PHOTOSYNTHESIS AND TRANSPIRATION IN

YOUNG <u>LARIX</u> <u>LEPTOLEPIS</u> AND TRANSLOCATION OF

^{14}C PHOTOSYNTHATE IN MATURE <u>LARIX</u> <u>DECIDUA</u>

By

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ABSTRACT

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The effects of light intensity and temperature on net photosynthesis
(Pn) and transpiration rate for leaves of three-year-old <u>Larix</u> <u>leptolepis</u>
trees was determined with an infrared, differential open gas analysis
system. Immature to recently mature, and mature long shoot (LS) foliage
borne on the terminal leader or first major branch apex, and interior
branch, respectively, was used for these measurements. Similar foliage
was sealed inside Mylar bags and CO_2 depletion of air inside bags was
measured by infrared gas analysis to determine CO_2 compensation concentration.

Net photosynthetic response to increasing levels of photosynthetic
photon flux densities (PPFD) was similar for each foliage position and
stage of maturity. Light compensation was between 25 and 50 μE m^{-2} s^{-1}.
Rates of Pn increased rapidly at PPFD above compensation intensity and
saturated at approximately 900 μE m^{-2} s^{-1}. Transpiration rates at constant temperature likewise increased with increasing PPFD and leveled
between 800 and 1000 μE m^{-2} s^{-1}.

Photosynthetic response to temperature was determined at saturating
PPFD and was also similar for all foliage positions. Pn increased
steadily from low temperatures to an optimum range between 15 and 21° C,

and at temperatures above 21° C Pn decreased rapidly. Transpiration rate, however, increased continuously with rising temperature up to the experimental maximum, suggesting that the rapid decline in Pn above 21° C was due to internal factors and not stomatal closure.

The lowest CO_2 compensation concentrations were 58 and 59 μl l^{-1} for the mature foliage of low and mid-crown branches respectively. The foliage borne at the apex of the terminal leader had the highest CO_2 compensation concentration of 75 μl l^{-1}.

In a second series of experiments leaves of both long and short shoots (LS and SS) borne on three-year-old first order branches of mature L. decidua were exposed to $^{14}CO_2$ and the distribution of fixed ^{14}C was traced after exposure. This was done on July 1, August 10, and September 8, and followed the course of LS growth from a period of rapid expansion to early bud set. Labeled foliage included SS borne in the middle of 3-year and 2-year branch increments (3YBI and 2YBI) or 1-year terminal LS (1YTLS).

In July, the vigorous growth of LS was approximately 50% completed and SS expansion had ceased approximately two months prior to this. The majority of ^{14}C fixed and transported by LS leaves was retained in 1YTLS, but basipetal transport of ^{14}C-photosynthate was detected in 2YBI, 3YBI, and main stem as early as 5 h after exposing TLS leaves to $^{14}CO_2$. The majority of ^{14}C fixed by 2-year and 3-year SS was transported to the 2YBI and 3YBI and was retained for local use. Movement of excess ^{14}C out of 2YBI and 3YBI was predominantly translocated basipetally to the main stem and downward. Similar patterns of ^{14}C distribution were observed in August when LS growth was much slower and nearly complete, and in September

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after LS had set bud. Progressively more ^{14}C, however, was retained in branch increments or basipetally transported.

Results suggest that 1YTLS growth is essentially self supported by July and contributes increasing amounts of photosynthate to older branch increments and main stem as the season progresses. Recovered ^{14}C in partitioned 2YBI and 3YBI also suggests that SS during this time contribute photosynthate almost exclusively to branch portions supporting these SS, older branch increments, and the main stem.

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CHAPTER I

LITERATURE REVIEW

Taxonomy and distribution. The genus Larix is one of six northern polytypic genera in the order Coniferales with extensive natural ranges (others are Cupressus, Juniperous, Abies, Picea, Pinus). Species in these genera typically show considerable variation in habitats and natural distribution, with some species restricted and local in occurrence, while others form extensive forests in northern glaciated regions (Li 1953).

There are ten species of Larix, with several varieties generally recognized. All are distributed in the coolest regions of the northern hemisphere (Ostenfeld and Larsen 1930; Rehder 1940). They occur spontaneously in mountain regions in the south and extend down to lowlands in the north where they form extensive forests. Recently two new species were described in central China (Chang and Fu 1978) and were added to a growing list of reported species. Whether these species are actually new remains to be substantiated, as much deviation from the taxonomic characters used to distinguish larch species exists. This is especially true where the natural range of a species is extensive, with large environmental differences, or where the natural ranges of two species overlap (Ostenfeld and Larsen 1930). Most new species described in the past were based upon insufficient observation, e.g., Wright's (1908) description of a new Larix species in Alaska.

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According to international rules of nomenclature, five of the _Larix_ species form a sub-genus. They are characterized by bracts of the cones which are longer than and protruding out of the cone scales (Ostenfeld and Larsen 1930). These species are all restricted in distribution to the mountainous regions of western North America and southeastern Asia. Western larch (_L. occidentalis_) attains the largest size of any larch species and occurs on the slopes and high valleys of British Columbia, Washington, Oregon, Idaho, and Montana. Of the five species in the sub-genus, it is the only one of commercial value. Alpine larch (_L. lyallii_) occurs in scattered stands in the higher elevations of the same mountain systems of North America as western larch. It grows as an upright tree at elevations higher than the krumholz forms of its associated species (Arno and Habeck 1972). _Larix graffithii_ is restricted to the south slopes of the Himalayas, while Masters larch (_L. mastersiana_) and Chinese larch (_L. potanini_) occur in the mountains of Central China. Chinese larch is reported to grow at 4800 m, an elevation higher than any other species in the _Pinaceae_ is found (Ostenfeld and Larsen 1930; Rehder 1940).

The other five species of _Larix_ vary in the extent and nature of their natural distribution. Japanese larch (_L. leptolepis_) is a mountain species, originally found in scattered stands on the island of Honshu, Japan. European larch (_L. decidua_) occurs from 150 m to 800 m in the mountains and high valleys of Austria, Switzerland, France, Italy, Yugoslavia, Czechoslovakia, Poland, Ukraine and Rumania. Dahurian larch (_L. gmelini_), Siberian larch _(L. sibirica_) and American larch or tamarack (_L. laricina_) have, in contrast, extensive natural ranges. Tamarack spans the North American continent from Newfoundland to Alaska.

Dahurian and Siberian larch essentially divide Eurasia. <u>Larix</u> <u>sibirica</u> extends west and north from Lake Baikal to northeastern Europe and beyond the Arctic Circle. <u>Larix</u> <u>gmelini</u> occurs in Eastern Asia from Lake Baikal to Korea in the south. It also occurs in Russia as far north as 73° N latitude where no other tree species grows (Ostenfeld and Larsen 1930; Rehder 1940; Polunin 1959).

<u>Genetics</u>. Most of the larch species are allopatric. The natural range of several species, however, overlap and spontaneous hybrids have been reported for each. Hybrids between <u>L</u> <u>sibirica</u> X <u>L</u>. <u>gemelini</u> occur frequently on the west side of Lake Baikal. Hybrids also occur in Central China where the natural ranges of <u>L</u>. <u>potanini</u> and <u>L</u>. <u>mastersiana</u> overlap (Larsen 1937; Bobrov 1973). The natural range of <u>L</u>. <u>occidentalis</u> and <u>L</u>. <u>lyallii</u> coincide geographically in many areas, but they are usually separated altitudinally. Hybrids have been reported, however, in a few areas of frequent disturbance where <u>L</u>. <u>lyallii</u> has extended its range below normal elevation limits (Carlson 1969; Carlson and Blake 1969; Arno 1972).

Species hybrids are produced readily from open-pollinated trees planted together or under controlled conditions. The two most famous spontaneous hybrids produced from open-pollinated trees are <u>L</u>. x <u>pendula</u> and the Dunkeld larch from Scotland. <u>Larix</u> x <u>pendula</u> was originally thought to be a native North American species that was introduced into Europe around 1800 (Oppermann 1923). More recent evidence indicated that <u>L</u>. <u>decidua</u> was first introduced into the United States and then returned to Europe as <u>L</u>. x <u>pendula</u>, a <u>L</u>. <u>decidua</u> x <u>L</u>. <u>laricina</u> cross (Ostenfeld and Larsen 1930; Larsen 1937).

The second hybrid, <u>L</u>. x <u>eurolepis</u>, originated from a spontaneous cross between <u>L</u>. <u>leptolepis</u> and <u>L</u>. <u>decidua</u> planted on the Dunkeld and Murthly estates in Perthshire, Scotland (Henry and Flood 1919). The expression in the hybrid of the best traits from the parent trees generated much interest in it for future planting in England. European larch had been present in England at that time since 1629 (MacDonald 1957) and was highly regarded for its rapid growth, straight stem, light branches, and durable wood. "In no other tree have such high hopes been placed, hopes which too often have led to disappointment" (Hiley 1919). The high susceptibility of European larch to the canker-causing fungus <u>Dasyscypha</u> <u>willkommii</u> prompted this statement. Japanese larch grown in England, on the other hand, was a lesser tree with coarse branches and not as favored as European larch. It was, however, very resistant to the larch canker. The Dunkeld hybrid combined the favored form and wood qualities of the European larch parent with the canker resistance of Japanese larch. When tested in England, Denmark, and other European countries, the Dunkeld larch was found to grow faster than both parent types (MacDonald 1957; Larsen 1956; Langer 1957), while similar reports have been made for the hybrid grown in the United States (Cook 1969; Holst 1974; Littlefield and Eliason 1938, 1957; Paton 1944).

Larch breeding programs intensified after heterosis was observed in the Dunkeld larch. The first controlled pollination of Japanese and European larches took place in Scotland between 1924 and 1925 and in Denmark in 1930 (Larsen 1937). The European larch used for this purpose in Denmark was said to be the "finest" tree in the country and required 29 m of scaffolding. Much of the later breeding research was reviewed by Larsen (1956) and general indications were that combination of any two

species was possible. Some species combinations that have produced
vigorous hybrids include: L. decidua x L. siberica, L. leptolepis
x L. gmelini, L. laricina x L. leptolepis, and L. occidentalis x
L. leptolepis (Wright 1976; Larsen 1934; MacGillivray 1967; Wang 1971).
Wright (1976) states, however, that only about one-fourth of the forty-
five possible species combinations have been attempted, and at least
five of these included L. decidua as one parent. Triploid individuals
have been produced by pollinating L. decidua with pollen from L. occi-
dentalis (Larsen 1956), but apparently no attempts at producing a tetra-
ploid from this triploid tree have been successful. One individual of
L. decidua growing in a private Danish arboretum was cytologically
identified as a tetraploid (Larsen 1956) but it was not produced by con-
trolled pollination. There is a possibility that this tree was introduced
from England as a variety of European larch (L. decidua var. pendula) and
thus may have been derived from a L. decidua x L. laricina.

Provenance studies. The use of larch (L. decidua in particular)
for reforestation increased during the 18th century when the original
forests of central Europe were being cut over. Interest in European
larch for this purpose was mainly based on its rapid growth and high
yield, strong valuable wood, and its ability to adapt to a variety of
sites, both inside and outside its natural range. This adaptability was
not uniform, however, and by the middle of the 19th century some plant-
ings had failed (Vincent 1958). It became apparent that European larch,
although of rather limited natural range, was quite variable.

The first comparative study of the growth of larch was initiated
in 1879 and several provenance studies were established shortly there-
after. Characteristics such as growth rate, wood density, time of spring

needle flush, and needle fall in autumn were found to be dependent upon the geographic origin of the trees studied (Ciesler 1914). McComb (1955) reviewed the European provenance studies and described the Alpen, Sudeten, Tatra, and Polen races of European larch.

In the United States, European larch was planted sporadically in Massachusetts, Connecticut, and Vermont after the Civil War. From 1860 to 1880 it was one of the most popular trees for planting in Illinois, Iowa, Minnesota, and the Dakotas. Later it was planted extensively in Pennsylvania and New York. Hunt (1932) reported on the performance and silvical characters of European larch plantings scattered throughout Massachusetts, Vermont, Connecticut and New York. The seed origin of these early plantations, however, could not be stated with certainty.

In 1944 the International Union of Forest Research Organizations (IUFRO) began an international study of geographic variation in European larch. A few seedlots of other larch species were also included in this early test. Henry Baldwin initiated the study in the United States and plantations were established in New Hampshire and New York. The four-year performance of the New Hampshire planting were reported by Baldwin (1949) and twelve-year results for both New Hampshire and New York plantings was published by Genys (1960). Reviews of all provenance experiments on European larch and the 1944 IUFRO study have been made. Early reports indicated that the best performance in Europe was obtained with Japanese larch followed by Sudetan provenances of European larch (Schober 1958). Later reviews, however, have indicated that early results were misleading and seven or more years are required for perform-ance to stabilize. The most recent data indicate that Sudetan provenances

of European larch grew best, while Japanese larch demonstrated only average performance (Giertych 1979).

A second international larch provenance test was initiated in the 1950's involving 68 provenances of larch tested in 14 European countries and the United States (Lacaze and Birot 1974; Schober 1976). The United States participation was organized by S. H. Spurr. Test plantations were established in southeastern Michigan and included 22 European larch provenances, one Japanese larch source and one F_2 progeny of Dunkeld hybrid larch. The 19-year performance of these plantations indicated that the best height and diameter growth were obtained from European sources having similar macroclimatic conditions as southeastern Michigan (Barns 1977). Japanese larch was most severely damaged by ice, but it and the Dunkeld hybrid had the greatest resistance to larch casebearer (Coleophora laricella) and the larch wooly aphid (Chermes strobilobius).

Japanese larch is restricted to a ca. 200 square km natural range between 900 to 2500 m on Honshu Island, Japan (Wright 1962). Despite its limited range, the performance of this species when tested in Europe has repeatedly been shown to depend on its geographic origin (Hattemer 1968, 1969; Langer 1961; Schönbach et al. 1966). United States experiments planted in New York (Stairs 1965), Maryland (Genys 1972, 1973), and in the North Central States (Farnsworth et al. 1972; Lee 1973) have also demonstrated the seed source diversity of Japanese larch.

The geographic variation of native North American species of larch is not well-documented. Tamarack has an extensive transcontinental natural range but little was known about its genetic variation until 1961 when a cooperative rangewide seed source study was initiated by the

University of Minnesota. Seed for this test was obtained from more than 50 sources and early height growth of seedlings planted in Minnesota and Wisconsin gave reasonable indication that there was geographic variation in the species (Pauley 1965). This was further indicated by the survival and height growth of these plantations eight and nine years after establishment (Jeffers 1975). More recent plantings of this range-wide provenance test were established in 1969 in Michigan by Michigan State University, but results have not yet been published.

Surpringly little information is available on the natural variability in _Larix occidentalis_, even though it is the largest of all larch species and is of great commercial value in North America. When planted or seeded outside its natural range, it is usually included for comparison with other larch species (Genys 1968, 1976) or for ornamental purposes. No significant efforts to determine inherent variability or adaptability to other climatic or geographic regions have been attempted (Schmidt et al. 1976). It is reasonable to expect, however, that a great deal of genetic variation exists in western larch and that a potential for selection of superior seed for plantation establishment within and outside its natural range exists.

Injury factors. Larch is generally considered relatively resistant to physical and biologic injury within the confines of its natural range. It is also resilient and capable of good recovery from injury that would kill or permanently disfigure other tree species. The greatest problems have occurred when the natural range of a larch species was extended by planting or exotic pests were introduced (McComb 1955; Hunt 1932). The severity of injury, however, varies between and within species and is

dependent on age, time of year, and geographic location.

The effects of fire on larch vary with species and age. Seedlings, saplings, and pole-sized larch are readily killed by fire (Sudworth 1918). Mature tamarack and Dahurian larch are also very sensitive to fire, but they seed in and occupy burned over areas readily (Roe 1957; Rozhkov 1966). Mature and overmature western larch, on the other hand, are considered the most fire-resistant tree in the northern Rocky mountains (Flint, 1925). This is attributed to its thick bark with low resin content, high and open branching, and low foliage flammability (Haig et al. 1941). Siberian larch also produces bark up to 25 cm thick on the lower trunk and is fire resistant on sites that permit deep rooting (Rozhkov 1966).

Species such as European, Siberian and western larch develop deep, wide-spreading root systems which make them moderately to highly resistant to windthrow. This is decreased, however, with age and degree of root rot or topography (Hunt 1932; Schmidt et al. 1976; Rozhkov 1966). Tamarack and Dahurian larch, conversely, produce shallow root systems and are subject to windthrow (Roe 1957; Rozhkov 1966).

Larch is generally not susceptible to damage by snow and ice due to its light branches and deciduous habit, but exceptions have been noted. Ice storms have caused severe damage to European larch planted in the northeast United States (Hunt 1932), while early wet snows cause bending of western larch sapling and pole stands with full complements of needles (Schmidt et al. 1976). Young western larch, however, are usually quite resistant to permanent snow damage and severely bent trees recouperate within six years (Schmidt and Schmidt 1979).

Noxious fumes tend to have less effect on larch than other conifers due to its deciduous habit. This is especially true when winter

air-inversions cause air pollutants to be particularly damaging (Hepting 1971). During the growing season gases such as fluorine and sulfur dioxide can injure larch foliage and young needles are very sensitive to these and other industrial pollutants, but susceptibility tends to decrease with age (Leaphart and Denton 1961).

When the natural range of European larch was extended by planting and seeding, particularly into the lowlands of Germany, the larch canker became a serious disease of this species (McComb 1955). In the United States this disease also is a tenacious problem with European larch (Hunt 1932), but tamarack is not affected by this canker and is relatively free of other stem diseases (Hepting 1971). The larch canker is also known to be a problem with Siberian larch in moist areas of its range (Rozhkov 1966), and has also proved parasitic to western larch when arti- ficially infected (Hahn 1934; Hahn and Ayers 1943).

Larch dwarf mistletoe (Arceuthobium larcis) is the most serious disease of western larch (Schmidt et al. 1976; Weir 1916). A foliage disease affecting eastern, European and western larches is the needle blight caused by Hypodermella laricis (Cohen 1967; Hepting 1971). Virtually all larch species are affected by Fomes species causing various root, stem and heart-rot diseases.

The insects causing the most serious damage to native or exotic larch species in North America are of European origin (Hunt 1932; Graham and Knight 1965). The larch sawfly (Pristiphora erichsonii) was first observed in the United States in 1880 (Hunt 1932) and has subsequently caused great losses in larch throughout the Northeastern and Lake States. The larch species most seriously affected by this insect in North America

is tamarack and, although repeated infestations reduce growth, moderate
to severe defoliations for six to nine years are required to cause
mortality (Drooz 1960). Other larch species planted in Maryland have
shown different levels of susceptibility to larch sawfly attack. Among
five species of larch examined, Japanese larch was most susceptible and
western larch the most resistant, but some geographic strains of Japanese
and European larch were less susceptible than others (Harman and Genys
1970; Genys and Harman 1976).

The second insect of European origin causing serious problems is
the larch casebearer. This is the most serious insect pest of western
larch, but it is also found world-wide on nearly every other species of
larch (Denton 1979). It was first observed in 1886 on European larch
in Northhampton, Massachusetts, but quickly established itself on native
tamarack (Hagen 1886). It spread rapidly west through the southern part
of tamarack's natural range. The first outbreak of casebearer in western
larch forests was discovered in 1957 near St. Maries, Idaho (Denton,
1958). From there the population increased and spread unchecked until
by 1972 over one-half of the western larch type was infested. Prior to
this, western larch was relatively free of insect pests compared to most
of its coniferous associates. Loss of tree growth is the most serious
damage caused by casebearer defoliation of western larch, although tree
mortality has occurred. In severe infestations of 5-year duration,
radial increment can be reduced by 97 percent (Denton 1979).

Another insect pest jeopardizing western larch is the western
spruce budworm (Choristoneura occidentalis). This insect preferentially
feeds on the current-years foliage of many conifers, but since 1962 it

has been observed to sever the current-year terminal shoots of western larch (Fellin and Schmidt 1967). This detracts from form and greatly reduces net annual height growth. If continued for a period of time, crooked boles and bushlike trees result (Schmidt and Fellin 1973; Fellin and Schmidt 1973).

Ecology. Larches occur naturally in the cooler regions of the northern hemisphere. They are well-adapted to northern continental or high mountain climates and extreme temperature fluctuations. In southern regions larch species also prefer cooler habitats and grow best on north and east slopes or valley bottoms. Southwest exposures are usually not favorable sites (Boe 1958). These species are also restricted to specific altitudinal zones (Arno and Habeck 1972; Boe 1958; Larsen 1930; McComb 1955; Saki and Okado 1971). Larix lyallii exemplifies the extreme of species adaptation. This species has an affinity for cold rocky sites, often at elevations above most of its associates. The growing season in these areas may be less than ninety days and is marked by average daily temperatures over 5.6° C. Larix lyallii east of the Continental Divide in Montana and Alberta is also capable of enduring winter minimum temperatures of -51 to -57° C. Likewise, larch species of the northern boreal forests of North America and Siberia are capable of withstanding extremely cold air and soil temperatures. In eastern Siberia, where mean annual temperatures may be less than -10° C, the ground is permanently frozen down to a depth of 250 to 400 m, and only 10 to 150 cm may thaw during the summer. Yet species like L. gmelini grow well in these unfavorable conditions and form extensive forests (Sakai and Okada 1971; Walter 1979).

Precipitation patterns throughout the entire range of larch are
varied. In relation to annual temperatures, however, precipitation
requirements may be rather exacting and delimit the natural distribution
of larch species. The range of L. laricina is one of the most extensive
in North America, and the variation in precipitation throughout this range
is considerable. Annual precipitation ranges from seven inches at
Fort Yukon, Alaska, to 55 inches in eastern Canada. The cooler tempera-
tures at Fort Yukon, however, reduce the precipitation requirement.
In the southern portion of its range L. laricina is characteristic of
bogs and swamps, but in the northwestern part, where annual temperatures
are reduced, it is found on drier upland sites (Fowells 1965). The dis-
tribution of L. occidentalis is also limited to areas receiving greater
than 18 inches annually (Schmidt et al. 1976; Fowells 1965). Extended
periods of drought occur, but the effect of this is balanced by low wind
velocities and retention of snow cover in its preferred habitat, and
moderate precipitation during May and June (Haig et al. 1941). European
larch likewise has a high moisture requirement, possibly greater than
that of any other European conifer (Burger 1945). Reflective of this are
transpiration rates for European larch which usually are higher than
those obtained for other associated coniferous species (Berger-Landefeldt
1936; Pisek and Cartellieri 1939).

The soil requirements of larch species are probably less exacting
as those of climate. European larch occurs naturally and grows well on
acidic soils derived from sandstone or clacarious soils derived from
limestone or dolimitic shales (McComb 1955). The results of planting
L. decidua in Europe and the United States indicate that deep, moist

soils with physical properties conducive to adequate drainage are more important than soil fertility for satisfactory growth (Aird and Stone 1955). Larix lyallii also occurs on extremely infertile soils and seems preferentially distributed on acidic substrates derived from quartzite, sandstone, and shale at timberline (Arno and Habeck 1972).

The best development of western larch is found on deep, moist, porous soils on mountain slopes or valley bottoms (Larsen 1940). The most common parent materials in the range of western larch are argillites and quartzites, and these soils may be gravelly, sandy, or loamy in texture. The one soil factor affecting western larch growth, however, is moisture-holding capacity. Thus, soil variations affecting the distribution of this species are also more likely to be physical than chemical (Schmidt et al. 1976).

The larch species with extensive boreal ranges grow on a wide variety of soil types and moisture conditions. Larix laricina is found commonly on moist peats and mucks of swamps or muskegs, and it can tolerate short periods of high water. Best growth, however, is obtained on rich, moist but well-drained, loamy soils bordering streams, lakes or swamps. It is also found on soils ranging from heavy clays to coarse sand. Thus, tamarack tolerates a wider variety of soil physical properties than any species discussed previously. Like the other species, though, it is sensitive to excess moisture and will not tolerate prolonged flooding (Fowells 1965). Siberian larch is also found on soils and conditions similar to tamarack. It is considered a poor competitor, however, and is not found on the most favorable sites unless the "dark taiga" coniferous species are set back by fire (Rozhkov 1966).

Growth and reproduction. Larch winter dormancy is broken early in the spring and is signaled by mitotic activity in the leaf primordia of vegetative buds, followed by apical divisions and leaf elongation (Owens and Molder 1979a). The buds begin to swell when daily mean temperatures reach 4 to 5° C and leaf emergence occurs about two weeks later (Arno and Habeck 1972; Tranquillini 1979). Terminal elongation, however, does not begin until average temperatures are 7 to 10° C and the foliage borne at the base of terminal shoots and on short shoots have fully expanded (Cook 1941; Fowells 1965; Owens and Molder 1979a). Short-shoot leaf expansion may take over 2 months but the foliage is able to photosynthesize early and may contribute to larch's rapid height growth once terminal shoot elongation begins (Tranquillini 1979).

Reproductive buds usually differentiate on young vigorous vegetative short shoots one year prior to pollination (Owens and Molder 1979b). These buds swell and the new reproductive strobilli emerge before leaf flush and develop rapidly thereafter. The wingless pollen are shed in mid-spring. The pollination mechanism in Larix species resembles that of Pseudotsuga mensiesii (Doyle 1945; Owens and Molder 1979c). The ovules of L. occidentalis cones are nearly fully enlarged prior to fertilization and development may proceed in the absence of pollination. This results common-ly in unfertile but normal-appearing cones (Owens and Molder 1979c) and may contribute to the low viability of seed produced by this species and L. lyallii (Arno and Habeck 1972; Shearer 1961). Ovulate cones ripen in late summer with seed shed through the fall and winter months.

Larch species are known to reproduce vegetatively when branches make contact with a soil substrate. Due to the light, deciduous nature

of their branches, however, this does not occur readily. <u>Larix</u> <u>decidua</u> will layer occasionally when branches are weighted down by heavy snow (Plesnik 1973) but this is much less common than with its spruce associates. The same is true for <u>L</u>. <u>laricina</u> when branches are covered by fast-growing sphagnum moss or by drifting sand. This species is also reported to produce root sprouts (Duncan 1954; Lewis et al. 1928).

Larch are intolerant, pioneering species and are often the first to occupy disturbed sites (Boe 1958; Roe 1957; Arno and Habeck 1972). Some shade is tolerated by seedlings at higher elevations, or in the southern part of a species range (Arno 1972; Boe 1958; McComb 1955; Roe 1957; Rozhkov 1966), but larches do not readily become established under their own canopy. In mixed stands a dominant position must be maintained for survival and some form of disturbance is required to regenerate a new stand of larch.

Fire has been one of the most important forms of disturbance for regeneration of many larch species and in its absence they are replaced by more tolerant associates. Western larch is considered a fire climax species (Kozlowski and Ahlgren 1974) in parts of its range and probably has the closest ecological relation to fire of all the larches.

Natural seeding is the preferred method of regenerating western larch (Schmidt and Shearer 1973). Some seedbed preparation is usually required for successful regeneration and broadcast burning is commonly used to accomplish this (Shearer 1975; Beaufait et al. 1977). Prescribed fire is often the preferred method due to reduced cost, limitation of topography, and nutrient release back to the soil (Artley et al. 1978). Thirteen-year-old western larch have been shown to grow about one-third

faster on broadcast burned areas than on mechanically scarified sites (Schmidt 1969). This increased growth on the burned site was attributed to the added nutrients. Establishment of tamarack stands on burned peatlands is also improved over establishment on adjacent unburned sites (Johnston 1973).

In natural stands early growth rate of larch generally exceeds that of its natural associates (Cunningham 1972; MacGillivray 1969; Sartz and Harris 1972). This is true for the first 90 years growth of western larch (Deitschman and Green 1965) which will reach five to six m in the first 20 to 30 years (Cummings 1937). Planted larch in the United States will also generally outgrow all native species for the first 25 years (Hunt 1932). Growth rates exceeding 0.6 m annually are common for both European larch and tamarack (Jeffers and Isebrands 1972; Lemmien and Rudolph 1968; Littlefield and Eliason 1956; Zavitkovski and Dawson 1978), while Japanese larch height growth may be over 1.0 m annually for 20 years (Isebrands and Hunt 1975; Turner and Myers 1972), The performance of planted Japanese or European larch is only surpassed by that of the Dunkeld hybrid (Holst 1974; Reck 1977).

The rapid height growth rate of larch is not always associated with increased dry matter accumulation when compared to other coniferous species grown under similar conditions. In a comparison of tamarack and jack pine (Pinus banksiana) grown under intensive culture, the tamarack produced two to three times the biomass of that measured in natural stands. This production, however, was less than that obtained with jack pine (Zavitkovski and Dawson 1978). Sweet and Wareing (1968) reported that height and diameter growth of Japanese larch was greater than

Pinus contorta and Pinus radiata planted in England, but the pines made up 25% of the growth difference after the larch lost its needles in the fall. At the end of the growing season Pinus radiata had produced more dry matter than the Japanese larch. The relative growth rate (RGR) of the larch exceeded the pines, but this advantage was reduced by the extended growing season experienced by the pine species. When compared to the hardwood sycamore (Plantanus occidentalis), a species having similar free growth and deciduous habits, larch displayed comparable patterns of CO_2-uptake and growth (Ledig and Botkin 1974).

Physiology. The growth potential of a tree depends not only on its photosynthetic rate but also on seasonal patterns of photosynthesis in relation to respiration, the duration of growth, and the distribution of photosynthate within the tree. Larch species do have patterns of growth unique among other north temperate coniferous species. Frampton (1960) described the seasonal periodicity of long shoot growth of L. decidua and suggested that the early and late leaves of long shoots were dimorphic in character. The seasonal growth of long and short shoots of L. laricina have also been described (Kozlowski and Clausen 1966a; Clausen and Kozlowski 1967), but leaf dimorphism of long shoots was not found in this species (Clausen and Kozlowski 1970). Long shoot and short shoot bud development was described for L. leptolepis (Fijimoto 1978), and more recently apical changes of long and short shoots of L. occidentalis were reported by Owens and Molder (1979a).

Terminal long shoots (TLS) bear leaves similar to those produced by seedlings. The terminal long shoot buds (TLSB) produced at the apex of long shoots are not totally preformed and consist of bud scales, basal

leaves, and long shoot (LS) leaf primordia. After release from dormancy
basal leaves elongate and new LS leaf primordia are initiated up the
flanks of the apex. Elongation of the shoot progresses slowly at first
until the basal leaves have fully expanded. The shoot then elongates
vigorously and then slows again. New bud scales and basal leaves are
formed and the first set of long shoot leaf primordia are initiated after
shoot elongation ceases but before the TLSB becomes dormant (Clausen
and Kozlowski 1970; Owens and Molder 1979a).

Axillary buds are initiated in the TLSB about the time of flushing
but all leaves along the axis of long shoots do not bear axillary buds.
The apices of these new buds differentiate into axillary long shoot buds
(ALSB) or short shoot buds (SSB). The ALSB act as TLSB do and initiate
the first LS leaf primordia before becoming dormant. The differentiated
SSB initiate leaves at the base of the apex and all but the last primordia
are present. Axillary SSB are preformed before becoming dormant and
each season they pass through the same phases of bud-scale and leaf initia-
tion to form a dormant preformed bud. Annual short-shoot elongation is
about 1 mm and the apex may live many years (Clausen and Kozlowski 1967;
Owens and Molder 1979a).

The apex of short shoots may differentiate into long shoots and
vice versa (Cook 1969; Owens and Molder 1979a). Short shoot differentia-
tion into long shoots usually occurs in young vigorous shoots. The leaves
initiated in the developing bud include basal leaves borne at the base
and the leaf primordia borne part way up the flanks of the apex. The
new dormant bud is no longer totally preformed as it was as a SSB and
will initiate new LS leaves the next season. The long shoot growth

will be the same as that from a TLSB.

The anatomical distinction between axillary SSB and ALSB in larch is apparent in the first year of development and before dormancy. This predetermination of SSB and LSB persists throughout the life of the short or long shoot and occurs each season as the buds develop. In _Ginkgo biloba_ anatomical differences between preformed SSB and LSB are not apparent before dormancy but becomes distinguishable after dormancy due to differential elongation (Gunkel and Wetmore 1946a, 1946b).

In addition to unique growth patterns, there are some aspects about larch photosynthetic physiology that may be unique. The rate of CO_2-uptake is often reported to exceed that of most coniferous species (Fry and Phillips 1977; Growin et al. 1980; Havrnaek and Benecke 1978; Larcher 1969). Likewise, net assimilation rates based on leaf weight and determined over extended periods or entire seasons exceed those of other species (Sweet and Wareing 1968; Growin et al. 1980). Larch foliage is less dense than other conifer leaves (Strong and Zavitkovski 1978), which may raise questions about the validity of these comparisons. Little doubt about larch's unique characters can be raised, however, when their growth and performance compares to or exceeds that of other species in a shorter period of time (Sweet and Wareing 1968; Tranquillini 1962).

Recently Fry and Phillips (1976) reported some intriguing results which place _L. leptolepis_ photosynthetic physiology intermediate between C_3 and C_4 species. They based this conclusion on phosphoenol pyruvate to ribulose _bis_ phosphate carboxylase activities, chlorophyll a/b ratios, initial products of $^{14}CO_2$ incorporation, CO_2 compensation concentration, and saturation light intensity. These results have not been substantiated

but it is difficult to envision a tree species so well-adapted to the coolest regions of the northern hemisphere possessing such characters.

Environmental effects on larch photosynthesis are in general not well-documented. With the exception of the high saturation irradiance reported for L. leptolepis (Fry and Phillips 1976, 1977), most environmental research has been performed with L. decidua. Much of this work, including the effects of air and soil temperature, humidity, wind velocity, and elevation have recently been compiled by Walter Tranquillini (1979) and assembled into a monograph on alpine timberline physiological ecology. The productivity and gas exchange of L. decidua as influenced by constant growth temperature has also been recently reported (Growin et al. 1980).

The anatomy and morphology of a few larch species have received some examination. The distribution of stomata and cross-section leaf anatomy has been described for L. decidua, L. leptolepis, and the hybrid L. X eurolepis (Gathy 1954) as well as a comparison of these characters between the races of L. decidua (Gathy 1959). Other studies have included epidermal wax deposits (Grill 1973), leaf surface area-leaf length relationships (Strong and Zavitkovski 1978), general structure and chloroplast ultrastructural characteristics (Fry and Phillips 1976), and ultrastructure of plastid development (Fry and Phillips 1977; Medghini-Bonatti and Boneta-Conta 1976).

CHAPTER II

PHOTOSYNTHESIS AND TRANSPIRATION BY
YOUNG LARIX LEPTOLEPIS PLANTS: C_3 RESPONSES TO
LIGHT AND TEMPERATURE

Introduction

From an economic standpoint, efficient growth of trees is that which

produces the maximum yield of desired products with a minimum amount of

silvicultural input. To the horticulturist this may mean the largest

possible yield of fruit. The forester, on the other hand, is more

interested in efficiently increasing the yield of wood. Yield is affected

by the interaction of various physiological, environmental, and genetic

factors controlling growth. Further, environment and genetic makeup

place limits on physiological capacity. Within these constraints the

growth potential of a tree depends on photosynthetic rate, seasonal pat-

terns of photosynthesis in relation to respiration, duration of growth,

and the distribution of photosynthate within the tree. Increasing or

altering any one of these physiological processes may increase tree

growth.

Trees in the genus Larix are unique among north temperate trees.

They are the only deciduous conifers found in northern habitats. Their

growth in plantations or natural stands is usually more rapid than any

of their natural associates (Hunt 1932; MacGillivray 1969). Terminal

extension and height growth is free and continuous in contrast to the

fixed growth pattern of most other northern confiers (Kramer and

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Kozlowski 1979). Larch displays distinctly different patterns of long
and short shoot growth (Clausen and Kozlowski 1967; Kozlowski and
Clausen 1966a; Owens and Molder 1979a). These two shoot types may have
different roles in the seasonal distribution of photosynthate. Short
shoots leaf-out early and may photosynthesize for over two months before
vigorous terminal and lateral long-shoot extension occurs (Tranquillini
1979). Larch photosynthetic rates and net assimilation rates (NAR) are
also characteristically higher than other conifers (Growin et al. 1980;
Larcher 1969; Sweet and Wareing (1968). Recently $\underline{L}$. $\underline{leptolepis}$ was
reported to have a photosynthetic physiology intermediate between C_3
and C_4 species, based on phosphoenol pyruvate (PEP) to ribulose $\underline{bis}$
phosphate carboxylase activities, chlorophyll a/b ratios, initial products
of $^{14}CO_2$ incorporation, CO_2 compensation concentration, and saturation
light intensity (Fry and Phillips (1976). These observations have not
been substantiated by independent workers nor have the environmental
effects on larch photosynthetic physiology been well-documented.

This study was performed to establish the photosynthetic response of
$\underline{L}$. $\underline{leptolepis}$ to different levels of photosynthetic photon flux density
(PPFD) and temperature, and to establish the CO_2 compensation concentra-
tion of plants grown under near ideal conditions. It was felt that
the pattern of response to these environmental variables would reflect the
basic photosynthetic physiology of the species and provide a base for
future studies.

Materials and Methods

Japanese larch (L. leptolepis Sieb. and Zucc., Gord.) were
established and grown in 5 X 5 X 30 cm paper bands filled with a peat-
vermiculite (1:1) media in the winter of 1979. The seedlings were main-
tained under optimal conditions for continuous growth (Hanover et al.
1976), with fertilizer and water added as needed. Seedlings were
repotted in May into 20 l plastic pots using a loam-sand (2:1) soil mix
and moved outside to grow under natural conditions until mid-August.
The repotted trees were then returned to the greenhouse and maintained
again under optimal conditions through the winter of 1980. All CO_2-
exchange determinations were performed in March and April, 1980, on
terminal immature and mature foliage. Average tree height at this time
was approximately 1 m.

The rate of CO_2 exchange in light or dark was determined in an open
gas analysis system (Sams and Flore 1979, 1981) by measurement of differ-
ential CO_2 concentrations with a Beckman 865 Infrared Gas Analyzer.
Steady state CO_2 exchange was determined with intact or excised shoots
placed into controlled environment chambers (Series 500 chambers,
15.3 X 10 X 10 cm, Paige Instruments). Temperature was controlled by
circulating water from a refrigerated bath through a finned aluminum
heat sink at the bottom of each chamber. Chamber air was circulated by
a variable speed fan (Pameter Model 900) incorporated into the aluminum
bottom of the chambers; Sams and Flore (1979, 1981) determined that this
reduced the boundary layer resistance to less than 0.2 s cm^{-1}.

Humidity of the air stream entering the chambers was controlled by saturating the air in water at a temperature equal to or lower than chamber temperature. The temperature of the air stream was then raised to chamber temperature before entering the chambers. The humidity of the air entering and exiting the chambers was monitored by a flow-through hygrometer (General Eastern Systems 1100 AP). Transpiration rates were determined by calculating the difference between water content of the air entering and exiting the chambers relative to the air stream flow rate and were expressed on a foliage dry weight basis as mg H_2O g^{-1} h^{-1}.

Chambers were illuminated by GE 400 W multivapor (metal halide) lamps. Light intensity was controlled by adjusting the distance between the light source and chambers or by inserting neutral-density filters between the light source and chamber. The GE 400 W lamps produce a spectral distribution of light high in the photosyntheticly active region (400-700 nm) and this distribution was unaffected by the neutral density filters (Sams and Flore 1979, 1981). Chamber PPFD was monitored by a LI-COR Model LI 188 integrating meter connected to LI-COR Model LI 190S quantum sensors incorporated into each chamber.

After photosynthetic and dark respiration rates were determined on mature or immature long shoot (LS) foliage of Japanese larch shoots, foliage was removed, weighed, dried at 75° C for 48h and re-weighed. Steady state CO_2 exchange was then calculated per unit fresh and dry leaf weight and the photosynthetic or dark respiration rate expressed as mg CO_2 g^{-1} h^{-1}. Net photosynthetic (Pn) response to light was determined by exposing each foliage type to PPFDs ranging from 0 to 2000 μE $m^{-2} s^{-1}$.

Chamber temperatures were maintained at 20 or 25° C for the light-response determinations.

Photosynthetic response to temperature was determined by measuring steady state CO_2 exchange while varying chamber temperature from 5 to 35°C. Foliage used to determine temperature response was exposed to saturating PPFD as determined in initial light-response experiments.

Dark respiration was estimated by measuring the increase in CO_2 concentration of the air in darkened chambers. Foliage for these determinations was allowed to equilibrate to chamber environment (20°C and saturating PPFD) and a steady state CO_2 exchange prior to darkening chambers. Dark respiration rates were calculated from the stable CO_2 exchange after chambers were darkened.

Carbon dioxide compensation concentrations for mature or immature (terminal) foliage was determined by adopting a rapid method developed by Dickmann and Gjerstad (1973). Terminal or proximal portions of branches were sealed in Mylar bags (20 X 36 cm) and allowed to reduce internal CO_2 concentration for 1 h. The seals were made by placing a longitudinally sliced foam rubber cylinder (2 to 4 X 3 cm) over the basal portion of the branch, wrapping the bag around the cylinder, and fastening with a Twist-em. A clamped section of Tygon tubing placed along side the branch was included in the seal to facilitate sampling the internal air. Measurement of mature foliage required cutting the closed end of a Mylar bag, sliding it over the branch and making two seals. All CO_2 compensation determinations were performed under green-house conditions where PPFD ranged from 300 to 600 $\mu E\ m^{-2}\ s^{-1}$ and air temperature inside bags was 25 to 25.9°C. After 1 h the air inside

the bags was manually expelled through the sample cell of a Beckman 864 infrared gas analyzer.

Results and Discussion

Light response. Pn response to different levels of PPFD was determined at three crown positions with LS foliage at varying stages of maturity. The terminal apex (Figure 2.1) and the first major lateral apex (Figure 2.2) included foliage ranging from newly initiated to recently mature leaves. The third position included mature foliage of the first major branch (Figure 2.3) basipetal to the foliage used in Figure 2.2. Different symbols on each light response curve represent replications for each foliage position.

Light compensation for all three foliage positions was between 25 and 50 $\mu E\ m^{-2}\ s^{-1}$. Intolerant species such as larch are generally considered to have higher light requirements for Pn, and these compensation intensities may at first seem low. The foliage of long shoots in Larix species, however, resembles that produced by seedlings (Frampton 1960). Photosynthetic capacity changes with the stage of development, and seedlings can generally make better use of low illumination than older plants (Larcher 1969). Light saturation was reached at approximately 900 μE $m^{-2}\ s^{-1}$ at all three foliage positions. The range of Pn values obtained beyond saturation in all three figures are higher than values obtained for other conifer species (Larcher 1969), and are consistent with those reported for Larix (Fry and Phillips 1977; Growin et al. 1980; Neuwirth 1967; Polster and Wise (1962). The overall shape of these curves is hyperbolic and typical of a response obtained with multiple leaves of a
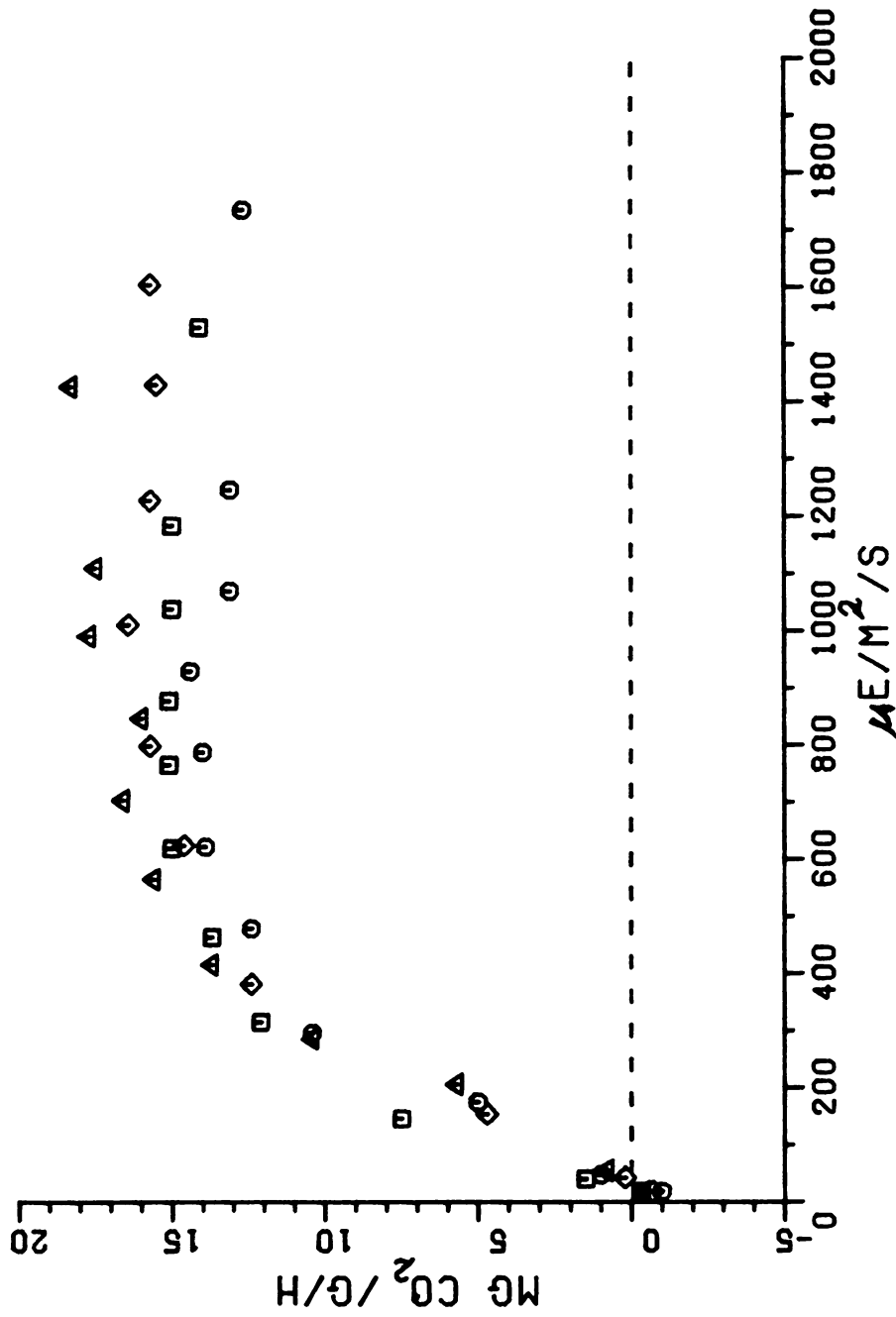
Figure 2.1. Photosynthetic response to PPFD for L. leptolepis leaves borne on the terminal leader. Long shoot foliage included newly initiated to recently mature leaves near the apex. Different symbols represent replications.
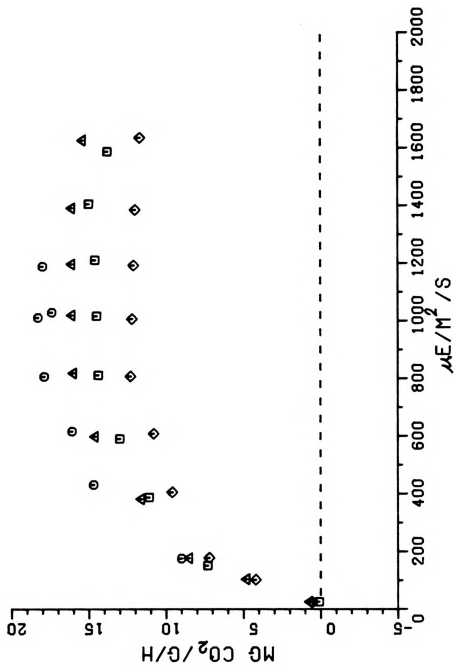
Figure 2.2. Photosynthetic response to PPFD for L. leptolepis leaves borne on the first major lateral branch. Long shoot foliage included newly initiated and recently mature leaves near the apex. Different symbols represent replications.
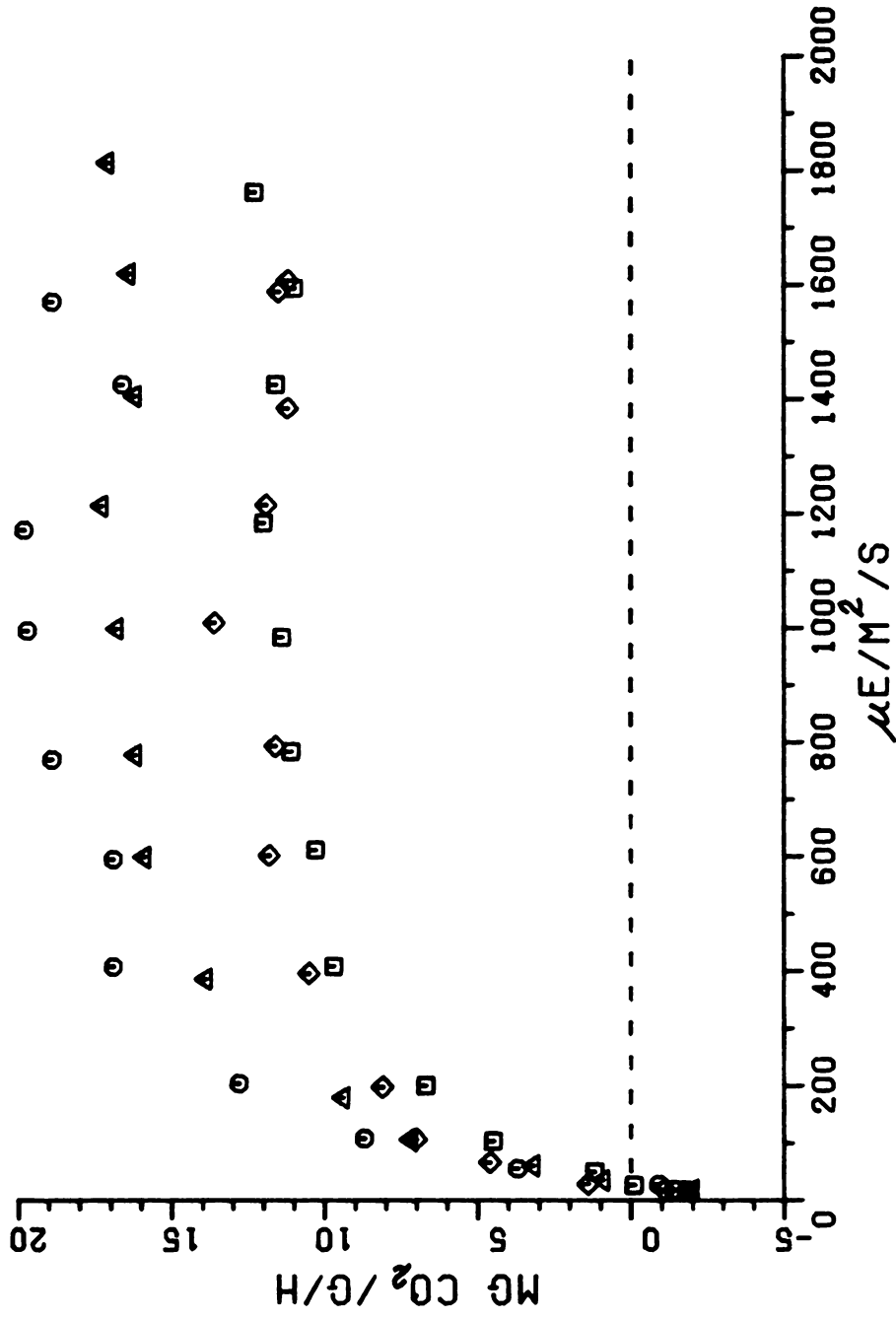
Figure 2.3. Photosynthetic response to PPFD for mature L. leptolepis leaves borne on the first major branch. Different symbols represent replications.

C_3 species (Leopold and Kriedemann 1975). Dark respiration rates obtained with replicates of all three leaf positions ranged from 0.9 to 1.8 mg CO_2 g^{-1} h^{-1}. A post-illumination burst of CO_2, typical of plants possessing a C_3 photosynthetic pathway, was not detected.

Average Pn values (from Figures 2.1, 2.2, and 2.3) plotted as a percent of maximum Pn clearly illustrate that light saturation was reached between 800 and 1000 μE m^{-2} s^{-1} (Figure 2.4). Previous work with L. leptolepis (Fry and Phillips 1976, 1977) indicated that individual leaves had higher saturation light intensities resembling those obtained with Zea mays L., a C_4 species. This was not found in the present study. Furthermore, the present measurements were made with multiple leaves which normally have even higher light saturation intensities than individual leaves (Lakso and Seeley 1978).

Temperature response. The effect of temperature on Pn was determined at saturating levels of PPFD (ca. 900 μE m^{-2} s^{-1}). The location of LS foliage used was similar to that used to determine light response curves.

Pn response to temperature for the terminal foliage of the leader and first major lateral branch is presented in Figures 2.5 and 2.6. Response to the leader foliage (Figure 2.5) to increasing temperature was similar for each replication up to an optimum range between 15 to 20°C. This steady increase in Pn as temperatures become more favorable is indicative of young leaves at or near full expansion (Leopold and Kriedemann 1975). Beyond the optimum range Pn dropped sharply and replication values were much more variable. This rapid decrease in Pn above optimum temperature probably reflects the adverse effects of high
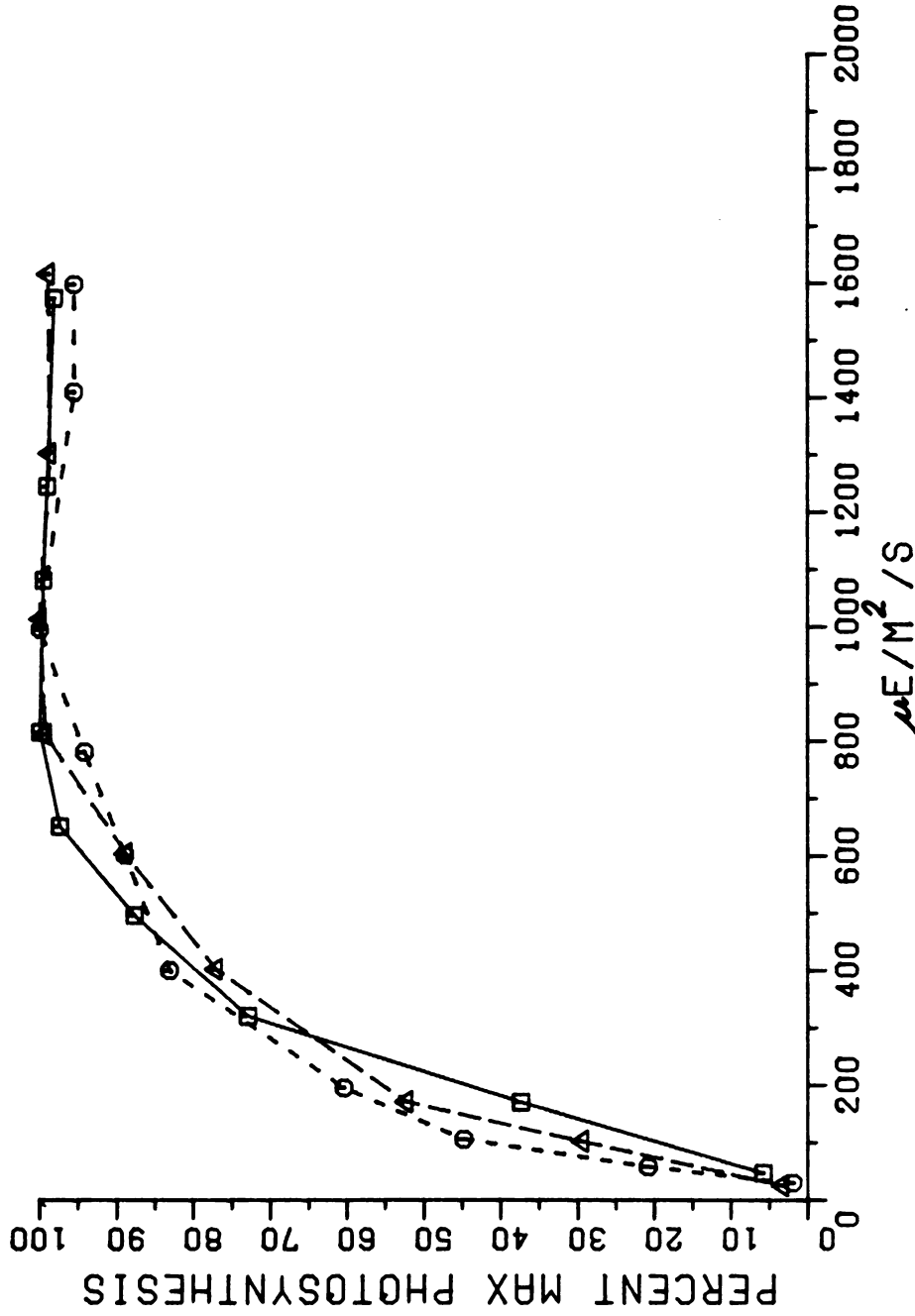
Figure 2.4. Light saturation of photosynthesis for L. leptolepis leaves from three crown positions. Symbols represent percent maximum net photosynthetic rate: Δ---Δ first major lateral branch foliage near the apex; □——□ terminal leader foliage near the apex; o---o mature leaves borne on the first major lateral branch. Maximum rates were 15.0, 15.4, 15.3 mg g^{-1} h^{-1}, respectively.
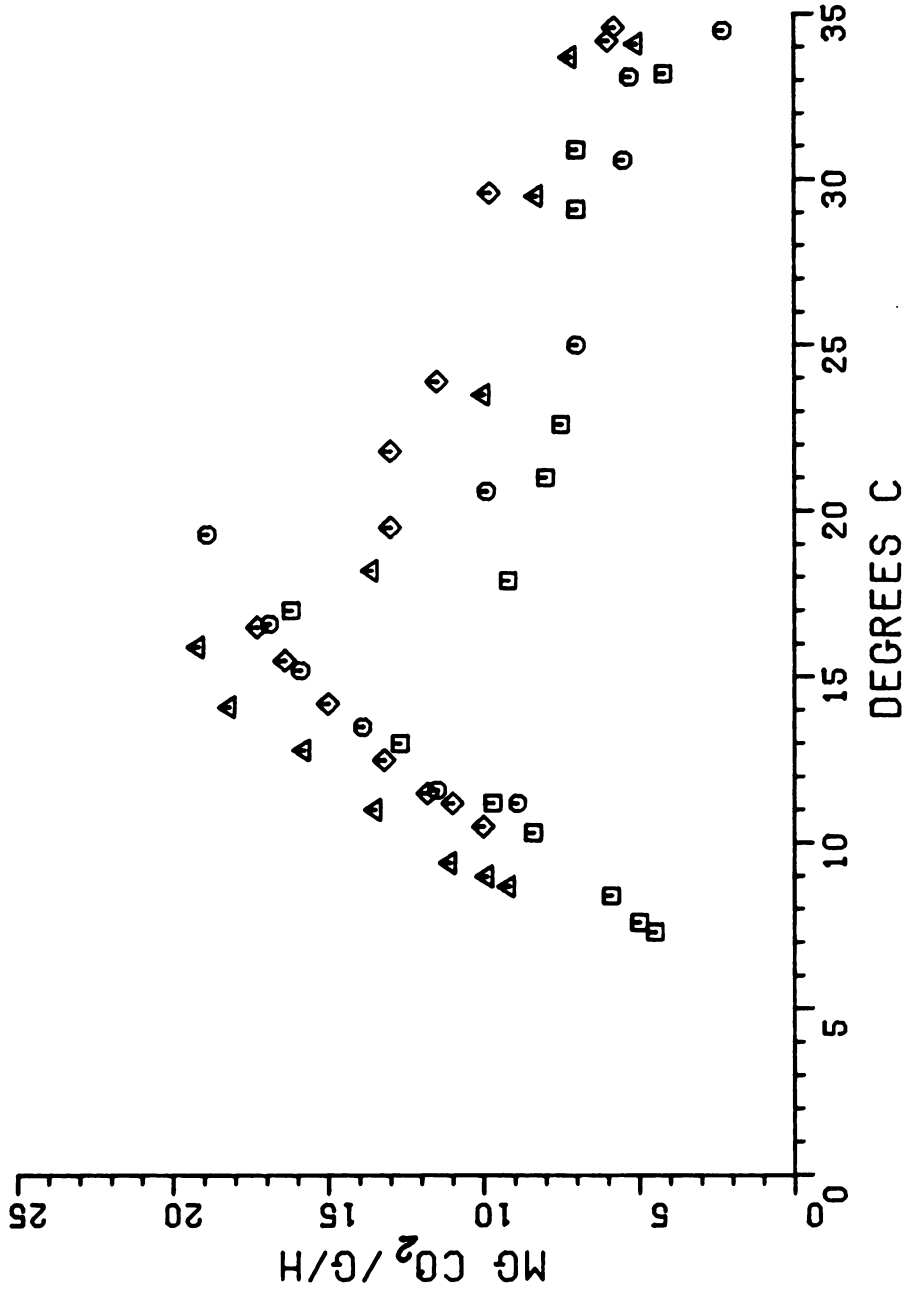
Figure 2.5. Photosynthetic response to temperature for *L. leptolepis* leaves borne on the terminal leader and measured at saturating $\overline{PPFD}$ (ca. 900 μE m^{-2} s^{-1}). Long shoot foliage included newly initiated and recently mature leaves near the apex. Different symbols represent replications.

Figure 2.6. Photosynthetic response to temperature for L. leptolepis leaves borne on the first major lateral branch and measured at saturating PPFD (ca. 900 μE m^{-2} s^{-1}). Long shoot foliage included newly initiated and recently mature leaves near the apex. Different symbols represent replications.

temperature on young foliage. Pn response to temperature curves for the terminal foliage of the first major lateral branch (Figure 2.6) were similar, except that maximum Pn values for all replications were higher than those in Figure 2.5. Response curves to temperature for mature leaves on the first major lateral branch displayed the greatest variation between replicates (Figure 2.7). The optimum temperatures for maximum Pn was less pronounced than in Figures 2.5 and 2.6, and the mature LS foliage appeared more tolerant to a broader range of temperatures.

The influence of temperature on growth, productivity and gas exchange of trees is dependent upon species and geographic origin (Hellmers 1963; Kramer 1957). The magnitude of temperature effects may also be modified by environmental variables such as light intensity, available CO_2, water, and preconditioning effects of environmental factors. In the present experiments, CO_2 exchange in response to temperature was determined in an open IRGA system at ambient CO_2 concentrations and saturation levels of PPFD. The trees were also greenhouse-grown and not allowed to become severely water stressed. The relatively constant temperature of the greenhouse may have had some preconditioning effects but results of previous work with larch indicate that this would be minimal. Growin et al. (1980) grew L. decidua at four constant temperatures ranging from 12 to 27°C. Optimal temperature for Pn, however, was 12°C for all growth temperatures.

The rate of photosynthesis in most temperate zone species increases from near 0°C to a maximum reached between 15 and 25°C (Kramer and Kozlowski 1979). Figure 2.8 illustrates the optimum range of temperature

Figure 2.7. Photosynthetic response to temperature for mature L. leptolepis leaves borne on the first major lateral branch and measured at saturating PPFD (ca. 900 μE m^{-2} s^{-1}). Different symbols represent replications.
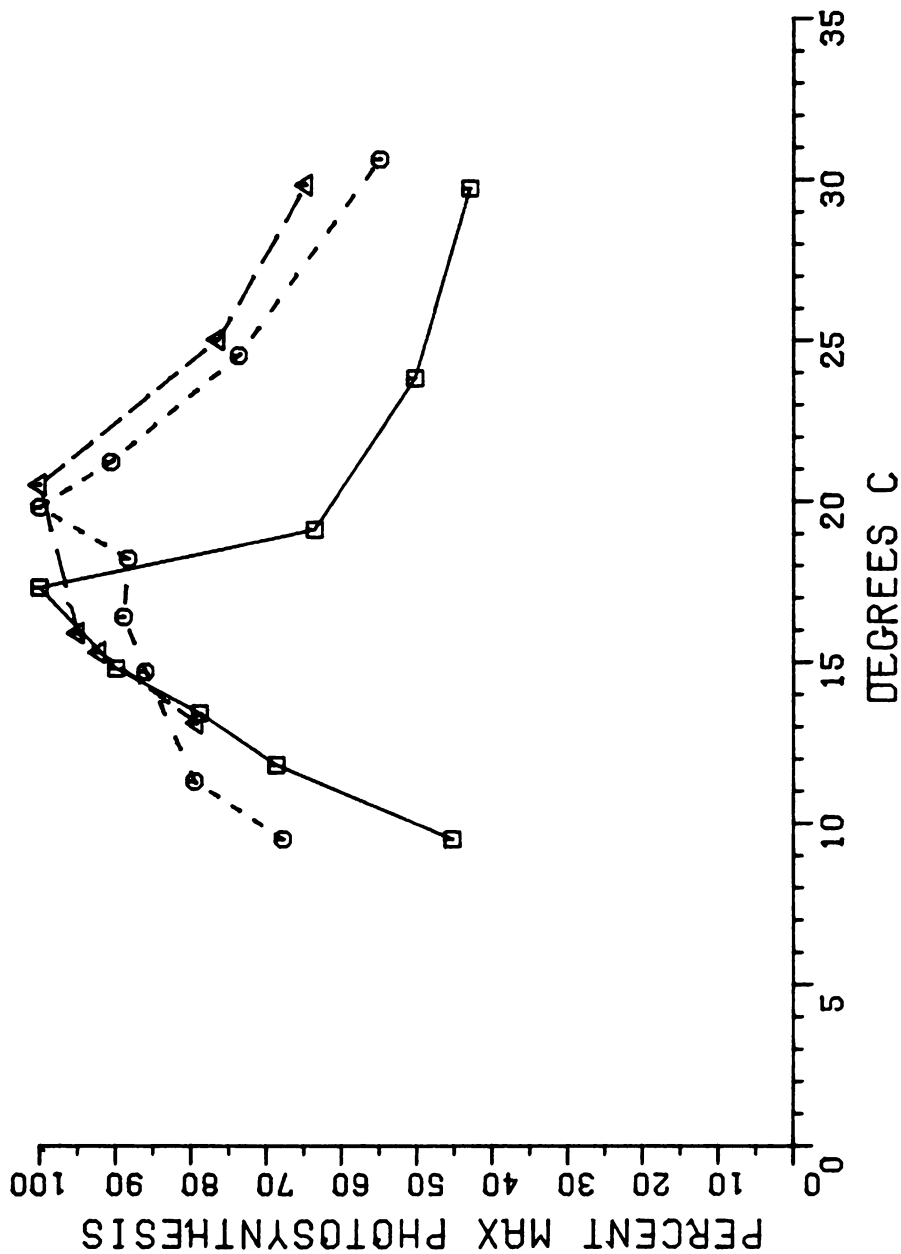
Figure 2.8. Optimum temperature for photosynthesis of L. leptolepis leaves from three crown positions and measured at saturation PPFD (ca 900 μE m^{-2} c^{-1}). Symbols represent percent maximum photosynthetic rate: ☐——☐ terminal leader foliage near the apex; $\triangle$----$\triangle$ first major lateral branch foliage near the apex; o----o mature leaves borne on the first major lateral branch. Maximum rates were 17.9, 21.6, and 17.1 mg g^{-1} h^{-1} respectively.

for the terminal and mature foliage obtained in this study. Average Pn
values are plotted as percent of maximum, which occurred between 17 and
21°C. This is consistent with temperature optimums established for C_3
species where maximum photosynthesis and quantum yield occur at tempera-
tures below 30°C (Björkman et al. 1975; Black 1973; Ehleringer and
Björkman 1977; Ehleringer 1979). The apparent sensitivity of terminal
leaves of the leader to temperature is also clearly shown in Figure 2.8,
but why the same degree of sensitivity was not shown by the terminal
leaves of the lateral branch is unexplained.

Transpiration rate. Changes in transpiration rate with increasing
light intensity for mature and newly initiated to recently mature leaves
borne on the first major lateral branch (same as Figures 2.2 and 2.3)
are presented in Figure 2.9 and 2.10, respectively. The curves resemble
those for Pn, although much more variation between replication values is
evident. Transpiration increased up to 800 to 1000 $\mu E\ m^{-2}\ s^{-1}$ then
leveled off, indicating that stomata were fully open at that light inten-
sity.

Transpiration rate response to temperature was determined on the
terminal leaves (Figure 2.11) and mature leaves proximal (Figure 2.12)
to the terminal leaves on a first major lateral branch. The rates of
transpiration below 20°C are consistent to those obtained for L. decidua
(Berger-Landefeldt 1936). Above 20°C transpiration rate increased
rapidly with temperature. Rates were determined at saturation PPFD
and the trees were well-watered so stomata apparently remained open up
to the maximum experimental temperature (31 to 33°C). These results
indicate that the rapid decrease in Pn above 20°C (Figures 2.5 to 2.8)
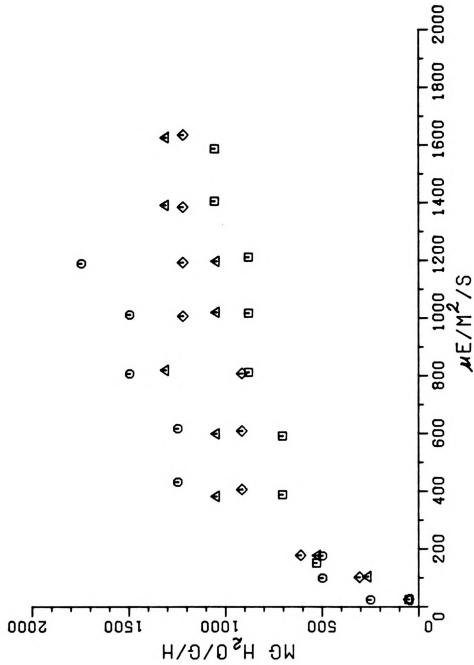
Figure 2.9. Transpiration rate response to light for _L. leptolepis_ leaves borne on the first major lateral branch. Long shoot foliage included newly initiated to recently mature leaves near the apex. Different symbols represent replications.
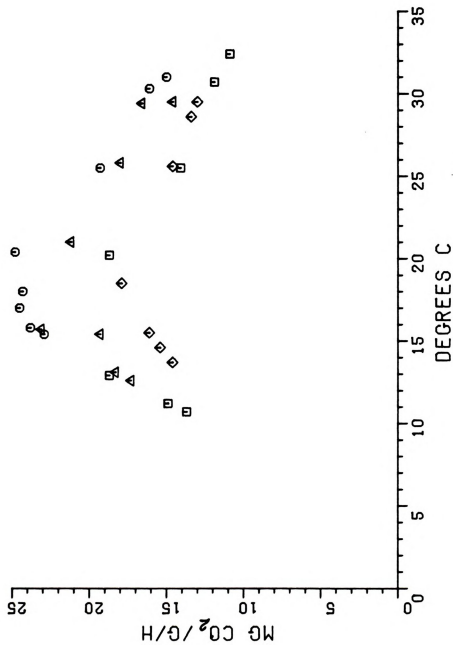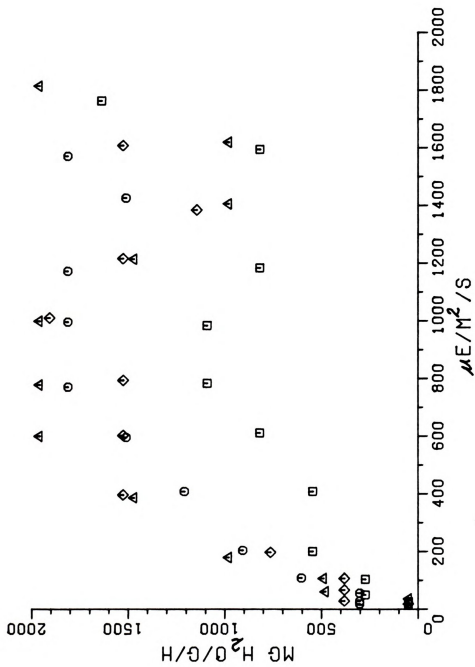
Figure 2.10. Transpiration rate response to light for mature L. leptolepis leaves borne on the first major lateral branch. Different symbols represent replications.
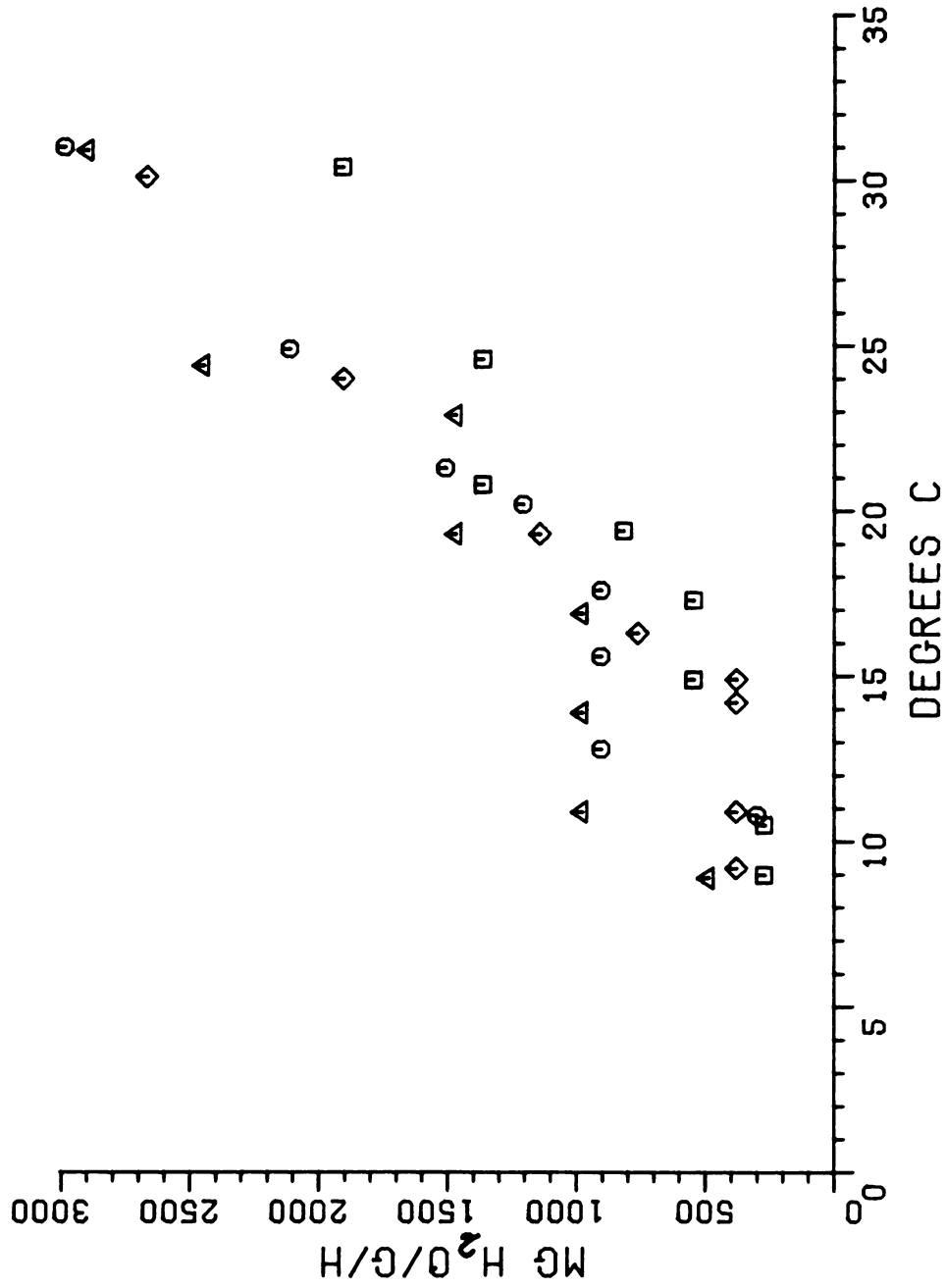
Figure 2.11. Transpiration rate response to temperature for _L. leptolepis_ leaves borne on the first major lateral branch and measured at saturating PPFD (ca. 900 μE m^{-2} s^{-1}). Long shoot foliage included newly initiated to recently mature leaves near the apex. Different symbols represent replications.
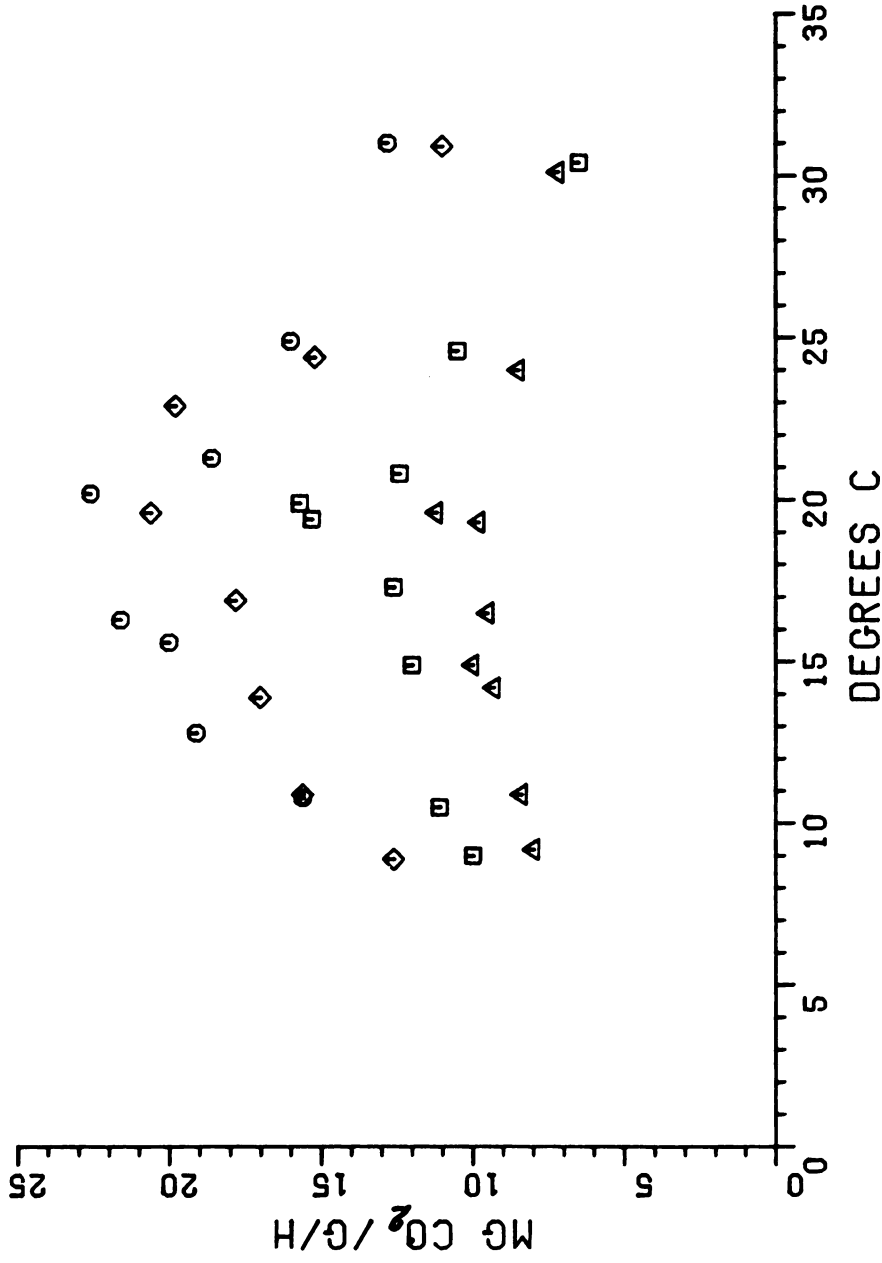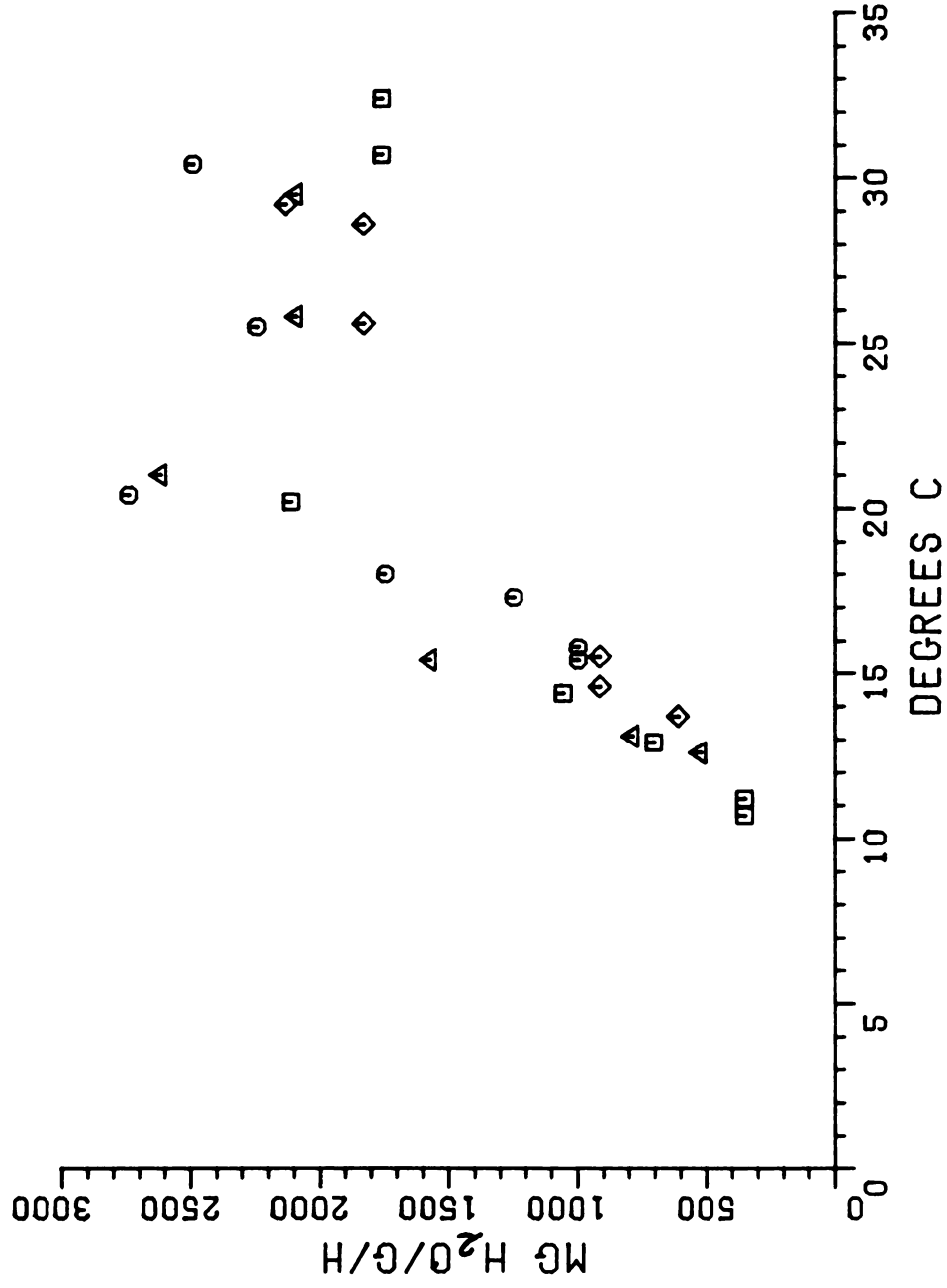
Figure 2.12. Transpiration rate response to temperature for mature L. leptolepis leaves borne on the first major lateral branch and measured at saturating PPFD (ca. 900 µE m^{-2} s^{-1}). Different symbols represent replications.

is due to internal factors and not stomatal closure. These internal factors would include antagonistic processes that increase with temperature and eventual inactivation of the CO_2-fixation apparatus at high temperature (Kramer and Kozlowski 1979). Investigations by Pisek et al. (1968, 1969) with different European conifers, including L. decidua, showed that this high cardinal, or compensation temperature, was passed at 36 to 38°C. Based on the rapid decline in the Pn above optimum (Figures 2.5 to 2.8), compensation temperature in the present study would probably have been close to those reported by Pisek et al. (1968, 1969).

CO_2 compensation concentration. The CO_2 compensation concentration of LS foliage was determined at various crown positions. Measurements were made at constant temperature and PPFD ranged from 300 to 600 $\mu E\ m^{-2}\ s^{-1}$. The lowest CO_2 compensation concentrations, 58 and 59 $\mu l\ l^{-1}$ were obtained with mature foliage borne on low and mid-crown branches. Foliage of the terminal leader had the highest CO_2 compensation concentration of 75 $\mu l\ l^{-1}$. These results agree with those obtained by Dickmann and Gjerstad (1973) who determined CO_2 compensation concentrations for numerous conifer and hardwood species, including L. decidua and L. laricina. The values they obtained for the larch species were mid-way between those obtained here with L. leptolepis and within the range of CO_2 compensation values for plant species with a C_3 photosynthetic pathway (Moss 1971).

Plant species that are intermediate between C_3 and C_4 have been reported (Kennedy and Laetsch 1974), and a large group of plants possessing crassulacean acid metabolism (CAM, a modified form of C_4 physiology)

are capable of shifting to C_3 photosynthesis (Ehleringer 1979; Hatsock and Nobel 1976). Woody arborescent plants, however, are of the C_3 type (Dickmann and Gjerstad 1973; Schaedle 1975). The only identified exceptions are the mangrove <u>Aegiceras majus</u> (Joshi et al. 1974) and several C_4 <u>Euphorbia</u> species of Hawaii (Pearcy and Troughton 1975).

Larch may have certain enzymatic characters similar to C_4 plants (Fry and Phillips 1976), but the photosynthetic responses to light and temperature determined in the present experiments were not suggestive of C_4 photosynthetic physiology. Light saturation occurred at a level below that characteristic of C_4 plants (Ehleringer and Björkman 1977; Björkman 1971; Gifford 1971; Leopold and Kriedemann 1975) while CO_2 compensation concentrations were within the range of C_3 species (Dickmann and Gjerstad 1973; Moss 1971). The optimum range of temperatures for maximum Pn was also well below that associated with species having C_4 physiology (Downton 1971). This low temperature optimum for <u>L</u>. <u>leptolepis</u> is probably indicative of its cool native habitat in the mountains of the Japanese island of Honshu. For larch species in general, their northern distribution and adaptation to some of the coolest regions of temperate zone forests is also not characteristic of the hot, dry habitats of most C_4 plants (Downton 1971; Stowe and Teeri 1978; Teeri and Stowe 1976).

CHAPTER III

14C-PHOTOSYNTHATE FROM SHORT SHOOTS AND LONG SHOOTS OF
MID- AND LATE-SEASON REDISTRIBUTION OF
MATURE <u>LARIX DECIDUA</u> TREES

Introduction

The contrasting growth of short shoots and long shoots of larch
(<u>Larix</u>) raise questions about the role each plays in the growth of the
whole tree. Long shoots increase tree height and lateral branch length,
with shoot extension continuing late into the growing season. They also
produce both early (preformed) and late (current season) leaves. This
seasonal pattern of leaf production and growth by long shoots resembles
that of "indeterminate" species such as <u>Populus</u> (Critchfield 1960) and
<u>Betula</u> (Kozlowski and Clausen 1966b). Short shoots, on the other hand,
arise from preformed primordia and complete expansion early in the
season. This resembles the determinant or fixed growth of species like
<u>Pinus</u>, <u>Acer</u>, or <u>Fagus</u>. The contribution, however, that one shoot type
makes to the growth of the other and of both to the tree as a whole is
not well understood.

According to Clausen and Kozlowski (1967), early long shoot growth
of <u>Larix laricina</u> was dependent upon stored reserves. Latter expansion
appeared to utilize current photosynthate produced by early leaves and
maturing late leaves. Short shoot growth was characterized by an early
flush of leaves followed by rapid leaf and shoot expansion which pre-
ceded long shoot growth. A similar pattern of growth has also been

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described for L. decidua (Tranquillini 1979) and L. occidentalis (Owens and Molder 1979a) and appears consistent in the genus.

The present study was performed to investigate the role of each shoot type during and after the period of vigorous long shoot growth. Leaves of long and short shoots borne on three-year-old branches of mature trees in the field were exposed to $^{14}CO_2$ and the translocation of fixed ^{14}C was traced at various times after exposure. This was done to further elucidate the photosynthetic contribution of each shoot type during this period of rapid growth.

Materials and Methods

Trees. This study was carried out at the Michigan State University, Department of Forestry Tree Research Center at East Lansing during the summer of 1980. Sample trees were Larix decidua Mill. planted in east-west windbreak rows and were 10 to 12 m in height. Experiments were performed on three-year-old first-order lateral branches located within 1 m of the top of the trees. Branch selection was based on age and similarity in length and vigor. Treatments were performed on foliage of three year short shoots (3YSS), two year short shoots (2YSS), and one year long shoots (1YTLS) borne on the third, second, and current seasons branch growth increments, respectively (Figure 3.1).

Translocation. On July 1 and August 10, short-shoot leaves borne on the middle portion of third- and second-year branch growth increments were exposed to $^{14}CO_2$ and allowed to photosynthetize for 1 h. Both distal and proximal portions of each branch increment relative to exposed
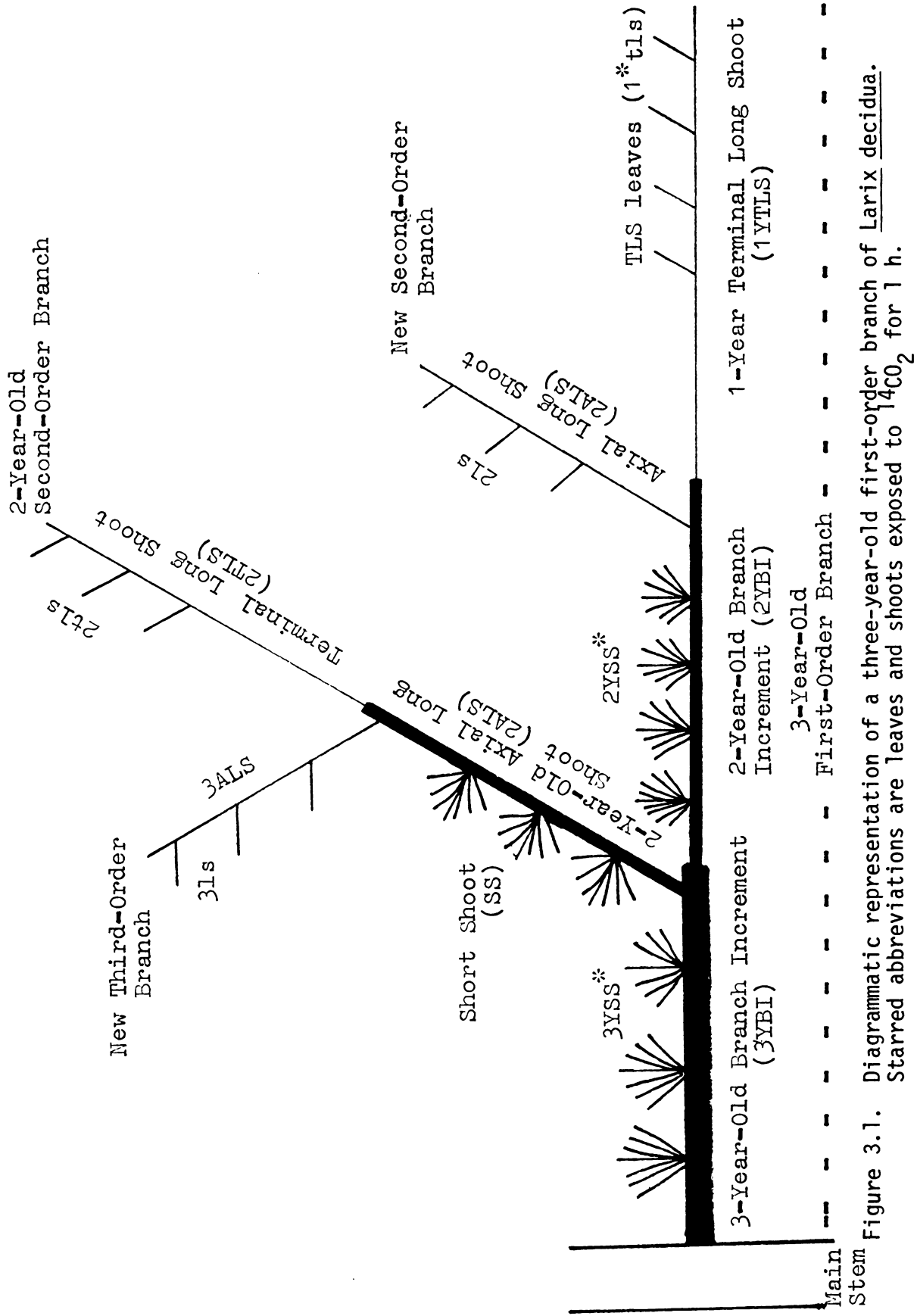
Figure 3.1. Diagrammatic representation of a three-year-old first-order branch of Larix decidua. Starred abbreviations are leaves and shoots exposed to $^{14}CO_2$ for 1 h.

foliage remained unlabeled. The same labeling procedure was applied
to all long shoot leaves of the current season's terminal long shoot.
A 4 ml beaker containing 0.1 mg $Ba^{14}CO_3$ (specific activity 277 µC mg^{-1})
was attached to each treated branch section and then enclosed in a
20 X 36 cm Mylar bag. Bag ends were sealed around the branch using foam
strips and wire ties. $^{14}CO_2$ was generated inside the bags by inserting
the needle of a 5 cc syringe through the bag and dispensing 2.0 ml
lactic acid (20% v/v) into the beaker. The syringe was withdrawn and
the hole sealed with cellophane tape. The Mylar bags were periodically
agitated to mix the gas inside and then removed after 1 h. At 5, 24,
and 48 h after labeling branches were excised and a bark sample was taken
from the main stem, directly above and below each treated branch, with
a 6 mm cork borer. Bark samples, branches, and foliage were then frozen
at -25° C. After freezing, branches were partitioned into leaf and
shoot types and third- and second-year branch increments were further
divided relative to labeled foliage position. These were dried at 75° C
for 48 h and then weighed.

    The same experimental procedure was repeated on September 8, with
the following exceptions. $^{14}CO_2$ was generated inside Mylar bags by
adding 2.0 ml lactic acid (20% v/v) to 1.0 ml Na_2 $^{14}CO_3$ (specific activ-
ity 25 µC ml^{-1}), and a 72 h sample was taken in place of the one at 5 h.

    <u>Radioactive determination</u>. Dried samples were ground in an aspirated
Wiley mill to pass a 40 mesh sieve. Subsamples of 7.0 to 8.0 mg were
taken from ground samples and placed in low potassium glass scintillation
vials. Subsamples were rehydrated for 2 hours by first adding 2 drops
of 80% (v/v) ethanol followed by 5.0 ml PCS (Phase Combining Systems,

Amersham Corp.) and then allowed to dark equilibrate for 24 h. The amount of subsample radioactivity was determined by liquid scintillation spectrometry with a TriCarb 2002 liquid scintillation spectrometer (Packard Instrument Co. Inc.). Sample radioactivity was, background subtracted, quench corrected by channels ratio method and expressed as distintegrations per minute (dpm).

Results and Discussion

In _Larix_ species the first leaves to flush in spring emerge from preformed buds borne on short shoots (SS). The stem of short shoots elongates only about 1 mm per year so they resemble clusters of needles along lateral branches and the main stem. The leaves of short shoots develop rapidly, and are capable of net photosynthesis (Pn) soon after flushing (Tranquillini 1979). This usually precedes terminal extension growth by 1 to 2 months. Increases in tree height and branch length occur by extension of long shoots (LS) produced by buds borne at the tree apex and distal portions of branches. Long shoot buds contain preformed leaves which flush shortly after short shoot leaves and are fully expanded before vigorous LS growth occurs. Little internode extension occurs between these leaves and they appear as clusters at the base of LS. New leaves are initiated up the flanks of the LS apex and their inter-node extension is greater than that of basal leaves.

By the July 1 exposure of foliage to $^{14}CO_2$, LS in the upper crown had completed approximately 1/3 to 1/2 of their final growth increment. Short shoots had flushed several months previously, but their contribution

to LS growth before this time is undetermined. Short shoot foliage, however, was capable of high rates of Pn by late April and early May. On May 5, for example, rates of SS leaves averaged 12 mg CO_2 g^{-1} h^{-1} at 19° C and saturating Photosynthetic Photon Flux Density (PPFD) (Chapter II).

July distribution of ^{14}C-photosynthate. Recovery of ^{14}C-photosynthate in July, 5, 24, and 48 h after exposure of the three foliage positions is presented in Tables 3.1-3.3. Specific activity (dpm/mg sample dry weight) and percent of total recovered translocate (TRT, excludes activity not transported from leaves exposed to $^{14}CO_2$) are tabulated according to major branch component and bark samples. Total activity (dpm/sample) is greatly affected by sample size, whereas specific activity is indicative of the metabolic activity and requirement for photosynthate regardless of size or weight. Percent TRT is also affected by sample size, but reflects the relative mobility and requirement for photosynthate by eliminating the activity retained in exposed leaves.

Terminal LS retained most of the ^{14}C fixed and transported from LS foliage (Table 3.1). Over 85% of the ^{14}C transported out of LS leaves after 48 h was retained in LS, reflecting their vigorous growth and photosynthate requirement. The specific activity of LS leaves over the same period dropped by nearly one-half and can be attributed to transport to the LS as well as high respiratory loss associated with young leaves (Kozlowski and Keller 1966). Long shoot net photosynthetic capacity, however, exceeded the needs of their elongating shoot. This is seen in the early ^{14}C activity found in 2YBI, 3YBI, and the stem bark samples 5 h after exposure of LS leaves to $^{14}CO_2$. Much of this ^{14}C-photosynthate

Table 3.1. Distribution of ^{14}C in 3-year first-order branches of L. decidua expressed as specific activity (dpm/mg) and percent total recovered translocate (%TRT). Terminal long shoot leaves were exposed to $^{14}CO_2$ for 1 h on July 1, and branches were removed 5, 24, and 48 h after.

	5h		24h		48h	
	dpm/mg	%TRT	dpm/mg	%TRT	dpm/mg	%TRT
3YBI			65	.15	156	.45
SS leaves	16	.02	69	.04	108	1.5
2YBI			645	11.7	198	7.6
SS leaves	1947	31.3	15	.2	21	.5
2ALS	74	.87	487	2.4	17	.18
21s leaves			53	.68	179	4.3
1YTLS	18292	67.8	42752	84.9	11633	85.2
tls leaves*	59109	-	60871	-	30900	-
Bark above branch	15	<.01	69	.01	30	<.01
Bark below branch	6	<.01	196	.03	399	.18

*Foliage exposed to $^{14}CO_2$.

appears to be moving toward the main stem as indicated by the steady decrease in specific activity recovered from 2YBI with time of sample, while that in 3YBI and bark samples increased over the same period. The high specific activity in the 2YBI after 5 h may represent a transient pulse of early mobile photosynthetic products moving toward stronger sinks in the tree. The pathway in the main stem also appears to be directed toward the base of the tree, as higher specific activities were found in the bark samples taken below each branch.

Labeled 2YSS leaves actively transported ^{14}C-photosynthate to the 2YBI (Table 3.2). This accounted for over 99% of the TRT in the branch sampled at 5 h, and about 63% at 24 h. Approximately the same proportion was found in 2YBI at 48 h and appears to have been retained there. Short shoot elongation was completed previous to this time so the retained photosynthate may have been required for radial growth. Some ^{14}C activity was found in the 1YTLS at all sample times, but the 104 dpm/mg at 48 h accounted for less than 1% of the TRT for the branch. The majority of ^{14}C-photosynthate not retained in the 2YBI was found in the 3YBI and bark samples. Again, transport in the main stem was predominantly downward.

The distribution pattern of $^{14}CO_2$ fixed by 3YSS leaves is similar to that of 2YSS (Table 3.3). The direction of transport is mainly basipetal, with the majority of ^{14}C-photosynthate retained in the 3YBI. Again, some specific activity is found in the 1YTLS as well as 2YBI indicating bidirectional translocation of photosynthate. Considerably more ^{14}C-photosynthate entered the main stem from 3YSS, however, than from younger branch sections. The specific activity of the bark sample

Table 3.2. Distribution of ^{14}C in 3-year first-order branches of L. decidua expressed as specific activity (dpm/mg) and percent total recovered translocate (%TRT). Second-year short shoot leaves were exposed to $^{14}CO_2$ for 1 h on July 1, and branches removed 5, 24, and 48 h after.

	5h		24h		48h	
	dpm/mg	%TRT	dpm/mg	%TRT	dpm/mg	%TRT
3YBI	29	.2	103	34.0	413	35.6
SS leaves	52	.05	54	2.4	18	.21
2ALS[a]	63	.49			4	.21
2YBI	50416	99.3	3752	62.6	2279	61.6
SS leaves*	13997	-	6388	-	14364	-
2ALS			4	.13	46	.64
2ls leaves					21	.84
1YTLS	4	<.01	5	.05	104	.31
tls leaves	3	<.01			24	.15
Bark above branch			32	.02	15	<.01
Bark below branch			73	.05	70	<.01

*Foliage exposed to $^{14}CO_2$.

[a]Includes all foliage, 2TLS, 3ALS, borne on 2ALS.

Table 3.3. Distribution of ^{14}C in 3-year first-order branches of L. decidua expressed as specific activity (dpm/mg) and percent total recovered translocate (%TRT). Third-year short shoot leaves were exposed to $^{14}CO_2$ for 1 h on July 1, and branches removed 5, 24, and 48 h after.

	5h dpm/mg	5h %TRT	24h dpm/mg	24h %TRT	48h dpm/mg	48h %TRT
3YBI						
SS leaves*	7197	97.5	707	92.8	5829	90.6
	41584	-	15524	-	23099	-
SS leaves	2565	1.7	58	1.2	775	7.7
2ALSa	63	.75	10	.80	4	.7
2YBI						
SS leaves	8	.05	5	.24	6	.23
					15	.25
2ALS	306	.01	12	.48	8	.12
21s leaves	305	.04	11	.9	11	.4
1YTLS						
tls leaves	7	<.01	5	.05	11	.05
			3	.41	9	.05
Bark above branch	50	<.01	27	.02	8	<.01
Bark below branch	10	<.01	2979	2.5	907	.06

*Foliage exposed to $^{14}CO_2$

aIncludes all foliage, 2TLS, 3ALS, borne on 2ALS.

below the treated branch represented over 2% of the TRT, and as indicated by the previous treatments (Tables 3.1 and 3.2), the majority of ^{14}C translocated to the main stem was directed toward the base of the tree. Rangnekar et al. (1969) reported similar downward transport of ^{14}C fixed by third-whorl lateral branches of _Pinus resinosa_ trees, whereas transport from the second whorl was predominantly upward. The position of third-whorl branches in the Rangnekar et al. study would be in approximately the same nodal position as the 3-year branches in the experiments described here.

The primary function of leaves on 2YSS and 3YSS in July appears to be providing photosynthate for maintenance of the branch section bearing them. Some excess photosynthate is translocated basipetally out of these branch sections, with the majority moving toward the main stem and the rest acropetally to the 1YTLS. That bidirectional translocation in these branch sections occurred is indicated by some basipetal movement of ^{14}C-photosynthate from the 1YTLS (Table 3.1). The reason for transport to the 1YTLS from 2YSS and 3YSS is unclear in view of the excess ^{14}C fixed by 1YTLS leaves and transported to the main stem. Young expanding leaves of _Populus deltoides_, however, have been shown to simultaneously import and export photosynthate (Gordon and Larson 1968), and a similar pattern may have been present in the LS leaves. Larson and Dickson (1973) also reported that the direction of import or export by leaves was dependent on the phyllotactic vascular connection between, and the distance from, other importing or exporting leaves.

The relative contribution of the foliage on various shoot types to the three branch increments is presented in Figure 3.2. By July the
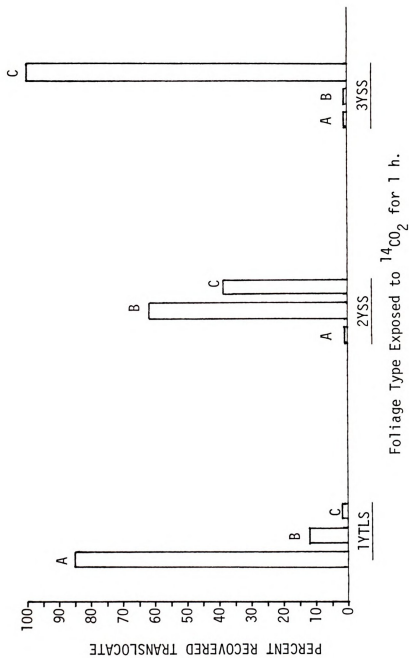
Figure 3.2 Relative distribution of recovered ^{14}C-translocate in (A) 1YTLS, (B) 2YBI, and (C) 3YBI 48 h after exposing different shoot foliage to $^{14}CO_2$ on July 1.

translocation pattern appeared almost exclusively basipetal. The foliage of each shoot type was capable of producing photosynthate in excess of that required locally. Further, the TLS appeared autonomous and able to support its own vigorous growth. This is similar to findings reported for other species that produce distinctly different short shoots and long shoots, e.g., apple (Hansen 1967).

August distribution of ^{14}C-photosynthate. Long shoots displayed a gradient of growth activity from upper to lower crown positions by the August 10 treatment of shoots with ^{14}C$_2$. The terminal leaders of trees were still actively growing and apical buds were not observed on long shoots of upper crown branches. The frequency of bud set increased toward the base of the tree, and long shoots without apical buds were not evident on branches above mid-crown.

The distribution of ^{14}C obtained after the August 10 treatment was similar to that of July 1 and is presented in Tables 3.4 to 3.6. Leaves on 1YTLS were exporters of ^{14}C-photosynthate as suggested by the specific activity found in older branch sections and the stem bark samples (Table 3.4). Again, the specific activity of 2YBI was high after 5 h and then decreased in 24 and 48 h samples. Conversely, the specific activity in 3YBI increased with time of sampling while transport to the main stem from 1YTLS was highest at 24 h, with more ^{14}C heading downward. These results further suggest that LS leaves on August 10 are capable of producing more photosynthate than required to maintain the growth of LS.

Some acropetal translocation of ^{14}C-photosynthate to the 1YTLS from 2YSS and 3YSS leaves was evident on August 10, but the majority

Table 3.4. Distribution of ^{14}C in 3-year first-order branches of L. decidua expressed as specific activity (dpm/mg) and percent total recovered translocate (%TRT) Terminal long shoot leaves were exposed to $^{14}CO_2$ for 1 h on August 10, and branches removed 5, 24, and 48 h after.

	5h		24h		48h	
	dpm/mg	%TRT	dpm/mg	%TRT	dpm/mg	%TRT
3YBI	8	.02	56	.1	253	1.3
SS leaves			47	.08	193	1.8
2YBI	1368	23.6	322	18.5	159	4.1
SS leaves	53	.6	10	.08	10	.3
2ALS			268	1.4	5	.1
2ls leaves			38	.47	155	7.4
1YTLS	14605	75.6	28286	79.2	19940	85.0
tls leaves	43339	–	41871	–	23561	–
Bark above branch	10	<.01	1628	.2	17	<.01
Bark below branch	3	<.01	4145	.42	470	.1

*Foliage exposed to $^{14}CO_2$.

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of movement appeared to be basipetal (Tables 3.5 and 3.6). Foliage on both the 3YBI and 1YTLS contributed substantial photosynthate to the main stem as the high specific activity recovered from the bark samples indicate.

The contribution of foliage on each shoot type to the three branch sections in August is seen in Figure 3.3. The pattern of distribution was similar to that obtained in July, but the proportion of ^{14}C-photosynthate translocated to older branch sections increased slightly. ^{14}C translocated from 1YTLS and recovered in 2YBI and 3YBI was about 2% higher and that from 2YBI to 3YBI about 7% higher than in July.

September distribution of ^{14}C-photosynthate. Recovery of ^{14}C-photosynthate 24, 48, and 72 h after exposure of the three foliage positions in September is presented in Tables 3.7 to 3.9. By September 8, apical buds had formed on the LS of upper crown branches, but the last LS leaves initiated were still immature. There was no visual evidence of bud set, however, in the terminal leaders at this time.

Compared to July and August, the specific activity of labeled leaves borne on all shoots decreased appreciably with time after treatment. Mobilization of fixed ^{14}C and basipetal transport was still very active, but increased respiratory loss could also have added to the decreased ^{14}C in labeled foliage. Ursino et al. (1968) found that over 50% of the ^{14}CO$_2$ incorporated by Pinus strobus seedlings late in the season was lost through respiration.

The predominant direction of ^{14}C transport in September was still basipetal, as was found in July and August, but greater proportion was translocated to 1YTLS from 2YSS at each sample time (Table 3.8).

Table 3.5. Distribution of ^{14}C in 3-year first-order branches of L. decidua expressed as specific activity (dpm/mg) and percent total recovered translocate (%TRT). Second-year short shoot leaves were exposed to $^{14}CO_2$ for 1 h on August 10, and branches removed 5, 24, and 48 h after.

	5h		24h		48h	
	dpm/mg	%TRT	dpm/mg	%TRT	dpm/mg	%TRT
3YBI						
SS leaves	13	1.4	177	35.2	357	42.8
	39	.4	33	1.9	28	.11
2ALS[a]	87	3.5				
2YBI						
SS leaves*	4582	94.5	2724	61.5	2640	55.8
	17461	-	4167	-	2179	-
2ALS			8	.21	32	.54
21a leaves	8	.09	9	.33	12	.67
1YTLS						
tls leaves	5	.01	8	.09	88	.25
	5	.02	3	.08	10	.19
Bark above branch			24	.04	9	<.01
Bark below branch			89	.09	87	.04

*Foliage exposed to $^{14}CO_2$.

[a]Includes all foliage, 2TLS, 3ALS, borne on 2ALS.

Table 3.6. Distribution of ^{14}C in 3-year first-order branches of L. decidua expressed as specific activity (dpm/mg) and percent recovered total translocate (%TRT). Third-year short shoot leaves were exposed to $^{14}CO_2$ for 1 h on August 10, and branches removed 5, 24, and 48 h after.

	5h		24h		48h	
	dpm/mg	%TRT	dpm/mg	%TRT	dpm/mg	%TRT
3YBI						
SS leaves*	2373 34448	93.3	820 33569	91.6 –	4695 16374	89.9 –
SS leaves	1891	3.5	65	2.3	455	6.1
2ALSa	77	2.4				
2YBI						
SS leaves	9	.2	12 7	.95 .3	8 11	.15 .19
2ALS	10	.28	8	.24		
2ls leaves	14	.27				
1YTLS						
t1s leaves	6	<.01	8 24	.1 .73	8	.08
Bark above branch	34	.01	38	.07	4	<.01
Bark below branch	7	<.01	1863	1.6	733	.09

*Foliage exposed to $^{14}CO_2$.

aIncludes all foliage, 2TLS, 3ALS, borne on 2ALS.
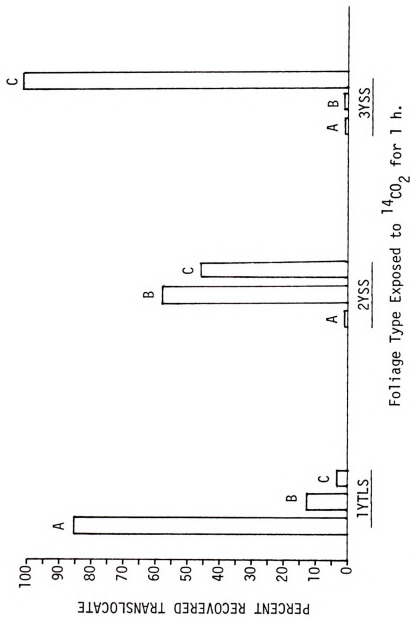
Figure 3.3. Relative distribution of recovered ^{14}C-translocate in (A) 1YTLS, (B) 2YBI, and (C) 3YBI 48 h after exposing different shoot foliage to $^{14}CO_2$ on August 10.

Table 3.7. Distribution of ^{14}C in 3-year first-order branches of L. decidua expressed as specific activity (dpm/mg) and percent total recovered translocate (%TRT). Terminal long shoot leaves were exposed to $^{14}CO_2$ for 1 h on September 8, and branches removed 24, 48, and 72 h after.

	24h dpm/mg	24h %TRT	48h dpm/mg	48h %TRT	72h dpm/mg	72h %TRT
3YBI	248	2.7	538	5.5	497	4.5
SS leaves	22	.29			13	.04
2YBI	1188	16.3	966	11.3	684	19.0
SS leaves	9	.2			22	.3
2ALS					269	.08
21s leaves					391	.16
1YTLS	5958	79.5	5018	82.8	426	75.5
t1s leaves*	24691	-	24171	-	6804	-
Bark above branch	801	.63	31	.04	43	.03
Bark below branch	221	.21	114	.16	191	.13

*Foliage exposed to $^{14}CO_2$.

Table 3.8. Distribution of ^{14}C in 3-year first-order branches of L. decidua expressed in specific activity (dpm/mg) and percent total recovered translocate (%TRT). Second-year short shoot leaves were exposed to $^{14}CO_2$ for 1 h on September 8, and branches removed 24, 48, and 72 h after.

	24h		48h		72h	
	dpm/mg	%TRT	dpm/mg	%TRT	dpm/mg	%TRT
3YBI						
SS leaves	553	53.2	1066	26.0	3195	48.5
2ALS[a]	76	1.0			9	.44
2YBI						
SS leaves*	3029	43.1	1291	70.0	911	47.6
2ALS	22532	-	8814	-	8296	-
2ls leaves					163	.31
1YTLS	324	.68	244	.61	1330	1.3
tls leaves	104	1.7	5	.18		
Bark above branch	24	.01	685	1.4	8	<.01
Bark below branch	548	.27	441	1.1	80	.10

*Foliage exposed to $^{14}CO_2$.

[a]Includes all foliage, 2TLS, 3ALS, borne on 2ALS.

This is also seen in the movement of ^{14}C fixed by 3YSS to 1YTLS and 2ALS after 24 h but not later (Table 3.9). It appears that the contribution of older SS to newer LS was greater late in the season than in July when vigorous LS growth occurred. Higher specific activities were also found in the main stem bark samples above the treated branch than earlier in the season. After 72 h, however, 3YBI still retained a large proportion of assimilated ^{14}C. This suggests that photosynthate is required for cambial growth or storage at this time in the growing season.

Distribution of translocated ^{14}C 72 h after foliage on various shoot types were labeled is presented in Figure 3.4. The recovered portion of ^{14}C fixed by TLS leaves and transported to 1YTLS was less than found in July or August, but the proportion transported to 2YBI and 3YBI increased. This reflects the termination of long shoot extension and increased excess photosynthate available for other areas of growth. Approximately equal amounts of ^{14}C-photosynthate were translocated from 2YSS to 2YBI and 3YBI, and a small amount was recovered in 1YTLS. Only a trace of the ^{14}C fixed by 3YSS was recovered in the 2YBI with the majority retained by 3YBI for local use or transported to the main stem.

The growth and development of LS from early July through the rest of the season is apparently largely autonomous and self-sustained. Long shoot extension was only 50% completed by July 1, but very little ^{14}C fixed by SS leaves on older branch sections was translocated to growing LS. Similar results in July were observed with young Pinus strobus where small amounts of photosynthate were translocated to current seasons needles from old needles (Shiroya et al. 1966). New needle and

Table 3.9. Distribution of ^{14}C in 3-year first-order branches of L. decidua expressed as specific activity (dpm/mg) and percent total recovered translocate (%TRT). Third-year short shoot leaves were exposed to [14]CO_2 for 1 h on September 8, and branches removed 24, 48, and 72 h after.

	24h dpm/mg	24h %TRT	48h dpm/mg	48h %TRT	72h dpm/mg	72h %TRT
3YBI SS leaves*	1688	89.7	1321	97.7	2838	97.8
SS leaves	1913	-	5105	-	410	-
2ALS[a]	302	2.2	415	.82	7	.64
	240	2.2			4	.35
2YBI SS leaves	341	.71				
2ALS	18	.48			5	.48
	16	.56				
21s leaves	19	1.2				
1YTLS	583	1.2				
t1s leaves	17	1.2				
Bark above branch	52	.09	305	.74	143	.03
Bark below branch	220	.32	245	.71	856	.26

*Foliage exposed to [14]CO_2.

[a]Includes all foliage, 2TLS, 3ALS, borne on 2ALS.
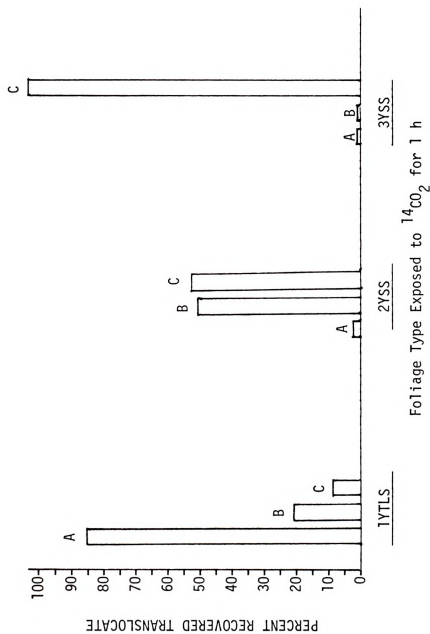
Figure 3.4. Relative distribution of recovered ^{14}C-translocate in (A) 1YTLS, (B) 2YBI, and (C) 3YBI 72 h after exposing different shoot foliage to $^{14}CO_2$ on September 8.

shoot expansion of pine is at or near completion by July and new needle maturity is reached shortly thereafter. The role of new leaves of conifers has been shown to shift from net importers to net exporters of photosynthate about this time (Gordon and Larsen 1968; Loach and Little 1973). Larch LS, however, were exporting ^{14}C-photosynthate when shoot and leaf expansion was only 50% complete.

The role of SS leaves in the current-season growth of LS is apparently very minimal by July. Short shoot leaves flush, expand rapidly, and photosynthesize for over two months before vigorous LS expansion occurs. Their contribution prior to July, when they function as previous-season's needles of other conifers, is probably considerable. Old needles in _Pinus resinosa_ have been shown by tracer studies to be very important in early season growth of new needles and shoots (Dickmann and Kozlowski 1970a, 1970b; Rangnekar and Forward 1969; Schier 1970). The role of old needles as exporters of photosynthate diminishes, however; when new shoot maturation is completed, these new needles then become the major producers (Gordon and Larson 1968; Loach and Little 1973; Ursino and Paul 1973). The phenologically older leaves of larch SS do not seem to fit this pattern.

Table 3.10 shows the specific activity of sections of 2- and 3-year branch internodes bearing SS leaves when leaves on the middle section were exposed to ^{14}CO$_2$. These data indicate that SS export considerable photosynthate to their supporting branches and elsewhere in the tree late into the growing season. The low activity found in sections distal to the treated leaves probably reflects the autonomous LS growth. This uneven distribution of specific activity also suggests that each short
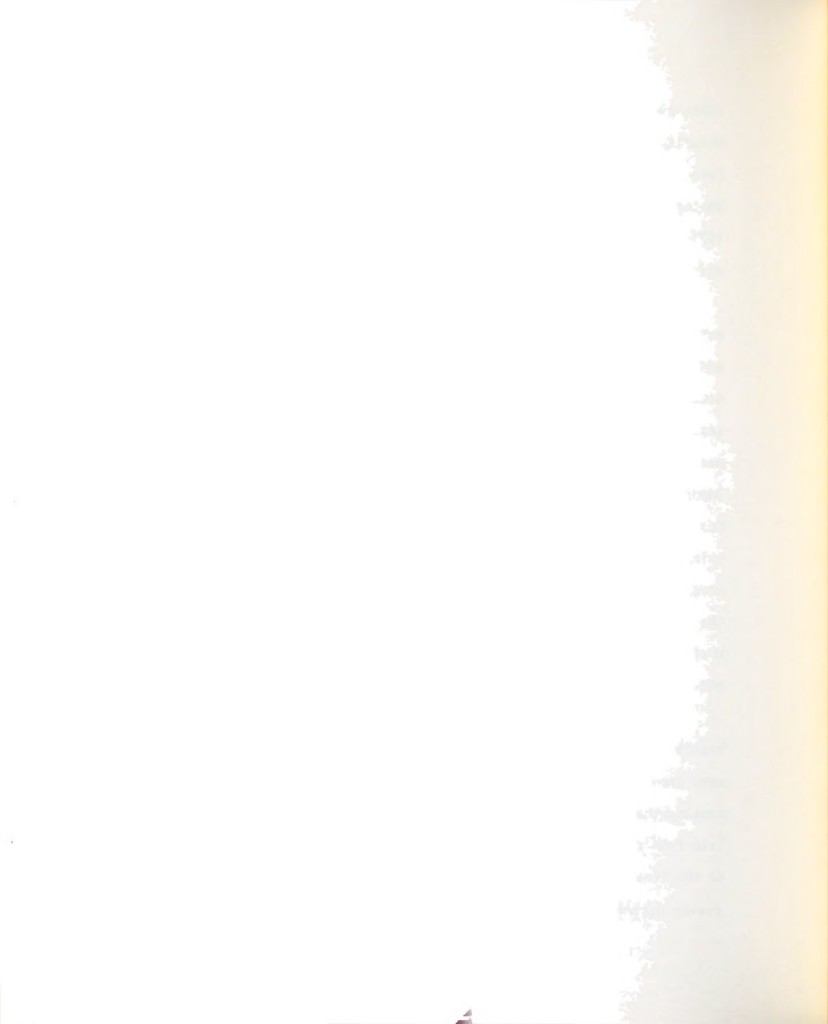
Table 3.10. Movement of ^{14}C in the 2- and 3-year branch internodes of 3-year branches relative to the section of each internode exposed to $^{14}CO_2$ for 1 h. Figures are specific (dpm/mg) obtained in partitioned branch sections.

	July			August			September		
	5 h	24 h	48 h	5 h	24 h	48 h	24 h	48 h	72 h
Partitioned 2YBI									
Acropetal			41			42			-
Labeled			2382			1953			706
Basipetal			2247			1864			1206
Partitioned 3YBI									
Acropetal		45	17	52	33	16	16	7	-
Labeled		3046	1704	3263	2730	1389	352	350	216
Basipetal		3099	823	2163	2867	754	583	612	211

shoot provides photosynthate for the growth of the portion of branch bearing it. The surplus, represented by the specific activity in sections proximal to the treated leaves, would be available for other growing tissues such as roots or stem cambium.

Long shoots of larch increase tree height and extend lateral growth of branches. Their vigorous growth lags behind that of SS and initially is at the expense of the phenologically older SS leaves. This would be similar to the pattern shown in non-deciduous conifer species. The results of these experiments, however, suggest that expanding LS of larch differ from other conifer species by becoming net exporters of photosynthate long before shoot and leaf expansion is completed. Short shoots resemble the prior-season needles of other conifers in that they are borne on older branch sections and produce leaves capable of net photosynthesis early in the season. Unlike previous season needles, leaves and SS are actually current-season growth and function as new shoots late in the season when they export large amounts of photosynthate.

CHAPTER IV

SUMMARY AND CONCLUSIONS

In the first series of experiments an infrared differential open gas analysis system was utilized to determine the effect of light intensity and temperature on net photosynthetic (Pn) and transpiration rate for leaves of three-year-old _Larix leptolepis_ trees. Immature to recently mature, and mature long shoot (LS) foliage was used for these measurements. This foliage was borne on the terminal leader or first major branch apex, and interior branch, respectively. Similar foliage was sealed inside Mylar bags and CO_2 depletion of the air inside bags was measured by infrared gas analysis to determine CO_2 compensation concentration.

The net photosynthetic response to increasing levels of photosynthetic photon flux densities (PPFD) was similar for each foliage position and stage of leaf maturity. Light compensation was between 25 and 50 $\mu E \ M^{-2} \ s^{-1}$. Rates of Pn increased rapidly at PPFD above compensation intensity until saturation was reached at approximately 900 $\mu E \ m^{-2} \ s^{-1}$. This hyperbolic pattern of Pn response to light is characteristic for multiple leaves of plant species possessing a C_3 photosynthetic pathway.

Dark respiration rates for all foliage positions ranged from 0.9 to 1.8 mg $CO_2 \ g^{-1} \ h^{-1}$. A post illumination burst of CO_2 was not detected.

Photosynthetic response to temperature was determined at saturating PPFD. Net photosynthetic rates of terminal leader foliage increased steadily from low temperatures to an optimum between 15 and 20° C. At temperatures above 20° C Pn decreased rapidly reflecting the sensitivity of the young foliage to adverse high temperature. Similar photosynthetic response to increasing temperature was obtained for the branch terminal foliage. Maximum Pn, however, was higher for all replications of this foliage position than observed with the leader foliage. Mature leaves of the first major lateral branches had a slightly broader range of optimum temperature than found for the terminal foliage positions. The adverse effect of temperature on Pn above optimum range also appeared less pronounced for mature leaves. Maximum Pn for all foliage positions occurred between 17 and 21° C, comparable to other north temperate trees. This was also consistent with the optimum temperatures for Pn established for C_3 plants.

Transpiration rates obtained for terminal and mature foliage of branches at increasing levels of PPFD resembled Pn response to light. Temperature was maintained at 20° C so rising transpiration rates appeared to be due to stomatal response to increasing PPFD. Transpiration rate leveled between 800 and 1000 $\mu E\ m^{-2}\ s^{-1}$ and remained fairly steady at higher PPFD.

Results of the transpiration rate response to increasing temperature indicated that the rapid decline in Pn above optimum range of temperature was due to internal factors and not stomatal closure. Transpiration rates increased continuously with rising temperature up to the experimental maximum. Rates of Pn, however, declined rapidly when temperature

exceeded the optimum range. If this decrease in Pn had been due to stomatal closure a similar decrease in transpiration rate would have been expected.

The CO_2 compensation concentration was determined for LS foliage at various crown positions. PPFD ranged between 300 and 600 $\mu E\ m^{-2}\ s^{-1}$ and temperature inside bags remained constant. The lowest CO_2 compensation concentrations were 58 and 59 $\mu l\ l^{-1}$ for the mature foliage of low and mid-crown branches respectively. The foliage borne at the apex of the terminal leader had the highest CO_2 compensation concentration or 75 $\mu l\ l^{-1}$. These values are similar to those obtained for other trees and plant species possessing a C_3 photosynthetic pathway.

In a second series of experiments leaves of both long and short shoots borne on three-year-old first order branches of mature L. decidua were exposed to $^{14}CO_2$ and the distribution of fixed ^{14}C was traced at various times after exposure. This was done on July 1, August 10, and September 8, and followed the course of long shoot growth from a period of rapid expansion to early bud set. Labelled foliage included short shoots (SS) borne in the middle of 3-year and 2-year branch increments (3YBI and 2YBI respectively) or 1-year terminal long shoots (1YTLS; current season increment).

In July, the vigorous growth of long shoots (LS) was approximately 50% completed and SS expansion had ceased approximately two months prior to this. At this time the majority of ^{14}C fixed and transported by LS leaves was retained in 1YTLS. Basipetal transport of ^{14}C-photosynthate, however, was detected in 2YBI, 3YBI and main stem as early as 5 h after exposing TLS leaves to $^{14}CO_2$. This indicated the 1YTLS leaves were

capable of producing photosynthate in excess of that required to support the rapid LS growth. The majority of ^{14}C fixed by 2-year short shoots (2YSS) was transported to the 2YBI where over 60% of the total recovered translocate (TRT) was retained 48 h after labelling 2YSS leaves. The predominant direction of movement of ^{14}C out of the 2YBI was basipetal to the 3YBI and main stem, but a small amount of ^{14}C was moved acropetally to the 1YTLS. This was less than 1% of the TRT. ^{14}C fixed by 3YSS was primarily transported to the 3YBI and retained for local use. Again a small portion of ^{14}C was transported to the 2YBI and 1YTLS, indicating bidirectional translocation, but most of that not retained in 3YBI was moved to the main stem. Movement of ^{14}C in the main stem from all branch increments was predominantly downward.

The distribution of ^{14}C-photosynthate transported out of labelled foliage in August was similar to that observed in July. Basipetal translocation from all shoots, however, was slightly increased in August. Terminal long shoot growth at this time was near completion and ^{14}C exported basipetally from 1YTLS after 48 h was approximately 2% higher than observed in July. The amount of basipetal transport of ^{14}C from 2YBI and 3YBI in August was also approximately 7% higher than in July.

Terminal long shoots of 3-year-old branches had recently set bud by September 8, but the last leaves initiated near the apex were still immature. Tree terminal leaders, however, were still actively expanding. The proportion of acropetal transport from 2YBI was higher than observed in July or August, but the majority of ^{14}C translocated from all foliage positions was still basipetal. 1YTLS actively exported to older branch increments and retained proportionally less ^{14}C-photosynthate reflecting

termination of LS expansion. ^{14}C fixed and transported by 2YSS leaves
was about equally distributed between 2YBI and 3YBI 72 h after labelling
foliage. The majority of labelled photosynthate from 3YSS leaves was
also retained in the 3YBI for local use. Even though the proportion of
^{14}C retained in 2YBI and 3YBI for local growth and storage was increased
over that in July or August, the specific activity in bark samples of the
main stem also increased. The proportion of this activity detected
above the branch was higher than observed previously and may be attributed
to the continued growth of the terminal leader.

The results of these experiments suggest that LS growth and develop-
ment is largely self-supported by early July when expansion is less than
50% completed. Active export of ^{14}C-photosynthate to older branch incre-
ments and main stem was observed in July and then increased in later
months. The current-season shoots of other conifers also become active
exporters of photosynthate, but this usually occurs after shoots have
expanded and needle maturation is completed. Shoot growth prior to this
is largely at the expense of older needles.

The contribution of short shoots to the growth of LS prior to July
was undetermined. Like the older foliage of other conifers they must
contribute to the early growth of new LS, as their leaves flush early and
are capable of Pn several weeks before vigorous LS growth begins.
Unlike the old foliage of other conifers, however, SS are current season
growth and as such are capable of major export of photosynthate through-
out the growing season. This, in conjunction with the early autonomy of
LS growth, may partially explain the rapid growth rate generally associ-
ated with larch species.

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