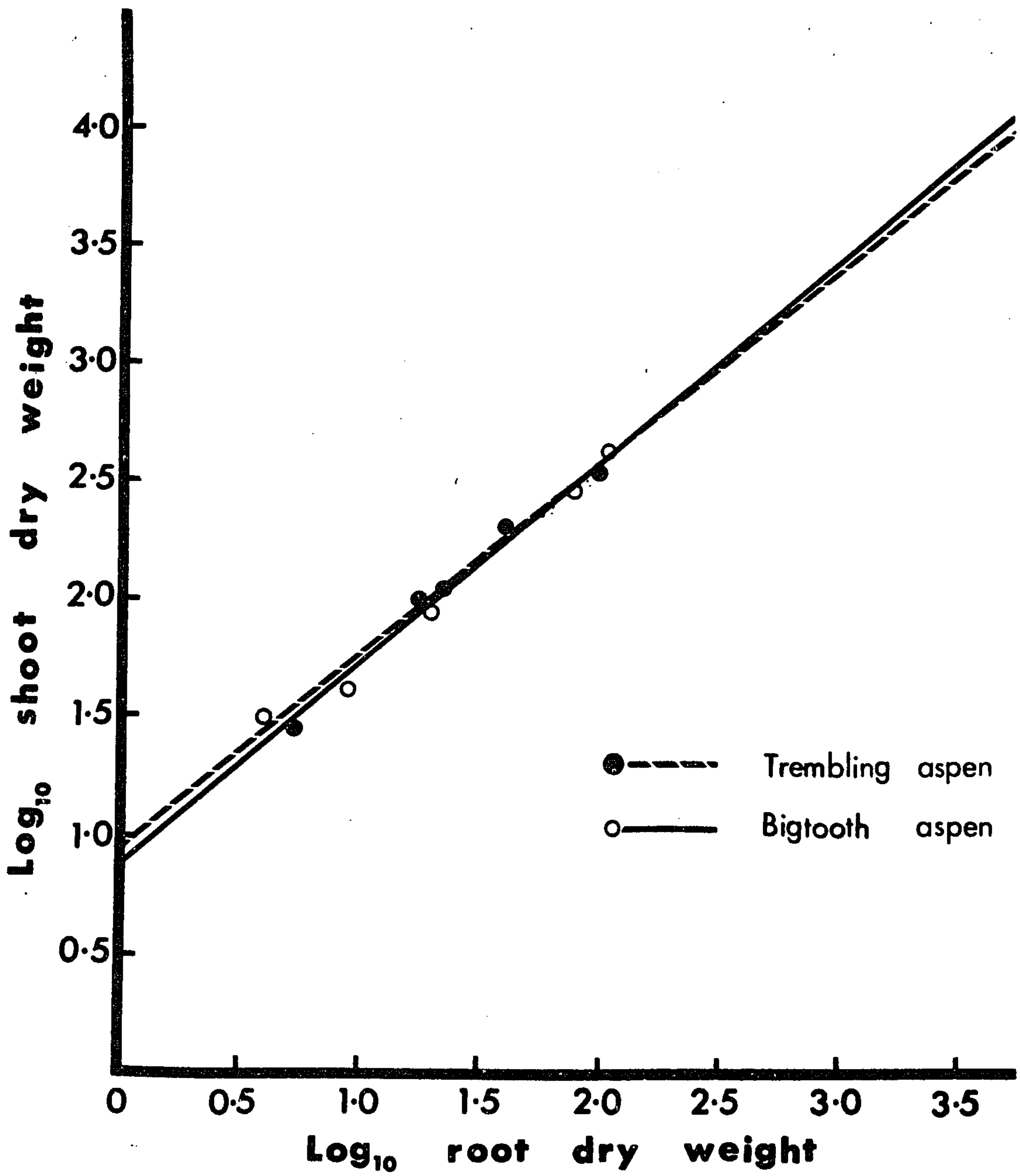
The regression of $\log_{10}$ shoot dry weight on $\log_{10}$ root dry weight was highly significant for both species (Table 4-1, Figure 4-7), as indicated by the high r^2 values. A comparison of slopes of the allometric formulae shows no significant difference between the regressions for the two species. The observed regression coefficient of less than 1.0 for both species would be expected. It indicates a proportionately smaller increase in shoot than occurs in root, resulting in the faster growth of roots than in the aerial parts of the plant. It is, however, significant that it falls in the same group as the conifers mentioned eariler, which characteristically have sub-unity regression coefficients for the allometric equation. Ledig (1970) has observed that there appears to be a trend from coefficients greater than 1.0 in annual plants (increase in shoot-root ratio with growth) to coefficients less than 1.0 in perennial plants (greater root-to-shoot growth). He attributed this to the greater additional function of storage and anchorage which the root takes on in woody perennials. It is conceivable that the added role of vegetative reproduction in aspen roots further depresses the magnitude of the regression coefficients.

Table 4-1. Equations for the regression of $\log_{10}$ shoot dry weight on $\log_{10}$ root dry weight of trembling and bigtooth aspens after 9 weeks of growth.

Species	Variables	Regression coeff (b)	Regression equation	r^2 value	Significance between slopes (t)
Trembling aspen	$y = \log_{10}$ shoot dry weight $x = \log_{10}$ root dry weight	0.82^{**}	$y = 0.92 + 0.82x$	.982	1.735, n.s.
Bigtooth aspen	$y = \log_{10}$ shoot dry weight $x = \log_{10}$ root dry weight	0.84^{**}	$y = 0.88 + 0.84x$	.986	

** = Significant at the 1 percent level respectively.

Figure 4-7. Comparison of regression of $\log_{10}$ shoot dry weight on $\log_{10}$ root dry weight between trembling and bigtooth aspens.



4·0
3·5
3·0
2·5
2·0
1·5
1·0
0·5
0
0·5
1·0
1·5
2·0
2·5
3·0
3·5
Log10 shoot dry weight
Log10 root dry weight
Trembling aspen
Bigtooth aspen

Summary and Conclusions

Observations from the present greenhouse study suggest that bigtooth and trembling aspens are very similar in their rooting habits at the seedling stage. They initially invest the major portion of their stored energy into the photosynthetic tissue--the shoot, thus effecting rapid growth. During the fast growth pace which ensues, the roots assume a relatively more rapid growth rate over the shoots. This probably reflects a strategy for ensuring the survival of the highly vulnerable seedlings (Ledig 1970), which seems essential for aspen seedlings in overcoming herbaceous competition.

CHAPTER V

PHOTOSYNTHESIS AND RESPIRATION OF ASPENS IN CONTROLLED ENVIRONMENT

Introduction

Photosynthesis and respiration are two of the key physiological processes that determine yield. Because of their importance short-term measurements have been widely employed as an index of growth potential of trees (Kozlowski and Keller 1966; Gatherum et al. 1967; Ferrell 1970; Luukkanen and Kozlowski 1972). But these physiological measurements on a short-term basis do not show any consistent correlation with yield data (Decker 1955), and would appear to vary not only with the species concerned, but also with experimental conditions. Thus, measurements on *Populus* have shown both high, low, and sometimes negative correlations with yield (Huber and Polster 1955; Gatherum et al. 1967; Luukkanen and Kozlowski 1972). Nevertheless, Ferrell (1970) noted the potential usefulness of genetic variation in such physiological processes as an aid in selecting fast growing genotypes.

Luukkanen and Kozlowski (1972) reported that clones from Aigeiros and Tacamahaca sections of the genus *Populus* differed significantly in their rates of photosynthesis and photorespiration. Thus by measurements of short-term rates of photosynthesis and respiration for trembling and bigtooth aspen, the present study aimed to determine:

(a) differences in photosynthesis and respiration between the two aspen species and how they correlate with dry matter yields

(b) how the observed differences in photosynthesis and respiration relate to variation in morphological structures, and their possible adaptive significance

(c) the variation in the above traits within each species

(d) how these measurements from the Leuce section of *Populus* compare with those reported for other sections of the genus.

Materials and Methods

During the summer of 1975, seedling of both aspen species were raised from seed obtained in a state-wide seed collection made earlier in the spring. They were grown in a peat-vermiculite soil mix, contained in 5cm x 5cm x 28cm poly-coated units (milk carton brand), and packed in groups of 36 in plastic milk cases. Details of the greenhouse growing procedure are described in Chapter III. Optimal water levels and fertilization (Peters 20-20-20) were maintained throughout the experiment.

Preliminary studies showed that similarly grown aspen seedlings reached their peak growth period between the seventh and tenth weeks from seed. Moreover, roots did not extend beyond the open bottom of the container until after the tenth week. Thus at the end of the ninth week from seed, seedlings were chosen from ten paried clones. Each pair (one from each species) was randomly chosen from within one of ten areas uniformly spread through the entire state of Michigan. The most healthy and vigorous seedlings from each clone were used in the subsequent study. Photosynthetic rate for each seedling was measured on a whole plant basis as well as for a single leaf in a closed environmental control system.

For the whole plant determination, the portion of the seedling above the root collar was sealed in a water-jacketed plexiglass chamber. Illumination was provided by three 400 watt color-improved mercury vapor lamps positioned one each on three sides of the plant chamber. No lamp was positioned on the fourth side which was used for equipment control. A 1000 watt lamp of the same type provided illumination from above the chamber. Light intensity measured from about the mid-crown position in the chamber, was 5,600 footcandles from above and 2,700 footcandles on the average from the sides. Light quanta as determined by a Lambda Quantum Sensor was 600 μeinstein $m^{-2}s^{-1}$ from above, and 467 μeinstein $m^{-2}s^{-1}$ from the sides. Relative humidity within the chamber was held at 60 ± 2%, temperature was 24.5 ± .5°C, and wind speed was 112 cm sec^{-1}. Any observable deviations in temperature were corrected for in the calculations. Each plant was preconditioned in this environment for at least 15 minutes before the rate of photosynthesis was recorded. At the end of the preconditioning period, uptake of CO_2 (net photosynthesis) was measured with a Beckman infrared gas analyzer by observing the rate of depletion of CO_2 between 330 and 270 ppm in the closed system. CO_2 was replenished to the closed environmental control system by opening the water-jacketed chamber lid to the laboratory air.

Dark respiration determinations were made at the end of each photosynthetic measurement by placing a black cloth over the plant chamber and observing the rate of increase of CO_2 in the system for at least one hour.

Preliminary studies (Chapter II) have shown that during their peak period of growth, trembling aspen produces a little over two leaves for each single leaf produced by bigtooth aspen. Thus for the single leaf photosynthetic study, determinations were made on the third expanded leaf of bigtooth aspen, which was regarded as the ontogenetic equivalent of the seventh expanded leaf used in trembling aspen measurements. The intact leaf was carefully sealed in a specially built water-jacketed plexiglass leaf chamber. A small pump circulated water from a large water bath through the plexiglass water jackets. Chamber temperature was regulated by varying the temperature of the water in the bath. Temperature was maintained at 26 ± 1°C. A 400 watt color-improved mercury vapor lamp located 75cm directly above the leaf chamber provided the illumination which gave 3,200 footcandles intensity and 500 μeinstein $m^{-2}s^{-1}$ inside the leaf chamber. A drierite column ensured a low relative humidity of the air in the small closed system. The velocity of air flow was maintained at 1500 cc min^{-1}. Net photosynthetic rate of the leaf was determined in a manner similar to that for the whole plant, by measuring the rate of depletion of CO_2 between 330 ppm and 270 ppm using a Beckman IR 215 infrared gas analyzer. CO_2 depletion by the leaf was allowed to continue to the CO_2 compensation point, at which no more uptake occurred.

Dark respiration of single leaves was also determined by following the rate of CO_2 increase in the system for at least one half hour.

Leaf surface area measurements were made electronically with a Lambda LI-3000 Portable Area Meter. The roots were carefully washed free of soil and the different plant parts packed separately for oven-drying and subsequent weighing.

The t-test was used to determine the significance of the differences in physiological and developmental parameters, both between the leaf and the whole plant of each species, and between the species themselves. The degree of relationship between the various measurements was examined with simple correlation analysis.

Results and Discussion

On total plant leaf area basis, there was no significant difference in net photosynthetic rate between trembling and bigtooth aspen, though the former had a higher value (Table 5-1). It is interesting that bigtooth and trembling aspen which belong to the section Leuce of the Populus genus have similar rates of photosynthesis to those for Aigeiros,but much lower than those for Tacamahaca poplars reported by Luukkanen and Kozlowski (1972). Moreover, photosynthetic rates of the apparently heterotic bigtooth aspen x white poplar hybrids examined by Gatherum et al. (1967) show no superiority over those of the aspens used in the present study.

Preliminary studies had shown that intact aspen leaves of either species attain their light saturation point when receiving 3000-3500 footcandles. Thus 3,200 footcandles of light used in the single leaf photosynthetic study allows the leaves to fix carbon under light saturation conditions, and their photosynthetic rates should reflect the full photosynthetic capacity of the leaves. Under these conditions, trembling aspen had a significantly higher net photosynthetic rate than bigtooth aspen. However, for either species, the difference in rates between the single leaf and the whole plant was very highly significant. The much higher observed photosynthetic rate in the single leaf would appear to partly reflect the importance of self-shading in the photosynthetic

Table 5-1. A comparison of developmental and physiological traits of trembling and bigtooth aspen seedlings at age 9 weeks.

	Trembling aspen[1]			Bigtooth aspen[2]		
	Whole plant	Single leaf	Sig. level	Whole plant	Single leaf	Sig. level
Net photosynthetic rate [P_s] ($mgCO_2dm^{-2}$ hr^{-1})	7.3	33.9[3]	**	5.4	21.0[3]	**
Respiration rate [R] ($mgCO_2dm^{-2}$ hr^{-1})	1.9	5.7	n.s.	1.5	4.5	n.s.
R/P_s	.26	.17		.28	.21	
Total photosynthesis ($mgCO_2hr^{-1}$)	34.8	15.4[4]	**	24.6	10.4[4]	**
Number of Leaves	25			15		**
Leaf area (dm^2)	4.91			4.90		n.s.
Dry weight (gms)	1.42			1.45		n.s.
Net assimilation rate ($mgdm^{-2}wk^{-1}$)	53.5			52.5		n.s.
CO_2 compensation point (ppm CO_2)		52			52	n.s.
Leaf weight ratio (LfWt/Total Wt)	.49			.53		n.s.
Specific leaf area (dm^2g^{-1})	3.48	3.21	n.s.	3.38	3.07	n.s.

[1]Mean of 10 seedlings

[2]Mean of 9 seedlings

[3]Significant between species at 1 percent level

[4]Significant between species at 5 percent level

process of the whole crown, and probably the effect of higher temperature in the leaf chamber. Bigtooth aspen which has significantly fewer leaves than trembling aspen showed a leaf photosynthetic rate 389% that of the whole plant. The relative superiority of trembling aspen leaf net photosynthetic rate, on the other hand, was 464% that of the whole plant. Furthermore, the 2° higher air temperature in the leaf chamber during the measurements could have contributed to the observed differences in photosynthesis between single leaves and whole plant. Dickmann (personal communication) noted that leaf temperatures in small chambers exceed air temperatures by as much as 5-6°. The increase in net photosynthetic rate with temperature is well documented, and has been shown to be very significant in several species of *Populus* (Luukkanen and Kozlowski 1972).

In both species, no significant difference was observed between the single leaf dark respiration and whole plant dark respiration rate. Furthermore, difference between species was not significant in this regard. It is nevertheless interesting to note that the value of dark respiration rate relative to net photosynthetic rate diminished substantially when the whole plant values are compared to single leaf values. This would also seem to be a reflection of increase in light intensity through self-shading elimination. However, photorespiration rate which was shown to be as high as dark respiration rate in other related poplar species (Luukkanen et al. 1972), is known to rise with increasing light intensity

(Jackson and Volk 1970), and was found to increase linearly with net photosynthetic rate in Populus clones (Luukkanen and Kozlowski 1972). The net effect of these two offsetting respiration rates with increasing light intensity may be important in the net photosynthetic production of the plant. No significant differences were observed between species in the following measurements: net assimilation rate (NAR), total plant dry weight, CO_2 compensation point, total leaf area, leaf weight ratio, and leaf area ratio. NAR is not a reliable index of photosynthetic efficiency of the leaves (Pollard 1972), but a measure of efficiency of carbon conversion and conservation (Ledig 1974). Thus, similarities of both species in NAR, as well as plant photosynthetic and respiration rates, would account for similarity in dry matter accumulation. The significant difference between species in net leaf photosynthetic rate under optimum conditions of light saturation probably should not be reflected in the net assimilation rate and dry matter accumulation. The seedlings, prior to the determinations, had developed under non-saturating light conditions, where self-shading was prevalent. On the other hand, isolated seedlings growing in open fields under full sunlight, as occurs in nature, would probably be photosynthesizing very near optimum conditions when water and nutrient supplies are ideal. If these observed patterns hold true in nature, one would expect trembling aspen to show superiority in dry matter accumulation in the seedling stages. However, measurements of photosynthesis and respiration over short intervals may not always correlate with yield data (Decker, 1955). As explained by Dickmann (1973), tree growth and dry matter production comprise an interaction of many factors, of which photosynthetic efficiency, respiration rate, and distribution of photosynthate are only a few. He further warned that any attempt to correlate growth with one single factor such as photosynthetic rate might fail.

Tables 5-2 and 5-3 show the degree of relationship between some of the measured phsiological paramenters. Most of the correlations were statistically non-significant. A few observed trends deserve pointing out. A negative correlation of -.47 was observed between plant photosynthetic rate and total leaf area as well as total dry weight (r = -.37) in trembling aspen, and even more so in bigtooth aspen (r = -.61 and -.65 respectively). Because leaf area is highly correlated with total dry weight in both species, and the bigger plants tended to have more leaves, the depressing effect of self-shading on net photosynthetic rate discussed earlier would be expected to rise with increase in dry weight. Leaf dark respiration rate correlated appreciably with leaf net photosynthetic rate in bigtooth aspen and significantly so in trembling aspen. It is not quite clear why under optimum light saturation conditions those leaves which show much higher net photosynthetic activity would be investing more energy to run their superior photosynthetic machinery.

Table 5-2. Simple correlations between physiological traits for 10 seedlings from 10 clones of trembling aspen in Michigan.

Physiological parameter	Correlation coefficient (r)[1] for:			
	Single leaf photosynthetic rate	Single leaf respiration rate	Whole plant photosynthetic rate	Whole plant respiration rate
Whole plant photosynthetic rt.	.42			
Single leaf respiration rate	.72*			
Whole plant respiration rate		.52	.41	
Plant leaf area	-.15	.15	-.47	-.03
Plant dry weight	.04	.33	-.37	-.13
Net assimilation rate	.35		.07	
CO_2 compensation point			-.41	

Physiological parameter	Correlation coefficient (r)[1] for:			
	Net leaf photosynthesis	Net plant photosynthesis	Plant leaf area	Plant dry weight
Plant leaf area		.17		
Plant dry weight	.02	.18	.84**	
Leaf weight ratio		.58		.23

*, **Significant at the 5 and 1 percent levels respectively.

[1]Degrees of freedom = 8

Table 5-3. Simple correlations between several physiological measurements for 9 seedlings from 9 clones of bigtooth aspen in Michigan.

Physiological measurement	Correlation coefficient (r)[1] for: Single leaf photosynthetic rate	Single leaf respiration rate	Whole plant photosynthetic rate	Whole plant respiration rate
Whole plant photosynthetic rt.	.21			
Single leaf respiration rate	.35			
Whole plant respiration rate		.29	.05	
Plant leaf area	-.47	.07	-.61	-.35
Plant dry weight	-.63	.04	-.65	
Net assimilation rate	-.30		.05	
CO_2 compensation point			-.65	

Physiological measurement	Correlation coefficient (r)[1] for: Plant dry weight	Plant leaf area	Net photosynthesis per leaf	Net photosynthesis per plant
Plant leaf area				-.39
Plant dry weight		.96**	-.32	-.42
Leaf weight ratio	-.40			-.27

*, **Significant at 5 and 1 percent levels respectively.

[1]Degrees of freedon = 7

The array of values for the physiological measurements made for each species (Table 5-4 and 5-5) indicates tremendous variation between clones. If this indication is representative of the true situation in nature, then the genetic variations in net and total photosynthesis, dark respiration, CO_2 compensation point and photorespiration discussed by Ferrell (1970) would appear to be strong in aspen populations. Hence, such measurements might prove useful in selecting for superior genotypes, especially if such desired superiority is shown to substantively correlate with superiority in these measurable physiological processes.

Summary and Conclusions

Observations in this study indicate further similarity between bigtooth and trembling aspen when grown under greenhouse conditions in close spacing. Seedlings of both species showed no significant difference in photosynthetic rate and dark respiration rate, as determined in a closed controlled system. Net assimilation rates, leaf area, dry matter accumulation, and CO_2 compensation points were also similar. Perhaps physiological processes in dense stands of young aspen suckers would follow a similar pattern. However, under optimum conditions when light is saturating, as probably happens with isolated young seedlings in the wild, trembling aspen would apparently have a higher net photosynthetic rate than bigtooth aspen, though all other measurements might remain similar.

Table 5-4. Physiological measurements on 10 seedlings from 10 clones of trembling aspen from different areas in Michigan.

Clone number	Leaf photosyn. rate	Whole plant photosyn. rate	Whole plant respir. rate	Net photosyn. per plant	Dry weight	NAR[1]	CO_2 compensation point
	$mgCO_2dm^{-2}hr^{-1}$			$mgCO_2hr^{-1}$	mg	$mgdm^{-2}wk^{-1}$	ppm CO_2
75-30	37.0	9.5	1.8	30.7	1862	52.4	58
-33	49.6	5.0	2.7	24.7	2774	51.1	52
-244	50.4	8.6	2.5	48.3	3678	59.6	55
-76	18.3	5.1	1.2	31.7	3666	53.6	57
-93	24.0	8.4	2.0	29.1	1833	48.0	45
-94	34.4	6.6	1.5	38.2	2770	43.5	47
-98	10.4	2.6	1.4	14.3	3266	54.0	58
-34	39.7	8.0	1.0	33.9	2912	62.4	49
-67	45.8	8.3	1.6	41.3	3327	60.8	58
-204	29.0	10.7	3.1	55.5	2822	49.5	43
$\bar{X}$	33.9	7.3	1.88	34.8	2891	53.5	52.2

[1]NAR = Net Assimilation Rate

Table 5-5. Physiological measurements on 9 seedlings from 9 clones of bigtooth aspen from different areas in Michigan.

Clone	Leaf photosyn. rate	Total plant photosyn. rate	Total plant respir. rate	Net photosyn. per seedling	Dry weight	NAR[1]	CO_2 compensation point
	$mgCO_2dm^{-2}hr^{-1}$			$mgCO_2hr^{-1}$	mg	$mgdm^{-2}wk^{-1}$	ppm CO_2
75-114	22.6	6.2	1.3	28.3	2715	54.2	43
-121	30.9	8.1	0.8	36.3	2374	48.1	57
-333	9.8	7.9	1.3	37.3	2943	56.6	40
-164	15.7	6.5	1.7	28.2	2731	57.3	50
-183	12.8	2.1	1.4	16.7	4104	47.1	52
-182	19.2	2.7	1.2	14.6	3094	52.0	56
-128	25.3	9.1	2.1	33.8	2009	49.2	43
-143	41.0	4.1	2.2	16.1	2297	53.2	61
-303	11.3	2.2	1.4	10.4	2852	54.7	65
$\bar{X}$	21.0	5.4	1.5	24.6	2790	52.5	51.9

[1]NAR = Net Assimilation Rate.

CHAPTER VI

BAREROOT VERSUS CONTAINERIZED PLANTING FOR ASPENS

Introduction

In any genetic study involving forest trees, the ultimate test is the performance of the test materials in the field. Survival is a primary factor in field establishment. However, survival of a nursery grown tree in its new plantation environment depends not only on the ecological and soil conditions of the new site, but also on the quality and physiological state of the planting stock used. The condition of the roots, whether seedlings are grown directly in the ground or in containers, can greatly affect overall survival in the field, especially in areas with prolonged periods of drought during the growing season (Miller and Budy 1974). The use of conventional bareroot planting materials has the strong advantage of being relatively inexpensive to produce; but some species are difficult to grow as bareroot stock, or are difficult to keep in good planting condition during handling, transporting, or outplanting when barerooted (Stein 1974). Stein (1974) further enumerated the advantages and objectives in the use of containerized seedlings. Miller and Budy (1974) showed that the survival and consequent growth of an outplanted seedling varies not only with the species, but especially with the nature and size of container used.

This study compared bareroot seedlings which were given cold storage period versus containerized aspen planting stock for survival and first season growth following field outplanting.

Materials and Methods

In Spring 1974, seeds and root segments were collected from 93 and 51 clones of trembling and bigtooth aspen, respectively, located throughout the state of Michigan. Seedlings were raised from the seeds, and young cuttings were obtained from the root segments as described by Farmer (1963) and Zufa (1971). The young trees were grown in the greenhouse during the Fall of 1974 as containerized plants. The containers were made out of tar-coated roofing paper 5cm x 5cm x 30cm deep, which were held in groups of 30 in wooden crates. The plants were preconditioned by greenhouse temperature regulation and moved outdoors in January 1975.

In late April when the ground had thawed, most of the seedlings were lifted for subsequent field planting. Trees which were considered too small for field planting were grown for another season in the nursery transplant beds. Among these seedlings a portion was randomly barerooted, packed with moist sphagnum moss, and kept in a cold room for 6 weeks before planting on nursery beds. The remainder were left outside in their original containers.

Both the bareroot and containerized seedlings were transplanted on June 6 into an irrigated bed 200 feet long and 4 feet wide. The trees were spaced at seven inches in a row and twelve inches between rows. Barerooted stock were planted on one half of the bed completely randomized, and the containerized stock were planted in their paritally degraded containers on the other half. In September, the amount of current-year growth was measured for all surviving trees. Height growth differences between the two aspen species and between the two types of planting stock were analyzed by the "t-test." The correlation coefficient was used to examine the performance of clones using both types of planting stock.

Results and Discussion

Survival results are shown in Table 6-1.

Table 6-1. Relative survival of barerooted and containerized aspen transplants.

	Planting material used as	
	Barerooted	Containerized
Total planted	776	368
Survived	389	320
Percent survival	50	87

Fifty percent of all the barerooted and stored trees survived by the end of September, compared to 87% survival for the containerized plants. A higher survival might have been expected from the barerooted stock because they were irrigated. Probably, the relatively long period of cold storage adversely affected the regeneration and growth of lateral roots. Moreover, new lateral roots were observed to have developed on some of the barerooted plants while in storage. It is conceivable that such young roots may have been damaged during planting, thus reduce the survival chances of the plant.

Data presented in Table 6-2 show that in both bigtooth and trembling aspen, the current-year growth was more than two times greater in containerized plants than in barrerooted plants.

Table 6-2. Comparisons of the current year height growth of barerooted and containerized aspen transplants.

Species	Total clones used	Planting stock		Sig. level	r^1
		containerized	barerooted		
		ht (cm)			
Trembling aspen	50	49^2	23^2	**	.27
Bigtooth aspen	42	20	13	**	.26

[1]r = Correlation between the height growth of containerized and barerooted stock of same clones, non-significant for either species.

[2]Height differences between species significant at 1 percent level.

** = significant at 1 percent level.

Trembling aspen, however, significantly outgrew bigtooth aspen irrespecitve of the kind of planting material used. At the time of planting, all the containerized stock had broken bud and had leafed out. Most of the barerooted stock, had broken bud and several had leafed out. Perhaps this apparent head start by the containerized plants was a factor in their relatively faster growth. Several other factors may have contributed to the disparity between growth rates. The failure to recover all the lateral roots, in addition to damage caused by their breakage during lifting, may have caused a considerable reduction in the absorptive surface of the young tree, which is needed to keep pace with the rapidly expanding transpiring surface of the shoot in the early part of the growing season. Stone et al. (1959, 1962) observed that the peak period of lateral root initiation in ponderosa pine and Douglas fir occurs in spring prior to terminal bud break. Several other woody plants have also been observed to exhibit periods of active root elongation in spring (Krugman and Stone 1966; Lanphear 1963; Stone and Schubert 1959; Stone et al. 1962). If this also applies to the aspens, it would appear that spring lifting of the young trees with its attendant damage to many lateral root meristems, and obvious disturbance of the rhizosphere, seriously hampers both the root initiation and root elongation potentials of the tree. Such problems do not exist with containerized plants. A reflection of the magnitude of these problems would be expected to show up in the relative growth of the plants following transplanting.

Correlation between the growth put on by barerooted stock and the current season's growth of containerized stock was strong, though not significant.

Summary and Conclusion

Observations in the present study suggest that higher survival and superior growth will be achieved in the first growing season following transplanting when aspen seedlings are planted out as containerized material, rather than barerooting followed by cold storage. Because the study was carried out in a well irrigated nursery bed, drought was not a factor in survival or growth. Either the storage treatment or damage and disturbance to the root system during lifting appear to be the most significant factors contributing to the differences in both survival and height growth. It is conceivable that the adverse effect of this root disturbance will be more profound in field plantings where a regular irrigation system may not be available. Genetic studies in forest trees are expensive to conduct, and the development of genetically improved planting material is even more so. Therefore, the success of further aspen field tests and plantation or seed orchard establishment employing improved aspen stock will be greatly enhanced by using containerized plants.

SUMMARY, CONCLUSIONS AND RECOMMENDATIONS

Trembling and bigtooth aspen showed much similarity in their developmental and physiological characteristics. Juvenile shoot development of the species showed very similar patterns of cumulative height growth, dry matter accumulation and leaf area in spite of significant differences in the number of leaves. Trembling aspen put on many more leaves, but bigtooth aspen compensated by producing much larger but fewer leaves.

Trembling aspen seedlings significantly outgrew those of bigtooth aspen in height in the greenhouse. Rapid height growth is an important strategy for overcoming herbaceous competition, and may be regarded as an adaptive advantage. Furthermore, bigtooth aspen seedlings have greater susceptibility to some juvenile diseases than trembling aspen (Graham et al, 1963). Thus trembling aspen seedlings may have a greater chance of survival in nature, which would contribute to the greater distribution of that species than bigtooth aspen, especially since seedlings play a substantial role in extending the range of aspens.

The very early manifestation of height differences between seedlings of the two species suggests that seed characters may be partially responsible. The differences between the species in seed weight estimated by Benson (1972), need to be more precisely measured. Further study of the seed anatomy--embryo size relative to cotyledons--employing scanning electron microscope techniques, is needed before seed size can be implicated as a factor in the observed differences. Duration of germination for seeds of the two species should be carefully observed.

Root development was very similar for both species. Root cuttings of both species sprouted equally well, seedlings produced lateral roots at the same rate, the roots showed similar growth rates and their dry weights were similar. A method probably more reliable for studying root development, which observes the growth of specific roots and patterns of lateral root development on a daily basis has been described by Stigter (1969), and is worth adopting for further studies of aspen root development.

Seedlings of trembling and bigtooth aspens also showed strong similarity in photosynthetic rates, respiration rates, net assimilation rate and CO_2 compensation point, when measured in controlled environments. However, under light sturating conditions typical of seedlings growing in the wild, single leaves of trembling aspen show higher photosynthetic and respiratory rates than leaves of bigtooth aspen.

Growth comparisons of seedlings and sucker-derived cuttings showed that seedlings grew at least three times as fast as cuttings for both species. Interruption of the development of the vegetative propagules by severing them from their mother root segments, as well as the extra energy required to form their own root systems, probably partially accounted for the growth differences observed. These apparent differences will be realized if the young trees are established in field plantations and allowed several growing seasons to adapt to their new environment. Any current season's growth measurement, then should be a true reflection of the relative performance of the propagule types.

Observations on seedling growth rates reveal significant differences between materials from different geographic areas. The results also gave an indication that sources from northern Michigan outgrow their southern counterpart in both aspen species. Field tests are needed to confirm these observations made from seedlings grown in the greenhouse before they can serve any meaningful purpose in guiding the selection of materials for further tree improvement work. A range-wide provenance test for both trembling and bigtooth aspens is essential to locate the fastest growing seed sources--a critical step in the improvement of any forest tree species.

Containerized young trees of both species outsurvived and outgrew the barerooted stock in first growing season performance after outplanting. Hence, by raising aspen seedlings in containers, a greater insurance is placed on the survival and fast establishment of the trees, especially when extensive genetically improved stock is used.

It is probably significant that in nearly all the measurements made on plant materials of both aspen species in this series of studies, bigtooth aspen consistently had higher coefficient of variation (Table 7-1). This indicates that there is more variability between individuals of bigtooth than trembling aspen in nearly all the traits measured. The relatively greater uniforminty observed among trembling aspen individuals cannot be adequately explained from results obtained in these studies. Further investigation of these species is required in order to bring out the apparent differences in intraspecific variability into sharper focus, as well as provide suitable explanations for their occurrence.

Table 7-1. Summary of coefficient of variation of several measurements made on bigtooth and trembling aspen.

Trait Measured	Coefficient of variation for seedlings of:	
	Trembling aspen	Bigtooth aspen
Sprouts per clone (1974)	.12	.11
Leaves per tree	.07	.07
Total leaf area (cm^2)	.14	.20
Plant dry weight (gms)	.14	.18
Net assimiation rate ($mgdm^{-2}wk^{-1}$)	.02	.04
Shoot-root ratio	.08	.11
Height (cm)	.06	.19
Longest root (cm) [ninth week]	.12	.17
Primary roots per seedling [9 wks]	.15	.17
Net photosynthetic rate ($mgCO_2dm^{-2}h^{-1}$)	.11	.17
Respiration rate ($mgCO_2dm^{-2}h^{-1}$)	.12	.10
CO_2 compensation point (ppm CO_2)	.04	.06

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