Abstract

Naturally well-pruned and poorly-pruned P. *virginiana* trees were selected. Branches from the select trees were used for determination of dead branch extractive content, phenol analysis and decay analysis. Although no phenolic differences were observed between well-pruned and poorly-pruned groups, extractive content and decay rates differed significantly. Branches from poorly-pruned trees contained 7.2% more extractives than branches from well-pruned trees. Decay rates (% weight loss/unit area) of branches from well-pruned trees were 35% geater than those from poorly-pruned trees. Results indicate that branch extractive content is one factor contributing to the natural pruning ability of P. *virginiana*.

Key words: Pinus virginiana (MILL), pruning, fungi. branch retention, extractives.

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Photosyonthetic CO,-Uptake and the Distribution of Photosynthate as Related to Growth of Larch and Sycamore Progenies

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Introduction

The growth of agricultural crop plants has been greatly improved through the efforts of plant breeders. It has become obvious that selective breeding can also improve the growth of trees to meet better the requirements of society (e. g. ZOBEL 1971), but there is a basic difference between agricultural crops and trees in the speed with which improvement can be attained. One of the most needed innovations in tree breeding is a technique for predicting the breeding value of species, provenances, strains, or families based on juvenile evaluation of their progeny. Even an imperfect correlation might increase genetic gain if it shortened the selection cycle sufficiently (NANSON 1970).

Our objective was to develop techniques useful for predicting which tree progeny or species was superior in growth. The present investigation represents a step in this direction, not a definitive result. Predictions of relative growth were made with a simulation model using as input: rates of photosynthetic CO_2-uptake, respiratory CO_2-emission, and parameters reflecting the way in which photosynthate is allocated for growth of leaves and other organs (see LEDIG 1974, 1969 for development of the model).

Prior to the present report, it had not been demonstrated that genetic variation in growth could be explained or predicted by growth models even in the short term. CO_2-exchange rates alone had failed to explain genetic variation in growth at least as often as they had aided such explanations, resulting in hesitance to pursue such techniques in breeding. Nevertheless, on balance the evidence suggested that the methods described below would be useful in predicting genetic differences in growth and might be developed as a potentially powerful tool for tree breeders.

Materials

Representatives of two deciduous genera, sycamore (*Platanus occidentalis* L.) and larch (*Larix* sp. MILL.) were chosen for study. Seed of European larch (*L. decidua* Mill.) was collected from a selected stand of particularly well-formed, rapidly-growing trees planted in Connecticut. For comparison, two other larches were obtained commercially from seed dealers. These were Japanese larch (*L. leptolepis* [Sieb. et Zucc.] Gord.) which is widely planted in Connecticut because of its rapid growth and Siberian larch (*L. sibirica* Ledb.) which is decidedly inferior in growth at these latitudes. To determine whether a correlation exists between physiological parameters and growth, it was necessary to ensure that there was variation, so greatly different species were chosen for comparison. For sycamore, three half-sib progenies were collected for comparisons. All three maternal trees were native to the area near Ossining, New York.

Methods

For an operational technique, it will be economic to make as few measurements as necessary, so the present investigation relied on measurements at what were hoped to be critical stages over two growing seasons. Even though controlled environments would have increased precision, seedlings were grown outside because we foresee that field or nursery environments will be necessary if these techniques are to be practical in a breeding program. Thus, normal climatic conditions and associated phenological events dictated the course of the experiment.

Several seeds were sown in late fall 1970 and in spring 1971 into each of several clay pots, ca. 20.3 cm top diameter at New Haven, Connecticut. The rooting medium was a 1 : 1 : 1 mix of sand, loamy top soil, and peat. Pots were sunk into the soil. Seed germinated in June 1971. In dry weather, seedlings were watered occasionally. Seedlings were subjected to some competition from herbaceous species because weeding was infrequent after germination was completed.

Beginning in late July 1971 and at periodic intervals until February 1973, potted seedlings were removed from the nursery and brought into the lab for measurement of photosynthetic rate, respiration rate, distribution of photosynthate, and harvest data. Measurements required several days. At each period, three pots each of the three larch species and the three sycamore progenies were used. In a few instances, accidents occurred in handling and there were less than three pots for particular lots. Each pot contained several seedlings, ranging from 3 in the second year for lots with rapid growth to 19 for slow-growing lots. Thinnings were made as necessary throughout the investigation. For measurements of photosynthesis and respiration by CO_2-exchange, the seedling tops were sealed in cylindrical plexiglass cuvettes of ca. 17.1 cm diameter with inlet and outlet ports. The height of the cuvette was varied with the height of the seedling. Seedlings were sealed into cuvettes with silicon rubber (RTV 11) a day or more before they were to be measured. The silicon rubber prevented gas exchange between the cuvette and soil atmospheres. Previous tests had indicated no phytotoxic effect of the silicon rubber if adequate ventilation was maintained during curing. Prior to measurement of CO_2-exchange rates, seedlings were well-watered.

CO_2-uptake was measured with an infra-red gas analyzer (Mine Safety Apparatus Co. Model 200) operated in a closed system. All measurements were conducted at a light intensity at plant top of 4500 ft-c supplied by a 1000 W mercury lamp, Sylvania H36-15GW/DX. Heating effects were reduced by interposing infra-red reflecting glass between the lamp and the cuvette. Air was circulated through the cuvette and the system at the rate of 4 l min^{-1} by a metal-bellows pump. Temperature was set to coincide with the long term mean daily maximum temperature for New Haven for each measurement periods as calculated from the Climatic Summary of the United States (U. S. Department of Commerce 1964). Dates of measurement and temperatures of measurement are listed in *Table 1*. Temperature was controlled within $\pm 0.5^0$ C using a temperature controller, converted freezer, and space heater in a system similar to that described by Ledig and Clark (1972). Respiration was measured as rate of CO_2-emission in the dark in the same system. For either dark or light conditions, at least 15 minutes were allowed for the seedlings to acclimate before measurement.

Table 1. — Dates and temperatures of measurement of CO_2-uptake.

Date	Temperature (^{0}C)
July 16—29, 1971	27
August 30—September 2, 1971	25
October 12—20, 1971	20.5[1]
March 17—28, 1972	7
May 31—June 6, 1972	21.5
August 14—18, 1972	26.5
October 17—November 9, 1972	20.5[1]

[1] Based on September-October mean daily maximum temperatures.

Following measurement, seedlings were harvested and divided into stem and leaves. Roots were washed free from the soil. Roots, stem, and leaves were dried at 90^0 C for at least two days before each was weighed to the nearest milligram. The distribution of photosynthate to leaf growth during each period was estimated by the ratio $\Delta L/\Delta T$, where ΔL is change in leaf dry weight and ΔT is change in total dry weight since the preceding harvest. The distribution of photosynthate to stem and roots was estimated by analogous ratios.

Using modifications of a model previously described (Ledig 1969), predictions of dry weight were made for each seedlot. Net growth (NET) in g dry weight d^{-1} was calulated on a daily basis as the difference between net photosynthesis in the light minus respiration in the dark:

$$NET = [P \times H_L \times L - R \times H_D \times S] \times .55,$$

where P = net photosynthetic rate in g CO_2 h^{-1} g^{-1} leaf dry weight,

R = dark respiration rate in g CO_2 h^{-1} g^{-1} shoot dry weight,

H_L, H_D = hours of daylight and dark respectively, determined for each day by a computer program described in Furnival *et al.* (1970),

L = simulated leaf dry weight as explained below,

S = simulated shoot dry weight (S = leaf + stem dry weight) as explained below.

Root respiration was not measured nor included in the calculation of NET. The factor 0.55 was calculated from data of Negisi (1966). It is an empirically determined ratio of g dry weight per g CO_2 assimilated in tree seedlings. For tops and roots of three coniferous species in several seasons, 50.00 ± 1.65 percent of the dry weight was carbon; i.e., the ratio of total dry weight to carbon weight was 1/0.50 (Negisi 1966). Very similar values are known for other plants. Because the ratio of carbon in carbon dioxide is 12/44, then net assimilation of 1 g CO_2 should result in an increase of $(12/44) \times (1/0.50) = 0.55$ g in dry weight.

To start the simulation, L and S were given initial values, observed at the first measurement date. Actual (observed) dry weight never entered the calculations after the first day of the simulation, although the decimal percent $\Delta L/\Delta T$ was calculated from dry weight measurements. For the second and each successive day in the simulation, new values were calculated for L and S and for the dry weight of wood (*i. e.*, root plus stem). To calculate a new value for leaf dry weight, leaf weight was incremented by a portion of NET for the preceding day:

$$L_n = L_{n-1} + \Delta L/\Delta T \times NET_{n-1},$$

where the subscript refers to the day of the simulation. NET could be negative, and in that case leaf weight would decrease. The procedure iterated day after day. Finally, the predicted growth of wood from the simulation was compared to the differences actually observed among seed lots after two growing seasons. The comparison of simulated with observed values was the objective and the test of the model.

Certain assumptions were necessary to extend the simulation over 2 years. First, net photosynthetic and respiration rates and ratios of $\Delta L/\Delta T$ were assumed to change linearly between measurement periods. For larch, leaves were assumed to fall immediately after the October measurements, which is not correct but does not bias the conclusions. For sycamore also, leaves were assumed to fall after the October measurements, which is very close to the truth. Also, leaf production of all sycamore progenies was fixed to begin on May 1 and leaf weight was set equal to 0.007 g at that time. For larch, leaf growth in the second growing season had just begun at the time of the March measurement so that arbitrary assumptions were unnecessary. None of the assumptions seemed to bias any seed lot relative other seed lots in this case but will of course lead to imprecision in predictions of dry weight growth.

Only the results for larch will be considered in detail.

Results and Discussion

Larch. — Only part of the seasonal change in rates of photosynthetic CO_2-uptake and respiratory CO_2-emission (*Figure 1*) was the result of inherent changes in photosynthetic capacity, because measurements were made at seasonal temperatures; *e. g.* in July 1971 CO_2-exchange rates were measured at 27° C while in March 1972 they were measured at 7° C (*Table 1*). In late spring or early summer, in both 1971 and 1972, Siberian larch had the highest rate of photosynthetic CO_2-uptake. However, its rate fell to the lowest by late August and continued to fall to very low or negative rates by October. In both years, the August and October rates were ranked from highest to lowest in the order European larch, Japanese larch, Siberian larch. The rank in August-October photosynthetic rate was the same as the rank in dry weight of woody portions (see *Figure 1, 2*) or total dry weight.

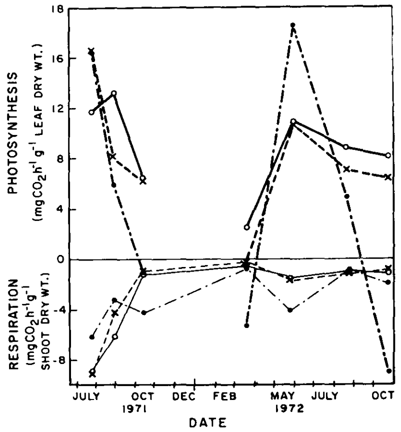

Figure 1. — Seasonal patterns in photosynthetic CO_2-uptake (heavy lines) and respiratory CO_2-emission (light lines) in three species of larch during their first two growing seasons; o = European larch, ● = Siberian larch, + = Japanese larch. (See *Table 1* for temperatures of measurement.)

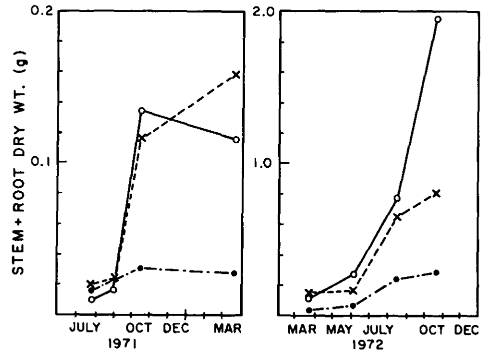

Figure 2. — Dry weight of three species of larch in their first two growing seasons. (Symbols as in *Figure 1.*)

There is a reason for comparing growth with October rates of photosynthesis in conifers. A good relationship between tree height and photosynthetic rate of excised branches was found in provenances of 7-year-old jack pine (*Pinus banksiana* LAMB.) when photosynthesis was measured in October (r = 0.85), while there was no relationship between growth to 7-years and photosynthetic rate in other months (LOGAN 1971). One explanation is that trees in which growth processes proceed most actively have high respiration rates during spring and summer when terminal, leaf, or cambial growth occurs and this obscures their potentially superior photosynthetic rates. In autumn when aboveground portions are not actively growing, trees with higher photosynthetic rates are more readily apparent. Our thesis, however, is that such relationships are fortuitous and become obvious only when factors other than rate of CO_2-uptake are relatively constant. Only integrative techniques, such as the model used here, can hope to be consistent predictors of growth.

Respiration rates were very high during early seedling development because seedlings had a high proportion of respiring tissue. By the second year, there was more woody tissue, resulting in lower rates of respiration g^{-1} shoot. Siberian larch had a notably high rate of respiration in October in both years.

The total area under the curve of photosynthetic rate (*Figure 1*) reflects the total photosynthesis g^{-1} leaf dry weight for the period. Again, the rank from highest to lowest was European larch, Japanese larch, Siberian larch. The high rates of photosynthetic CO_2-uptake for Siberian larch in early summer were more than offset by the superiority of European and Japanese larch in late summer and autumn. Similar observations were made by LEDIG and PERRY (1969) for loblolly pine during its first growing season when assimilation rate was measured by growth analysis techniques.

There were apparently no peculiarities of $\Delta L/\Delta T$ (*Figure 3*) that would reverse the trends in growth caused by differences among species in photosynthetic CO_2-exchange. In fact, the low ratio of $\Delta L/\Delta T$ for Siberian larch acted in the same direction as its low net seasonal photosynthetic rate. For European larch, the extended growth of leaves in late summer and retention of these leaves late in the autumn and winter interacted with its characteristically high autumn rate of photosynthetic CO_2-uptake to enhance its superiority in dry weight growth.

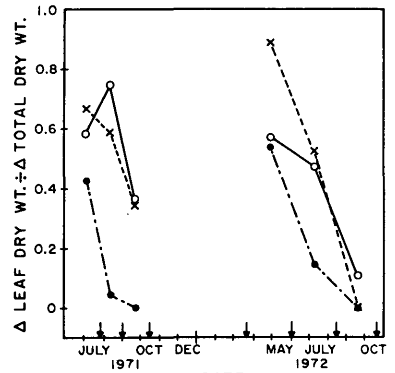

Figure 3. — Seasonal changes in the distribution of assimilate as measured by the proportion of total growth devoted to leaf growth, $\Delta L/\Delta T$, in three species of larch during their first two growing seasons. Arrows indicate dates of harvest. (Symbols as in *Figure 1.*)

Estimates of photosynthetic and respiratory CO_2-exchange and $\Delta L/\Delta T$ for each period were used in the iterative computer model to simulate growth for each of the three species. The growth simulator ranked the species from highest to lowest in exactly the same relative order as their observed dry weights at the end of two growing seasons *(Figure 4).*

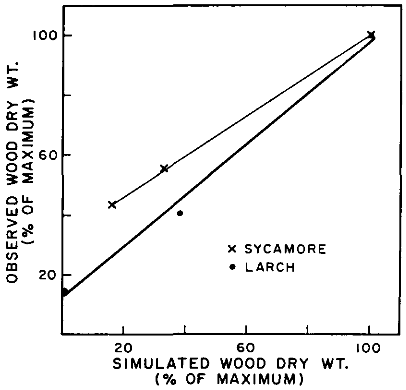

Figure 4. — The relationships between relative dry weight after two growing seasons and dry weight predicted by a model based on CO_2-uptake and the distribution of photosynthate for three larch species and three half-sib progenies of sycamore. Values expressed as percent of maximum, because simulated values were as much as 3 times greater than observed values in larch and up to 24 percent greater than observed in sycamore.

Sycamore. — As for larch, highest rates of photosynthetic CO_2-uptake in sycamore occurred in spring or early summer. There were only slight and inconsistent differences between the three half-sib progenies in rate of photosynthetic CO_2-uptake. Neither rates of photosynthetic CO_2-uptake in October nor in any other month were related to observed differences among progenies in dry weight. Nor were the areas under the curves of photosynthetic rate over the season related in any simple fashion to dry weight growth. Therefore, differences in growth could not be explained by reference to rates of photosynthetic CO_2-uptake alone.

Respiration in the dark was initially high when the seedlings consisted largely of respiring tissue but declined as the quantity of woody, non-respiring tissue increased during development. After the winter decline, respiration increased again from March to June. There were no differences among progenies.

Distribution of assimilate to leaf growth was highest in the spring or early summer and decreased to near zero in the period from mid-summer to autumn. In fact, by mid-October in both years some of the lower leaves had fallen, resulting in negative values of $\Delta L/\Delta T$. The ratio $\Delta L/\Delta T > 1$ in spring 1972, indicated that total seedling dry weight decreased between March 24 and June 3 because of net loss due to respiration while leaf production occurred, probably at the expense of stored carbohydrates in the stem and root (Rutter 1957, Tepper 1967). Progeny S2 enjoyed a slight advantage in leaf production in both years, but whether the advantage was sufficient to favor S2 in growth could not be readily determined by inspection of the $\Delta L/\Delta T$ trends.

Together with rates of CO_2-uptake, the differences in distribution of growth to leaves did have an important effect in the growth model. Predictions based on the growth simulation, ranked the progenies from highest to lowest as S2, S1, S3 which was their observed rank in dry weight. It is more interesting to note that dry weight of S1 and S3 changed in rank with period of measurement and this was predicted by the simulator.

General. — All larch species and sycamore families had maximum rates of CO_2-uptake sometime from June to August. By mid-August or October, rates had decreased from earlier levels. The pattern is similar to that reported for other deciduous species (Schulze 1970, Logan and Krotkov 1968, Saeki and Nomoto 1958), but differs from that usually observed in evergreens, which reach or maintain maximum rates in September or October *(e. g.* Bourdeau 1959, Clark and Bonga 1970, McGregor and Kramer 1963). Apparently, senescence of leaves begins early in deciduous species, whether gymnosperm or angiosperm, while evergreen leaves retain most of their capacity until temporarily curtailed by cold weather.

Winter photosynthesis did not appear to be of great importance in larch or sycamore because five of the six species or progenies suffered dry weight losses from stem or roots during the first winter. This contrasts with the results of Perry (1971) for sweetgum and loblolly pine and of Rutter (1957) for Scots pine. The difference may reflect differences between species or the climates in which they were grown. The climate in North Carolina where winter accumulation of dry weight was observed in sweetgum and loblolly pine or southern England where Scots pine showed positive winter rates of net assimilation are milder than the climate in Connecticut.

During the mild winter of 1972-1973 that followed their second growing season, European larch retained some leaves and had positive rates of photosynthetic CO_2-uptake even in February. Photosynthetic CO_2-uptake at 3^0 C (mean daily maximum temperature for February) was greater than that at 15^0 C, indicating acclimatization to low temperatures. Q_{10} for dark respiration was 2.4 *(Table 2).* Because net CO_2-uptake is possible at low temperature, the capacity to carry on photosynthesis in winter could be important in some years, even as far north as Connecticut.

Conclusions

The objective of the study was to test whether a computer model of dry matter growth based on CO_2-exchange

Table 2. — Rates of net CO_2-uptake at 4500 ft-c and CO_2-emission in dark respiration for European larch in February 1973 (± one standard error).

Temperature	Net Photosynthesis	Respiration
(C)	(mg CO_2 $h^{-1}g^{-1}$ leaf dry wt.)	(mg CO_2 $h^{-1}g^{-1}$ shoot dry wt.)
3^0	0.82 ± 0.09	0.13 ± 0.02
15^0	0.70 ± 0.16	0.38 ± 0.03

rates and the distribution of photosynthate could discriminate among genetically different groups. Observed dry weight entered the model only when seedlings were tiny germinants to provide initial conditions. Subsequent dry weight was calculated from net assimilation accumulated on a daily basis over two years. Leaf growth was simulated by adding a fraction of each day's assimilation. During the two-year period, seedlings increased in weight more than two orders of magnitude. Families or species that were the smallest initially had the greatest dry weight at termination (e. g. *Figure 2*). The reversals were predicted by the simulation.

The model was successful in discriminating among genotypes; it ranked species of larch and families of sycamore in the same relative order as their observed dry weight at the end of two growing seasons. Although ranking was accurately described, actual dry weight values deviated considerably from simulated values, particularly for larch, resulting in part from failure to account for root respiration. No single variable taken alone, either cumulative photosynthetic rate, photosynthetic rate in October, or the distribution of growth, was a consistent predictor for both larch and sycamore nor were they expected to be.

The deficiencies of this investigation are obvious. Nevertheless, the potential of the technique for tree breeding invites further exploration. The present report is a logical step in the development and testing of a practical model to predict genetic differences in growth. While the descriptive value of the model was demonstrated, its predictive value was not tested. Seedlings must be destructively harvested to determine trends in the distribution of growth among leaves, stem, and roots. The model will have predictive utility only if seasonal photosynthetic patterns and $\Delta L/\Delta T$ trends remain constant, enabling the iterative procedure to extrapolate growth to rotation age using seedling parameters. Otherwise, the model is no improvement over measurement of growth directly. It is hoped that we will soon be able to attempt the next step; *i. e.*, to make comparisons of model predictions based on seedling measurements with the yield of older trees of the same genotypes.

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Summary

Comparisons were made among seedlings representing three species of larch and three half-sib progenies of sycamore during a two-year period. Photosynthetic CO_2-uptake, respiratory CO_2-emission, and the distribution of photosynthate were measured periodically. Estimates of the parameters were substituted into an iterative computer model of growth to simulate the increase in seedling dry weight. The simulation ranked both the larch species and the sycamore progenies in the same relative order as their observed dry weight after two growing seasons and, in fact, accurately predicted reversals during the period. With further development, the model may have utility in the selection of superior species, provenances, families, or clones in a program of tree improvement.

Key words: Early tests, simulation, growth models, genetic variation, seasmal patterns in CO_2-exchange.

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