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ECOPHYSIOLOGY OF A DECIDUOUS TIMBERLINE TREE, LARIX LYALLII PARL.

by

© James Harlan Richards

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY
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PLANT ECOLOGY

DEPARTMENT OF BOTANY

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FACULTY OF GRADUATE STUDIES AND RESEARCH.

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Ecophysiology of a Deciduous Timberline Tree, Larix lyallii Parl.", submitted by James Harlan Richards in partial fulfilment of the requirements for the degree of Doctor of Philosophy in plant ecology.

Lawrence C Bliss

Supervisor

James M Mayo

Kenneth O. Higginbotham

Walter Moser

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Date October 23, 1980

DEDICATION

To my early ecology teachers:

Harlan Richards
Velma Richards
Ellen Heeren
Jack Whiting
John Marr
Martyn Caldwell

ABSTRACT

The deciduous timberline conifer, Larix lyallii Parl., suffers 30 to 64% less winter desiccation damage than sympatric evergreen conifers. Overwintering buds are tolerant of low midwinter water potentials (-4.0 to -5.0 MPa) and water contents (100-150%). They maintain high turgor (> 1.0 MPa) through the winter. A large resistance to water flux between the bud and xylem develops in October and maintains the relative isolation of the bud until February. Because of this large resistance, decreases in the xylem pressure potential in late winter and spring are not transmitted to the buds. The combination of these physiological and morphological features makes L. lyallii not only extremely resistant to, but also tolerant of, winter and spring desiccation. These characteristics give this species a significant advantage over evergreens in timberline environments, and explain how it can maintain upright growth well above the limits of sympatric trees.

The significant advantage over evergreens gained by this species in the wintertime is balanced by summer disadvantages. These disadvantages result from the adaptations that appear to be necessary for alpine larch to maintain a positive carbon budget. The adaptations include: high maximum net assimilation rates (dry weight basis) due to the high leaf area to weight ratios of the deciduous needles, and high light compensation and saturation points. The low mass needles are susceptible to large reductions of photosynthetic capacity in response to relatively low atmospheric demands. This response, together with the high light compensation point of wintergreen needles on young trees, prevents alpine larch from growing at elevations much below the timberline.

The light response restricts this species to open habitats which are common at the forest limit.

Alpine larch also suffers long-term reductions in photosynthetic capacity when subjected to soil moisture deficits. This, in addition to reductions caused by high atmospheric demands, limits L. lyallii to regions where regular summer rainfall maintains high soil moisture availability and high atmospheric humidity; or it is restricted to sites where edaphic factors contribute to both reliable soil moisture and cool temperatures which reduce atmospheric demand.

Desiccating winter conditions contribute to the differences in damage suffered by L. lyallii and sympatric evergreens, and Alpine larch's requirement for reliable summer moisture appears to be a result of its deciduous habit. Based on these ecophysiological studies and the distribution pattern of deciduous timberline trees, it is hypothesized that both moist summer and desiccating winter conditions are necessary for the occurrence of deciduous trees at timberline.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

A wide variety of tree species occurs at the northern and altitudinal limits of tree growth. They display a range of growth habits, from needle-leaved evergreen to broad-leaved deciduous. In addition, the pattern of vegetation and physiognomy of individual trees is extremely variable from one timberline region to another.

This variety has led to a multitude of terms describing vegetation boundaries and physiognomic types at timberlines (see Hustich 1966; Tranquillini 1966, 1976; Wardle 1968; Löve 1970; and Baig 1972). A general definition of timberline will be used here. Thus the timberline is not a narrow linear boundary at the upper or northern limit of continuous forest, nor the absolute limit of tree growth, but is the ecotone between forested and non-forested land (Wardle 1974, Tranquillini 1979). This general definition of timberline is useful at all timberlines especially at the northern limits of forest growth and on tropical mountains. Here the ecotone is often quite broad and there are no distinct boundaries in either vegetation pattern or tree physiognomy (Hustich 1966, Troll 1973). The limitation of such a general definition is encountered when attempting to compare elevations of timberlines with very different patterns of vegetation or ecotone breadths. In this case the more strictly defined terms describing vegetation pattern or tree physiognomy, i.e. forest limit, tree limit (>2 m and upright), and krummholz limit, will be used.

The floristics of timberlines and the distribution of trees of various growth habit have been reviewed by Hustich (1966), Baig (1972), Troll (1973), and Wardle (1974). Although the diversity at timberlines makes generalization difficult, some patterns are apparent (Fig. 1a and b). Evergreen needle-leaved trees are dominant over long stretches of timberlines in boreal and temperate North America, Europe, and parts of Asia, while evergreen broad-leaved trees dominate in tropical regions and in New Zealand and Australia. The importance of deciduous trees at timberline is often underestimated, but is of particular significance for this study. The distribution of deciduous timberline trees will be described in some detail (refer to Fig. 1a and b).

DISTRIBUTION OF DECIDUOUS TIMBERLINE TREES

The most important deciduous timberline trees are included in two genera: *Larix* and *Betula*. Species of *Alnus*, *Populus*, *Salix*, *Chosenia*, *Sorbus*, *Fagus* and *Nothofagus* are also important deciduous timberline trees, but their distribution or dominance is somewhat restricted.

Larix sibirica[1] and *L. gmelini* (=*L. dahurica*) dominate the northern timberline of Eurasia. *L. gmelini* is undoubtedly the most widespread and important deciduous timberline species. It reaches farther north (72.5° N) than any other erect tree. In addition to the area where these two *Larix* species share dominance with evergreen conifers, they form a pure larch forest which covers approximately 4.5 million km^2 in N. Eurasia. *L. gmelini* in far northeast Eurasia extends more than 1000 km beyond the limit of *Picea sibirica* (=*P. obovata*), and is joined only by the dwarf conifers *Pinus pumila* and *Juniperus communis* (Ostenfeld and Larsen 1930, Tseplyaev

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[1] *Larix* nomenclature follows Ostenfeld and Larsen 1930.

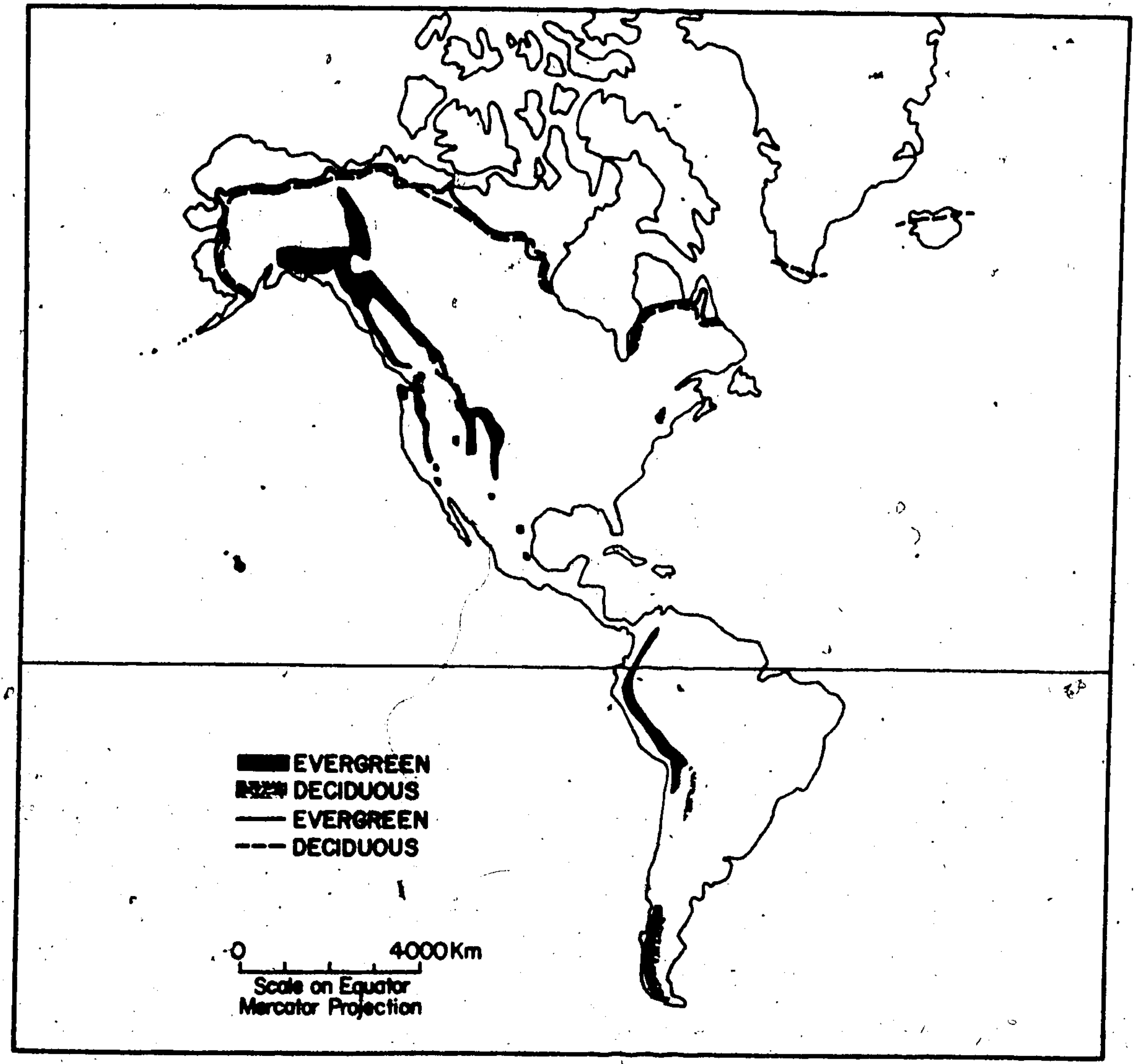

Figure 1a. Generalized distribution pattern of evergreen and deciduous trees at alpine and arctic timberlines in the Western Hemisphere.

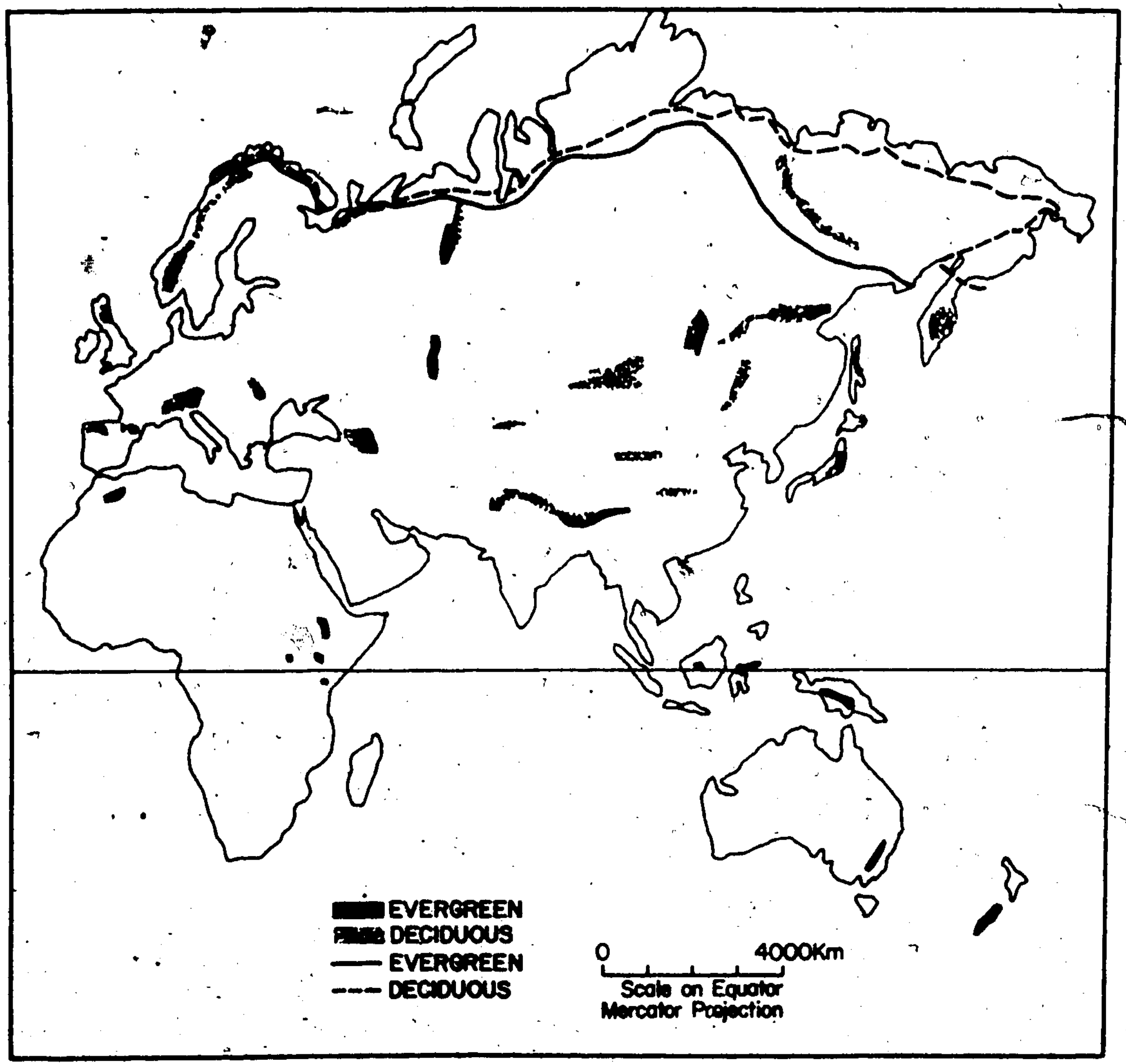

Figure 1b. Generalized distribution pattern of evergreen and deciduous trees at alpine and arctic timberlines in the Eastern Hemisphere.

1965, Hustich 1966, Arno 1970).

West of 120° E the northward extension of L. gmelini is less impressive, but even here and throughout the range of L. sibirica the larches form the northernmost forests. These two species are also important at alpine timberlines in the Ural, Verkhoyansk, Altai, and S. Khamar Daban Mountains, and in the mountains of the northern and northeastern provinces of China (Suslov 1961, Wang 1961, Epova 1965, Gorchakovskii 1965, Kuvaev 1965, Tseplyaev 1965, Stanyukovich 1973).

At the northern timberline of North America L. laricina is often present, but rarely dominates or grows farther north than the evergreen spruces, Picea mariana and P. glauca (Marr 1948; Ritchie 1959, 1960; Drew and Shanks 1965; Larsen 1965, 1974; Hustich 1966; Rowe 1972; Elliot 1979).

Of the seven remaining Larix species, two (L. mastersiana and L. occidentalis) cannot be considered timberline trees. L. kaempferi sometimes forms timberline in Japan (Franklin et al. 1979). L. griffithiana and L. potanini are important timberline trees of the northern provinces and southeastern plateau regions of China, and in the bordering Himalayan valleys. Both species are restricted to high elevations and often form a distinct forest zone above the forests of other montane-boreal conifers (Ostenfeld and Larsen 1930, Wang 1961). L. decidua has a relatively wide altitudinal range, but is an important timberline tree in the Central and Western Alps (Ellenberg 1963). L. lyallii is restricted to the upper subalpine forest and timberline ecotone in the N. Cascades and Central Rocky Mountains (see Ch. II and III). It is readily apparent from this survey that the deciduous genus Larix dominates a wide range of timberlines in the Northern Hemisphere.

Species of *Betula* are as important as larches at alpine timberlines, but have restricted distribution at the northern limits of tree growth. They nearly always form a zone of birch woods above or beyond the limits of evergreen trees. At northern timberlines *B. pubescens* (Greenland, Iceland, Scotland, Fennoscandia) and *B. ermani* (Kamchatka) form homologous vegetation types in areas with extremely oceanic climates (Walter 1968, Hämet-Ahti and Ahti 1969). One or the other of these species or their subspecies is important at alpine timberlines in Scandanavia, the N. Urals, S. Sakhalin, and Japan. (Hustich 1966, Ahti et al. 1968, Troll 1973, Kullman 1979).

B. utilis woodland forms the alpine timberline at very high elevations (3900 - 4200 m) in the northwest Himalaya and Karakoram ranges, and on Tirich Mir in the Hindu Kush (Schweinfurth 1957, Walter 1968, Baig 1972, Troll 1973). Further west, in the Caucasus, *B. verrucosa*, *B. litwinowii* and several other species sometimes form the timberline (Baig 1972, Troll 1973). *B. verrucosa* is also locally important in the Cantabrian Mountains of northern Spain (Walter 1968, Troll 1973). There are many small areas where birches are found at timberlines in the mountains of Eurasia (Hustich 1966, Baig 1972). It is again apparent that deciduous species, in this case, *Betula* spp., are important timberline trees.

Fagus sylvatica forms the upper timberline in oceanic areas of Europe (W. Pyrenees, Cantabria, S. Alps, etc.) (Baig 1972, Troll 1973). In the Scandanavian mountains, the Carpathians and Caucasus of Eurasia, and the Presidential Range of northeastern N. America, *Sorbus* species often grow in the timberline ecotone. *Populus*, *Salix*, *Chosenia* and

Alnus spp. are locally important in alluvial habitats all along the northern timberline, and in some mountain areas (Hustich 1966, Baig 1972).

Alnus jorulensis is presently an important timberline species on the eastern slopes of the central Andes, but this is a much disturbed timberline area and evergreen *Polylepis* spp. may be the 'true' timberline tree (Ellenberg 1958 a, b; Troll 1973; Wardle 1974). In the southern Andes two deciduous species, *Nothofagus pumilo* and *N. antarctica*, form the timberline in rain shadow areas from 40° to 55° S (Hueck and Seibert 1972). This distribution is analagous to the distribution of *L. lyallii* in the N. Cascades, where it occurs in rain shadow areas.

A feature common to many deciduous tree-dominated timberlines is the zone of woodland above the evergreen subalpine forest. Species of *Betula*, *Larix* and *Nothofagus* show this pattern distinctly at alpine timberlines (for examples see Wang 1961, Hämet - Ahti and Ahti 1969, Arno and Habeck 1972, Troll 1973, Quintanilla 1977). The pattern is also apparent with *L. gmelini* and species of *Betula* north of the boreal dark conifer forests (Tseplyaev 1965, Hustich 1966, Hämet-Ahti and Ahti 1969).

This brief review shows clearly that deciduous species occur in nearly as many timberline areas of the world as evergreens. Their importance has been underestimated, however.

CAUSES OF TIMBERLINES

In the long search for the cause(s) of timberlines, most physiological studies have been done on evergreen, needle-leaved trees in three genera, Pinus, Picea and Abies (Tranquillini 1979). This is understandable given the geographic facts mentioned above. Recent reviews by Larsen (1974), Wardle (1974) and Tranquillini (1979) thoroughly document our present understanding of the causes of timberlines. A very brief outline follows, with reference to alpine timberlines (see also Chapters IV and V). Physiological studies of deciduous timberline trees are then reviewed, based mainly on Tranquillini (1979).

Daubenmire (1954) reviewed seven different hypotheses explaining the occurrence and position of alpine timberlines. Recently, it has been shown that two of these hypotheses are interrelated. The combination has been proposed as an explanation for alpine, and perhaps northern, timberlines formed by a wide variety of species (Wardle 1971, 1974; Tranquillini 1976, 1979).

The two hypotheses are: 1) winter and spring desiccation of leaves and buds determines the limit of tree growth; 2) summer conditions, by their effects on carbon uptake, shoot growth, and maturation, prevent tree growth beyond the position of the 10°C isotherm for mean temperature of the warmest month. The position of this isotherm corresponds well with the positions of timberlines (Brockman-Jerosch 1919).

Winter and spring desiccation of leaves and meristems often reaches lethal levels at timberline, stunting or deforming trees.

This is the cause of the well-known krummholz growth forms found above the forest limit. Resistance to desiccation decreases rapidly above the forest limit as a result of thinner cuticles and incomplete maturation of shoots. Cuticle thickening and tissue maturation are slowed because of low temperatures, frequent frost and lack of photosynthate. Summer conditions thus determine the susceptibility of timberline trees to winter damage.

This general hypothesis has been based almost entirely on studies of evergreen trees, and is most relevant to them. Among evergreens, a few exceptions have been reported (Slatyer 1976, Marchand and Chabot 1978, Black and Bliss 1980). The physiology of only one deciduous timberline species, Larix decidua, has been studied extensively. In a pioneering study, Tranquillini (1962, 1964) compared the carbon budgets of L. decidua and Pinus cembra at timberline near Obergurgl, Austria. He found, on the average, that the deciduous larch daily fixed twice as much carbon per gram dry weight of leaf than did pine. Seasonally, on a dry-weight basis, larch fixed 47% more carbon than pine. The smaller difference resulted from the much shorter growing period of larch than of pine (107 vs. 181 days). However, on the basis of trees of the same size, the pine, due to its much greater mass of leaves, fixed 50% more carbon than the larch (Tranquillini and Schütz 1970).

Other comparative studies of evergreen and deciduous trees have shown similar results; i.e. that high fixation rates allow deciduous trees to make up for their shorter growing season (Sweet and Waring 1968, Schulze et al. 1977). Deciduous trees remain at a disadvantage, however, when compared with evergreens on a tree to tree or area basis, because of the much greater photosynthetic biomass maintained by evergreen trees.

Studies on a number of deciduous species have shown that environmental conditions at timberline may significantly reduce photosynthetic rates. Timberline deciduous trees, like evergreens, are acclimatized (and are probably genetically adapted) to lower temperatures than individuals of the same species from lower elevations (Mooney et al. 1966, Pisek et al. 1969, Slatyer and Morrow 1977). Nevertheless, photosynthetic rates are still often below maximum because of even cooler average conditions (Tranquillini and Turner 1961). Low soil temperatures also have been shown to reduce photosynthesis. Benecke (1972) determined reductions of similar magnitude in L. decidua, Alnus viridis, Picea abies and Pinus mugo.

Light may also limit photosynthesis at timberline because of increased cloudiness. Photosynthetic rates of L. laricina and Picea mariana near timberline in Labrador were often depressed by low light levels (Auger 1974, Vowinckel et al. 1975). Net production of Fagus crenata in Japan declined 50% from 550 m to 1550 m. Thirty-seven percent of the reduction was due to fog, and an equal amount to the shortened growing season (Maruyama 1971).

The relatively windy conditions at timberlines may reduce photosynthetic rates. A. viridis and Sorbus aucuparia, like Picea abies, had reduced rates at relatively low wind speeds. However, L. decidua and Pinus cembra were almost unaffected by wind speeds common during the growing season at timberline (Tranquillini 1969, Caldwell 1970).

Low soil moisture also reduced photosynthetic rates in L. decidua. However, as soil water potential fell, the larch showed a slower relative decline than either Pinus cembra or Picea abies (Havranek and Benecke 1978). In response to low atmospheric humidity, the spruce showed much greater photosynthetic reductions than the larch and the pine, which were about equal (Tranquillini 1963). Nevertheless, low soil moisture and atmospheric humidity are not usually experienced by timberline trees (Tranquillini 1979).

Apparently the environmental conditions which reduce photosynthetic rates at timberlines, as compared to lower elevations, do not differentially affect deciduous or evergreen trees. The response of individual species to these factors, in addition to the high maximum photosynthetic rates and phenological and morphological characteristics of deciduous trees, as shown before, determine the relative amount of carbon fixed by deciduous versus evergreen trees.

Dark respiration rates of deciduous timberline trees are higher than those at lower elevations, as with evergreens, and are extremely variable from species to species (Pisek and Winkler 1958, Pisek and Knapp 1959, Maruyama et al. 1972).

Needled shoots of L. decidua respired twice as vigorously as Pinus cembra, but relative to seasonal net photosynthetic uptake the percentage lost by respiration was slightly less for larch (7.7%) than for pine (8.8%) (Tranquillini 1962). Stem respiration rates of S. aucuparia and A. viridis were lowest among the trees studied by Tranquillini and Schutz (1970). L. decidua had moderate rates, and Pinus cembra quite high rates. Through stem respiration, larch lost 16.9% of seasonal net photosynthesis and a similar sized pine lost 23.1%. These sums are much less than stem respiration losses at lower altitudes because of the lower temperatures at timberline. Relative seasonal root respiration losses are also low at high altitudes, due to low soil temperatures and low root : shoot ratios (Tranquillini 1979). Timberline trees, both deciduous and evergreen, have exceptionally low respiratory losses, mainly as a result of low temperatures. This allows them to maintain a more positive carbon balance than would be expected from analyses of photosynthetic capacity alone.

Net primary productivity of timberline trees is much lower than that of trees at lower elevations, and the limited data suggest that deciduous trees show somewhat lower productivity than evergreens, especially at timberlines. In Norway *Picea abies* produced 4.5 t·ha^{-1} at 180 m and 2.0 t·ha^{-1} at 800 m, while *Betula verrucosa* declined from 5.2 t·ha^{-1} to 1.2 t·ha^{-1} (Mork 1942). Fromme (1963) showed an order of magnitude difference in accumulated dry weight of 20 yr *L. decidua* trees on different soils at timberline. Tranquillini (1979) uses these data and similar data on *Nothofagus solandri* (Wardle 1971) to argue that "the hypothesis that the tree limit occurs where the total photosynthetic production of leaves is consumed by respiration of the nonphotosynthetic plant organs resulting in zero net production (Boysen-Jensen 1949) is thus not valid for the alpine treeline." This reasoning is supported by the previously mentioned studies which have shown the very low respiratory cost of nonphotosynthetic organs at timberline.

Several phenological and winter water relations studies of *L. decidua* support the general two-part timberline hypothesis. Shoot growth of potted larch seedlings was reduced at timberline (1950 m) to 17% of that in the valley (700 m), more because of lowered growth rates than by the shortened growing period (Tranquillini and Unterholzner 1968). Benecke et al. (1978) and Benecke and Havranek (1980) correlated shoot growth rate to temperature for several timberline species being tested for reforestation in New Zealand. L. decidua, in New Zealand, began shoot growth two months after the leaves were fully extended and completed growth very late in the season at all altitudes in both Europe and New Zealand. A. viridis also had a much shorter period of shoot growth at timberline than at lower altitudes, and appeared to continue growth until deteriorating conditions forced its cessation (Benecke 1972). Thus both larch and alder probably entered the winter season at timberline with incompletely matured current year shoots. Low temperatures, besides having a direct effect on shoot growth, may also have an indirect effect by reducing available photosynthate.

Incomplete shoot maturation was shown for L. decidua by the reduction in cuticle thickness, 8% from valley floor (1000 m) to forest limit (1950 m) and an additional 14% at tree limit (2100 m) (Platter 1976 in Tranquillini 1979). This reduction was slightly less than that shown by Pinus cembra and about one-half that of Picea abies. Baig and Tranquillini (1976), studying Picea abies, showed that the reduction in cuticle thickness is less when the growing season is long and warm than when it is cool and short.

The rate of water loss in winter from tree limit L. decidua shoots was twice that of valley floor samples, presumably because of the decreased cuticular resistance (Platter 1976 in Tranquillini 1979). Water contents of some tree limit shoots dropped below the critical 50% (of dry weight) level, but none of the samples from the forest limit or valley floor fell below 75%.

Ivanoff (1924 a, b) measured the winter transpiration rates of sixty deciduous tree species and five evergreen conifers. Although the five *Larix* species studied were among the eight slowest transpiring deciduous trees, four of the five evergreens had lower water loss rates than the larches. Northern or mountain species nearly always had lower transpiration rates than southern or lowland species. Winter transpiration was 300 - 400 times less than summer transpiration. Unfortunately Ivanoff (1924 a, b) does not give enough data to calculate water vapor conductances for comparison to modern data.

To summarize, it appears that the deciduous conifer, *L. decidua*, is limited at timberline by winter and spring desiccation. The endogenous phenological pattern is modified by summer conditions so that the time for growth and maturation of shoots is limited. Summer environmental conditions also affect shoot growth and maturation directly, and indirectly through effects on photosynthesis. The incompletely matured shoots are increasingly susceptible to desiccation damage at higher elevations where summer and winter conditions are less favorable. This pattern agrees with the general timberline hypothesis developed from study of evergreen trees.

The typical zonation of deciduous woodland above subalpine evergreen forest is not found with *L. decidua*. Whether a timberline is advancing or is in elevational equilibrium, the occurrence of deciduous trees above (or north of) evergreens suggests that they have some advantage. Because of the lack of integrated physiological studies, the expectation that deciduous trees might have different constraints than evergreens, and the possible advantage mentioned above, a study of both winter and summer ecophysiology of a typical, deciduous, timberline tree (Larix lyallii Parl.) was undertaken.

OBJECTIVES

The general objectives of this study were to evaluate the relative advantages and disadvantages of the deciduous versus evergreen growth habits in timberline environments. Advantages and disadvantages of the deciduous habit were hypothesized in the context of a simplified carbon budget model (Fig. 2). Detailed objectives for the winter and summer studies are given in Chapters IV and V, respectively.

It was hypothesized that L. lyallii would have:

1) significantly lower wintertime shoot mortality than sympatric evergreens, by either avoiding or better tolerating desiccation stress;
2) higher photosynthetic capacity than sympatric evergreens, under limits set by timberline environmental conditions (see Fig. 2. Note: the effects of mineral nutrient deficiencies and mycorrhizal symbionts could not be included in this study);
3) needle and shoot growth patterns which would allow optimum utilization of the cool, short timberline growing season for photosynthetic carbon dioxide uptake;
4) severely curtailed photosynthetic rates in response to soil or atmospheric drought. This limitation was predicted to be especially severe for small trees on warm, well-drained sites.

It was hoped that quantification of the photosynthetic capacity of L. lyallii, the factors which limit that capacity, and the amount of

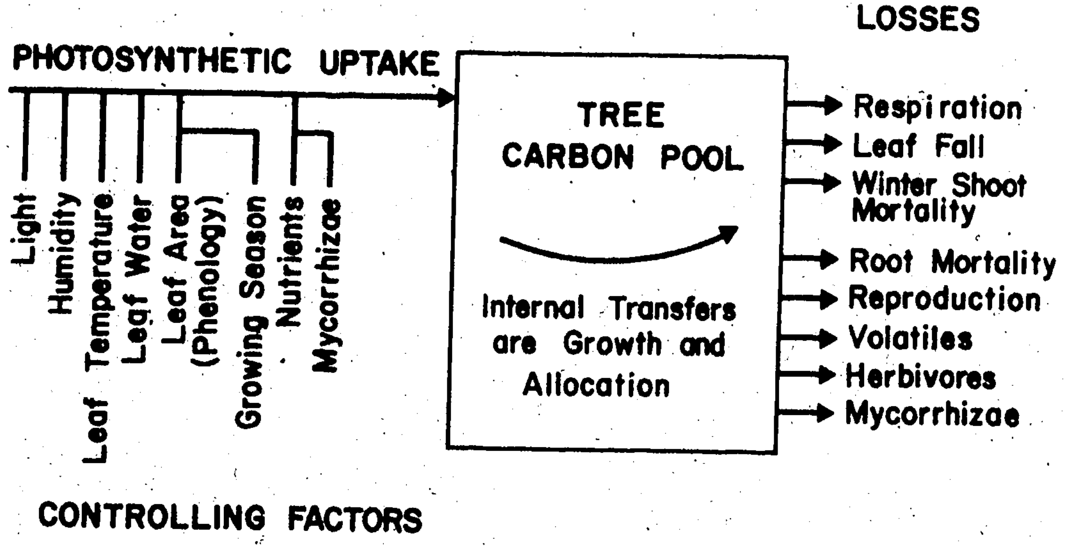

Figure 2. Simplified carbon balance diagram for a timberline tree. Major factors controlling uptake of carbon, as CO_2 by photosynthesis, and pathways of carbon loss are shown.

carbon loss by respiration, leaf fall and winter shoot mortality, would allow explanation of some of the distributional peculiarities of the species. For example: Why is L. lyallii restricted to timberline habitats? How does it maintain upright growth above krummholz of sympatric evergreens? Why is it limited to rain shadow areas in the N. Cascades? Clues to an understanding of the distribution of deciduous timberline trees worldwide, and a broader knowledge of the causes of timberlines were also expected.

CHAPTER II

DESCRIPTION OF THE STUDY AREA

Two intensive, and one extensive, study sites were chosen that provided a range in the environmental variables hypothesized to be most important in determining the timberline of Larix lyallii. The sites were situated in the Middle Creek cirque of the Marmot Creek Basin Experimental Watershed, Kananaskis Valley, Alberta (Fig. 3). The Basin lies on the east slope of Mt. Allan and is approximately 80 km west of Calgary in the Front Ranges of the Rocky Mountains. All three study sites were easily accessible year round, had similar soils, drainage, and elevation, and were on smooth slopes where the elevation of timberline was not affected by edaphic factors such as cliffs or talus.

In addition to meeting the criteria established for site selection, these sites had the advantage over other possible areas in the Canadian Rocky Mountains of being in a research watershed where hydrologic, meteorologic and other studies have been in progress since 1962. The data available from these studies have been very valuable in this research, and will be incorporated into the appropriate discussions which follow.

The south-facing site (Fig. 4) was on a 20° slope of SSE aspect at an elevation of 2250 m. It was at the forest limit in an area of reproducing, perhaps advancing, alpine larch with scattered islands of Abies lasiocarpa, Picea engelmannii, and an occasional Pinus contorta. The north-facing site (Fig. 5) was at an elevation of 2225 m on a 22° slope of NNW aspect, directly across the cirque floor from the south-facing

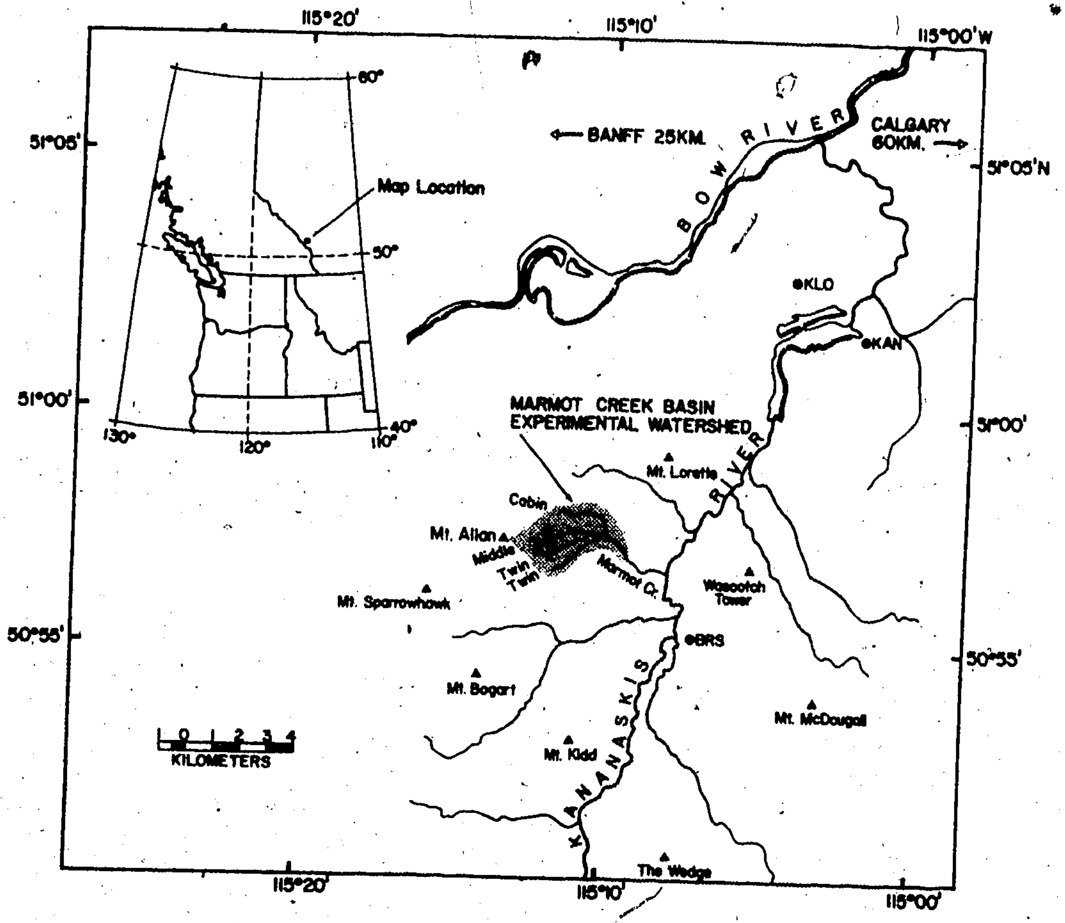

Figure 3. Location of study area and sites: south-facing (S), north-facing (N), and krummholz (K). Nearby weather stations (◎) are also shown: Kananaskis (KAN), Kananaskis Lookout (KLO) and Kananaskis Boundary Ranger Station (BRS).

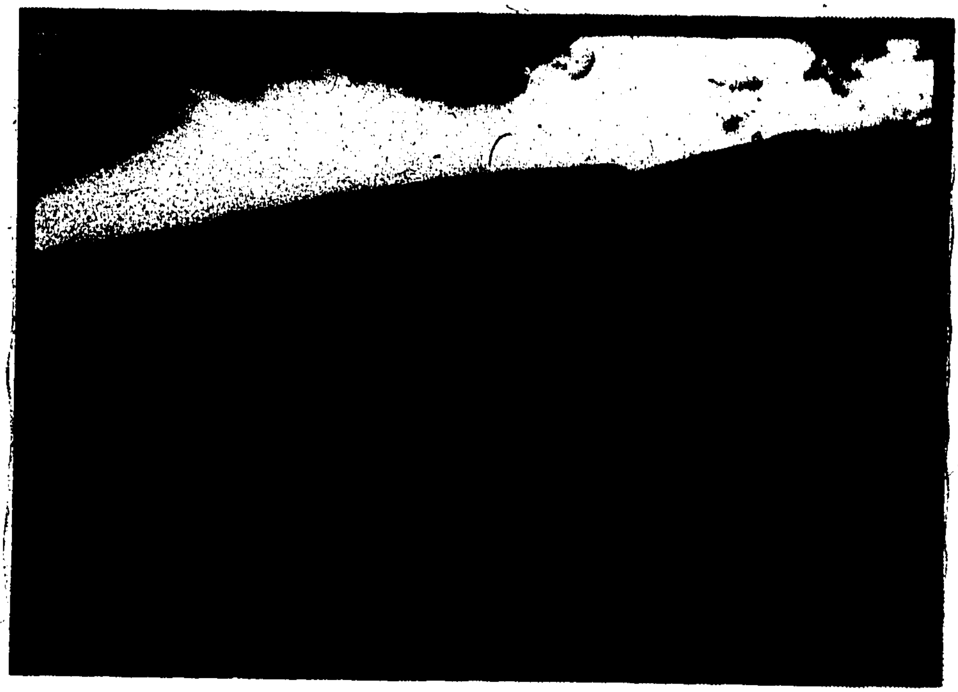

Figure 4. South-facing study site at the forest limit in Middle Creek cirque. Photograph taken on 4 July 1977.

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Figure 5. North-facing study site in opening in mature Larix lyallii woodland in Middle Creek cirque. Photograph taken on 19 July 1976.

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site. It was located about 75 m below timberline in an opening in mature alpine larch woodland where there was abundant larch reproduction; A. lasiocarpa was sub-dominant in the woodland. Both sites were laid out as approximately 40 x 100 m plots along the contour. Detailed descriptions of the soils, associated vegetation, and stand structure are given below.

Above the north-facing site and just above the forest limit, a third site (Fig. 6), for less intensive sampling, was located in mixed L. lyallii and A. lasiocarpa krummholz. This was an exposed ridge-top site with negligible slope, at an elevation of 2300 m. The ground vegetation was alpine in character, being dominated by Dryas octopetala and Oxytropis podocarpa.

The study sites, although situated in the eastern portion of the Rocky Mountains, are very representative of subalpine L. lyallii forests found along the Continental Divide (compare Barg 1972, Arno 1970). The Marmot Creek Basin Experimental Watershed was also chosen to be representative of mesic, high altitude, subalpine forests, and is more so than one might expect from its front range location (Water Survey of Canada 1962-1976).

GEOLOGY

The bedrock and structural geology of the Mt. Allan region has been described by Crockford (1949), Norris (1957, 1971), Bielenstein (1969), and Halliday and Mathewson (1971). Surficial geology and Quaternary history of the nearby Bow Valley was described by Rutter (1972) and similar work in the Kananaskis Valley has been reported by Stalker (1973), Osborn and Jackson (1974), and Jackson (1978). Studies of the geology, surficial

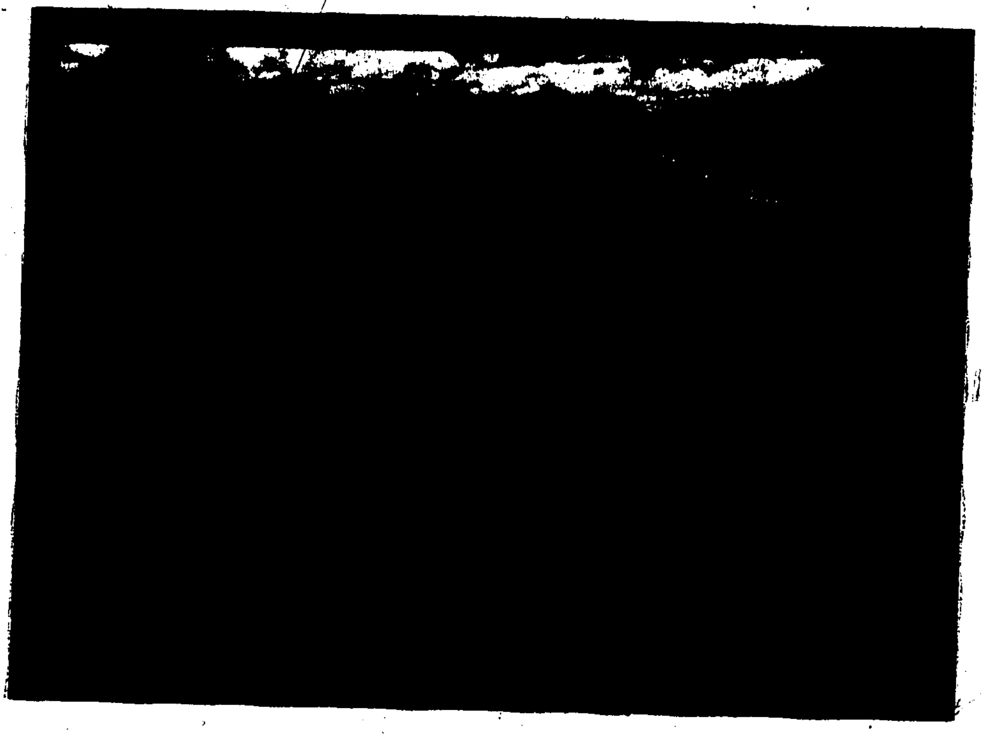

Figure 6. Krummholz study site on the south rim of Middle Creek cirque. Photograph taken 6 July 1976.

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materials and soils, and their hydrologic significance in the Marmot Creek Basin have been completed by Stevenson (1967) and Beke (1969). Much of this and other literature is reviewed by Osborn and Jackson (1974) for the Kananaskis Valley. Only a brief description will be given here. The predominant rocks of the Front Ranges are Palaeozoic carbonates, which are resistant to erosion and form the major peaks and ridges (Rutter 1972). The ridges formed by Mts. Sparrowhawk, Bogart, Kidd, and The Wedge along the Rundle fault, and by Mt. Lorette, Wasootch Tower, and Mt. McDougall along the Lac des Arcs fault are examples (Fig. 3). In belts between the ridges formed by major thrust faults are found the less resistant Mesozoic, clastic rocks. Three such NNW - SSE trending belts cross the Kananaskis Valley (Osborn and Jackson 1974). Mt. Allan lies in the central belt, which is known as the Cascade Coal Basin (Norris, 1957).

Mt. Allan (2805 m) is the highest peak in the region which is composed of Mesozoic rocks. It has probably been preserved because of its well-developed synclinal structure, albeit overturned, and its thick capping by massive, relatively resistant conglomerates of the Blairmore Group (Crockford 1949). The conglomerates and other rocks of the Pocaterra member of the Blairmore Group are lower Cretaceous in age and probably were freshwater deposits (Gibson 1977). Below these rocks lie the sandstones, conglomerates and shales of the coal-bearing Kootenay Formation, a complete section of which can be seen on Mt. Allan (Norris 1957). This formation is predominately non-marine and Juro-Cretaceous in age. It overlies the Jurassic sandstones, siltstones and shales of the Fernie Formation (Gibson 1977).

Glacial ice occupied the Middle Creek cirque on Mt. Allan, probably during pre-Wisconsin and Wisconsin times, up to approximately 2300 m elevation.

Sub-aerial freeze-thaw and mass-wasting processes have produced the broken, angular rubble to be seen on the slopes of Mt. Allan above this elevation. During the Neoglacial, ice probably only occupied a small portion of the upper part of the Middle Creek cirque (Stalker 1973). Thus the surficial materials on both study sites are a mixture of till and colluvium, both derived mainly from the Blairmore and Kootenay conglomerates, sandstones, and shales.

These materials have probably been open to colonization by trees since the retreat of the last Wisconsin glaciers, between 9000 BP (Rutter 1972) and 11000 BP (Stalker 1973). Mazama ash dated at 6700 BP occurs throughout Marmot Creek Basin (Beke and Pawluk 1971). A discontinuous ash layer found at 10-15 cm depth on the south-facing study site indicates that the surface there has not been substantially disturbed since the Mazama eruption. Although the surface was available and stable, climatic (Hypsithermal and Neoglacial) and bio-geographic factors would have controlled the advent and dynamics of forest, and specifically alpine larch woodland, on the study sites.

CORRELATION OF ALPINE LARCH TO SUBSTRATE TYPE

Arno (1970) and Arno and Habeck (1972) have noted the positive correlation of alpine larch to acidic substrates throughout its range. This correlation is certainly true in the Kananaskis Valley where nearly all of the well-developed populations occur on substrates derived from rocks of the Fernie or Kootenay Formations, or of the Blairmore Group. Because of the restricted occurrence of these acidic substrates at high elevations in the Front Ranges of the Southern Alberta Rocky Mountains, alpine larch also has a restricted, patchy distribution. In the Main Ranges lying along the Continental Divide, quartzitic sandstones become an important rock type (Rutter 1972); and it is on substrates derived from these rocks that the more widespread populations occur. Neither here nor in the Front Ranges is alpine larch totally excluded from substrates derived from carbonate rocks. Near both Mt. Sir Douglas and Mt. Joffre at the headwaters of the Kananaskis River, well-developed stands of L. lyallii, and indeed the highest elevation individuals observed in the Kananaskis Valley, grow on limestone. It must be remembered that even on calcareous substrates, the soil in the rooting zones of the subalpine trees is usually quite acidic.

That alpine larch rarely occurs on calcareous substrates in the Southern Alberta Rocky Mountains is partially explained by the cliff-forming nature of the widespread Palaeozoic carbonate rocks. Many areas of timberline elevation, which is the only habitat of alpine larch, are steep cliffs or at the base of them where regular rockfall prevents the establishment of trees. However, there are some topographically amenable areas with calcareous substrate at timberline where alpine larch does not occur. Arno and Habeck (1972, p. 431) suggest that "because of the extremely rocky and open nature of L. lyallii habitats, it seems unlikely that more vigorous competition from calciphilitic (sic) conifers could be the sole factor inhibiting larch from basic substrates." The mechanism(s) by which L. lyallii shows a preference for non-calcareous substrates remains an intriguing research problem, and an important one if the factors controlling the distribution of this species are to be understood.

SOILS

The soils of Marmot Creek Basin have been studied and mapped by Beke (1969). Timberline profiles are poorly developed, usually uniformly very acidic throughout, low in available nutrients, and relative to soils at slightly lower elevations, show less illuviation of colloids. Podzolization is the major soil-forming process. It has been studied by Blake and Pawluk (1971), who also described the pedogenic role of volcanic ash layers in these soils. Osburn and Jackson (1974) and Carroll (1978) review other soil studies in the Kananaskis Valley.

Although the characteristics mentioned above are true of soils inhabited by <u>L. lyallii</u> throughout its range, there is wide variation in some properties of those soils. For example, organic matter, Ca, N, P, and K contents all varied by a factor of ten among sites studied by Arno (1970). Degree of stoniness, although usually very high, can also vary greatly. Because of this variability, analysis of the soils on the study sites was thought desirable. This would allow more accurate assessment of the nutrient status of the sites, verify the similarity of the soils on both sites, and provide data for comparison with other alpine larch sites and for the conversion of gravimetric water contents to water potentials.

Methods

Soils at the two intensive study sites were described in the field and samples of each horizon analyzed for selected physical and chemical properties. They were then classified according to The System of Soil Classification for Canada (Can. Soil Surv. Comm. 1974) and according to the U. S. soil classification system (Soil Survey Staff 1975).

Descriptive terminology follows C.S.S.C. (1974) and color was determined in diffuse sunlight according to Oyama and Takehara (1967).

All analyses were done on the <2 mm fraction. Textural analysis was by the hydrometer method (Bouyoucos 1951). Moisture retention as percent of oven dry weight (O.D.W.) was determined by the pressure plate technique at -0.03, -0.10, -0.30, -0.80, and -1.50 Mpa. Dry weight was determined after 24 hr at 105° C. The pH was determined on a soil-water paste (1:1) by glass electrode. Organic matter, N (NO_3^- only), P, and K contents, and conductivity were determined by the Alberta Soil and Feed Testing Laboratory. Extractable cations and cation exchange capacity were determined by the Alberta Soil Survey after extraction with NH_4OAc at pH 7.

Soil moisture and temperature were determined during the physiological studies and are given in Chapters IV and V.

Results and Discussion

The soil profile on the north-facing site is deeper and has a much thicker A horizon (Table 1). Greater understory plant cover and production, and probable slower decomposition result in greater organic matter additions to the solum. A longer snowmelt period causing more percolation has led to slightly deeper profile development. Coarse fragment content in the upper horizons is relatively low. This ~~results~~ from freeze-thaw physical weathering processes, which are predominant over chemical weathering in cold high mountain soils such as these (Retzer 1974). Soils on both sites are rapidly drained because of the steep slopes and coarse textured parent materials. Angular, and somewhat platy fragments, often lying flat and parallel to the slope within the solum, indicate that colluvial materials have been deposited on, and perhaps mixed with, the till

Table 1. Characteristics of Alpine Dystric Brunisols of Middle Creek cirque, Marmot Creek Basin.

HORIZON	DEPTH (cm)	>2mm (%)	% of <2mm			BULK DENSITY (g cm^{-3})	pH	COND. (mmhos)	ORGANIC MATTER (%)	N (NO$_3$ ONLY)	P	K	EXTRACTABLE CATION (meq/100g)				TOTAL EXCHANGE CAPACITY (meq/100g)	BASE SATURATION (%)	COLOR (dry) 10 YR-___	COMMENTS
			SAND	SILT	CLAY				(ppm)				Ca	Mg	Na	K				
										NORTH - FACING SITE										
O	6-0	0	-	-	-	-	4.9	-	-	-	-	-	-	-	-	-	-	-	-	Moss, forb and graminoid remains and larch needles.
A_1	0-15	16	53	32	15	.8-.9	4.3	.4	12	<1	29	40	8.1	1.6	.3	.2	26.9	38	4/2; Grayish yellow brown	Wavy 1-2cm thick charcoal layer at base.
B_1	15-30	21	42	43	15	1.0-1.1	4.8	.3	10	<1	38	34	6.8	1.1	.4	.1	23.9	35	4/4; Brown	
BC	30-40	45	54	24	22	-	4.8	.2	5	<1	50	71	6.4	1.4	.1	.2	14.6	55	4/3; Dull yellowish brown	Very thin clay skins.
C	40+	49	52	25	23	-	4.8	.2	5	<1	55	78	5.5	1.3	.3	.2	12.2	60	4/3; Dull yellowish brown	Very thin clay skins.
										SOUTH - FACING SITE										
O	2-0	0	-	-	-	-	4.9	-	-	-	-	-	-	-	-	-	-	-	-	Larch needles and shrub parts; discontinuous.
A_1	0-5	25	61	23	16	-	4.6	.4	13	<1	41	90	13.5	2.0	<.1	.4	24.6	65	3/2; Brownish black	
B_1	5-30	37	53	22	25	1.1-1.2	4.0	.3	7	1	61	60	3.9	.8	.1	.2	17.0	29	5/2; Grayish yellow brown	Discontinuous ash layer present.
C	30+	44	59	22	19	-	3.8	.2	5	<1	70	62	1.9	.6	<.1	.2	11.9	23	4/3; Dull yellowish brown	Grading to rock rubble below 100cm.

veneer in the Middle Creek cirque (Stevenson 1967). All horizons show weak, fine, granular structure with friable consistence. Texture varies only slightly. The A horizons are sandy loams, and show only a small loss of clay. B and C horizons are sandy clay loams or in one case a loam. Boundaries between horizons are consistently clear and wavy except between the BC and C on the north-facing site, which is diffuse. A slight difference in moist color and clay skin thickness serves to differentiate these otherwise very similar horizons. Retzer (1965) mentioned that thin accumulations on stones in the deeper parts of the B and C horizon in alpine soils are composed of 70% silt and 20% clay, the silt resulting from freeze-thaw weathering.

The lower B and C horizons on the north-facing slope were saturated and very cold (ice crystals were found) when the soil pits were dug in mid-July. Groundwater discharge occurs on this slope at similar positions higher in the cirque, indicating that the groundwater table may be very close to the surface. No medium or coarse roots were found in the C horizon, suggesting that deep root growth may be prevented. Solifluction lobes and small soil hummocks are present on the north-facing slope near the study site. Thus congeliturbation has probably destroyed any ash layer that may have been present. Evidence of solifluction (sorted stripes) is apparent on the south-facing cirque wall, but well above the study site. Colluvial processes appear active, however, and are probably responsible for the disruption of the ash layer that was deposited on the south-facing site. Where the ash layer is present, the B horizon appears redder and more fine grained and may even appear multi-layered. Carroll (1978) noted similar B horizons in a meadow just below this site. The apparently more podzolized nature of such a profile is not the result of more active podzolization, but results from the stratification of colluvium and ash (Beke and Pawluk 1971).

The soils on both sites are strongly acid and very infertile (Table 1). The average pH is in the more acid half of the 3.9 - 5.7 range found by Arno (1970) on alpine larch sites. The soils on the study sites are only slightly less acid than well-developed podzols in the tree-limit ecotone on Mt. Katahdin, Maine (Bliss and Woodwell 1965). Total nitrogen analyses were not done on the study site soils. Arno (1970) reported a range of ammonium contents from <1 to 25 ppm, with a mean of 5.8 ppm for alpine larch sites. Beke (1969) reported 0.2% total nitrogen for alpine larch site soils in Marmot Creek Basin. These values suggest very low levels of nitrogen availability, as would be expected in these coarse textured, acidic soils. Likewise, the availability of phosphorus is probably very low because of the acidity and fixation by hydrous iron and aluminum oxides (Brady 1974, Beke 1969). Potassium, although present in greater quantity than nitrogen or phosphorous, is in very low concentration on the cation exchange complex. It is probably extremely limiting, especially when considered with the selective uptake of this element by subalpine vegetation (Hanawalt and Whittaker 1977).

Total cation exchange capacity (TEC) of these soils is moderate (17 - 27 meq/100 g in A and B horizons) in comparison to other high altitude soils. Subalpine soils in the Sierra Nevada developed in granitic substrates (Hanawalt and Whittaker 1976), the podzols on Mt. Katahdin (Bliss and Woodwell 1965), and well-drained alpine soils in Montana developed on limestone or metamorphic rocks (Nimlos and McConnell 1965) have TEC's ranging from 4 - 15 meq/100 g in the A and B horizons. The TEC of well-drained, loamy, alpine soils in the Front Range of Colorado ranges from

12 - 58 meq/100 g (Retzer 1962). Organic matter content is relatively high (12 - 13% in A, 7 - 10% in B) compared to well-drained soils developed on a range of parent materials (Retzer 1974). High organic matter content probably contributes significantly to the moderate levels of TEC.

Calcium is present on the exchange complex in moderate to high amounts compared to the soil mentioned above, but it and other exchangable bases are probably not readily available because of the high exchange acidity (Brady 1974). The more even distribution of Ca and Mg in the profile, and the lower concentrations in the A horizon on the north-facing site are probably due to the greater amount of percolation.

The soils on the study sites are very similar in horizonation and physical and chemical properties. They are poorly developed, very acid and infertile. Podzolization is the main soil-forming process evident in these soils, but its action is not strong. Both soils are classified as Alpine Dystric Brunisols (C.S.S.C. 1974). Beke (1969) noted the similarity of Marmot Creek Basin Alpine Dystric Brunisols to the Arctic Brown soils of Alaska described by Tedrow et al. (1958). In the U. S. soil classification system, the study site soils are classified as Typic Cryochrepts (Soil Survey Staff 1975), but it must be noted that the base saturation requirement of the Typic subgroup (60% in some horizon above 75 cm) is just met on the north-facing site. Because of variability, some pedons might be classified as Dystric Cryochrepts. Very similar soils in the alpine of Banff National Park have been described by Knapik et al. (1973). They occur there under <u>Phyllodoce glanduliflora</u> and <u>Antenneria lanata</u> communities. Both of these species are important on the north-facing site in Middle Creek cirque.

Beke's (1969) study of the soils of Marmot Creek Basin had the objective of determining their hydrologic characteristics and interpreting these for watershed management purposes. Infiltration rates were found to be generally higher than the maximum recorded rainfall rates for the Basin. Depth to an impeding horizon was closely correlated to moisture capacity, both total and available. Capacity for available water (12.4 cm) and total water (25.9 cm) were high in the Dystric Brunisols. On the basis of minimum infiltration rate and depth to the impeding horizon, Beke (1969) found that, of all the soils of Marmot Creek Basin, water retention was best in Alpine Dystric Brunisols and in poorly developed Degraded Dystric Brunisols, which occur at slightly lower elevations.

Soil moisture retention curves, used to determine soil water potentials from gravimetric water contents in later chapters, are given in Fig. 7. The curves for the B horizon agree well with expectations based on Slatyer (1967) for a sandy clay loam, and show the greater total (50% O.D.W. versus 16 - 17% O.D.W.) and available (17% O.D.W. versus 8 - 9% O.D.W.) moisture content of the A horizon.

Several properties of the soils on the study sites are of considerable importance to alpine larch as a deciduous timberline tree species. The lack of an impeding horizon, high infiltration rates, and high coarse fragment content lead to rapid, deep percolation of water into the subsoil. This, and the relatively high storage capacity in the available range, is probably of great importance to the success of alpine larch, particularly on the south-facing site. These soil characteristics provide a relatively large reservoir of available water that is easily recharged by summer rains. Deep snow accumulation on these sites assures that this reservoir is fully charged at the beginning of the growing season.

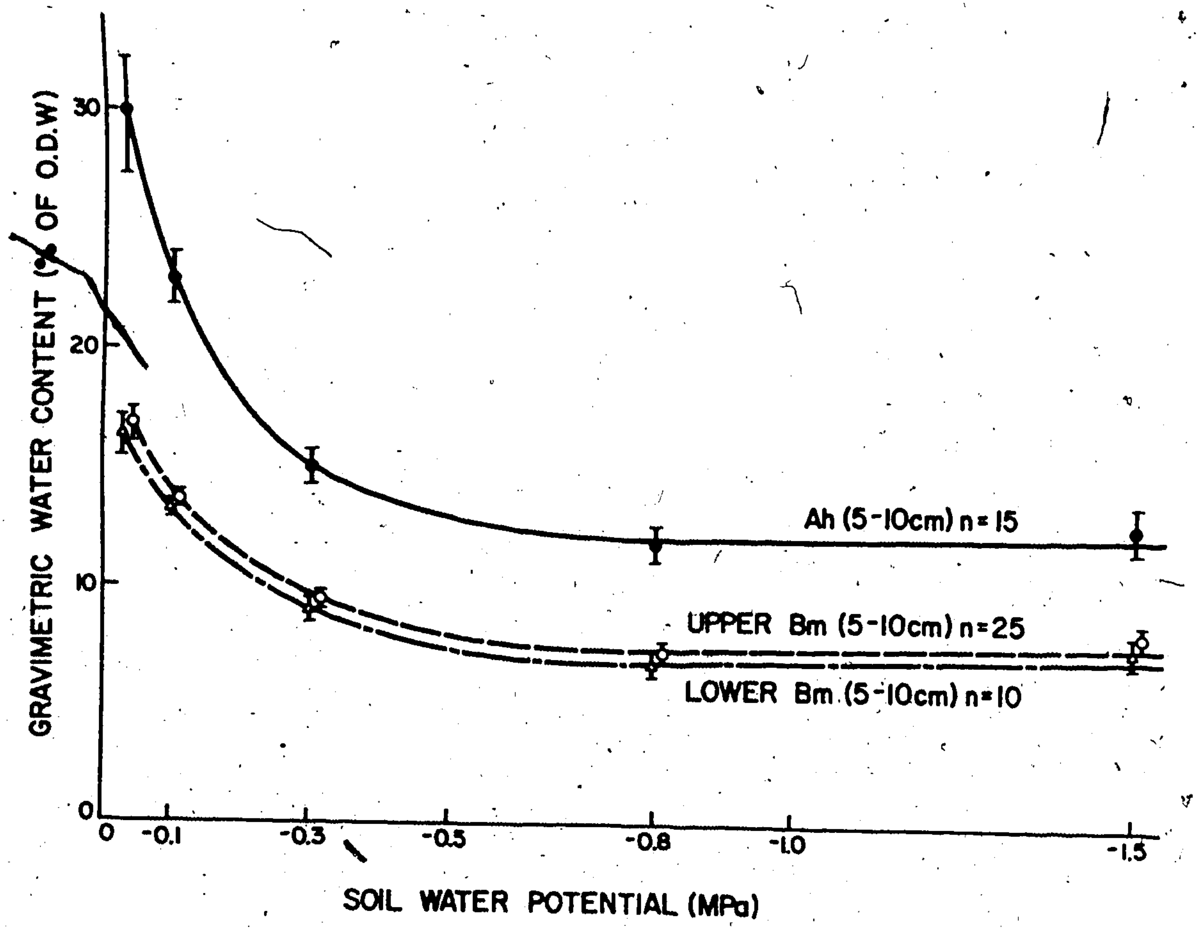

Figure 7. Water retention curves for composite samples, pooled when no between sample differences were found. Means and 95% confidence limits are given.

Further discussion of this point in relation to the species water budget will be found in Chapter V.

Monk (1966) and others (see Small 1972a) have shown that evergreens are often more important than deciduous species in low pH and low nutrient habitats. Small (1972a, 1972b) has shown that, in acidic bogs in the boreal region where growing seasons are short and nutrient uptake extremely difficult, evergreenness may provide a considerable advantage in maximizing production per acquired unit of mineral nutrients. More recently, Waring and Franklin (1979) have also shown advantages of evergreens over competing deciduous trees in regard to the particular nutrient regimes of the Pacific Northwest.

Based on these considerations, the deciduous habit of alpine larch in the strongly acid, infertile, and cold soils of the study sites, and Pacific Northwest timberline regions in general, is all the more suprising. Tikhonov (1963) notes that compared with pine, larch has beneficial effects, which include weakened eluviation of clays, and increased humus, TEC, percent base saturation and pH, on the podzolic soils of the Urals. The beneficial effects are attributed to the liberation of large amounts of ash elements by the rapidly decaying larch needles. Whether alpine larch has similar effects is not known; however, it probably is not particularly nutrient conservative, and also would be expected to have higher nutrient requirements than sympatric evergreen conifers.

One of the major adaptations of L. lyallii (and its mycorrhizal associates) to timberline habitats may be its ability to efficiently extract and use mineral nutrients. Study of the nature of this adaptation will probably provide clues to the reasons for the preference of this species for acidic substrates. Unfortunately, research on these aspects of the ecology of alpine larch could not be included within the scope of the present study.

VEGETATION

The vegetation associated with L. lyallii over its natural range has been documented by Arno (1970). Alpine larch itself is restricted to the timberline ecotone, while associated species are more widely distributed in the subalpine forest and lower alpine zone. A distinct pattern of habitat types was not apparent (Arno and Habeck 1972). This was attributed to the individualistic responses of the various species to the highly variable complex of environmental conditions at timberline. Baig (1972) in his study of timberline vegetation in Alberta, and Del Moral (1979) who studied alpine and subalpine vegetation in the Wenatchee Mountains, Washington, describe a number of alpine larch community types based on both understory and tree species composition and importance. Arno's (1970) hydric-mesic-xeric understory indicator species correlate well with several of these community types.

A description of the vegetation on the Mt. Allan study sites was undertaken to document the elevational banding of alpine larch, to provide a basic understanding of the dynamics of the alpine larch populations on the study sites and to allow comparison to the vegetation described by previous workers. Interpretation of the vegetation data provided a basis for developing hypotheses based on moisture availability.

Sampling Procedures

Stand structure was sampled at each site in three 10 x 10 m plots. Numbers and heights of all trees in each of seven base diameter (DAB) classes were determined. On both the N and S slopes, the size class distribution of alpine larch appeared to be bimodal; therefore, increment core sampling was stratified. On each site, eight large (> 17 cm DAB) and 14 - 16 sapling-sized (3 - 7 cm DAB) trees were cored to provide ages. Small trees, 30 on the north-facing and 26 on the south-facing site, were cut off at their bases and sectioned for aging.

The physiological studies described later were concentrated on the small (≤2 cm DAB) and sapling-sized (3 - 7 cm DAB) trees because of the difficulty of adequately sampling larger trees, and because of the importance of the establishment and early growth phases in the success of intolerant species.

Cover and frequency of understory species were determined in seven 1 x 1 m quadrats in each of the six larger plots. Quadrats were positioned at coordinates chosen from a random numbers table. The same set of coordinates was used in all plots.

An elevational transect from 1960 m in the subalpine spruce-fir forest to 2300 m at timberline wa established along the ridge separating Middle and Twin Creek subbasins in Marmot Creek Basin (Fig. 8). At 100 m elevation intervals, three 2 x 15 m belt transects were laid out and the base diameter of all trees > 1.4 m tall was measured. Trees ≤ 1.4 m high were counted and cover of major understory shrubs and herbs was estimated.

Results and Discussion

L. lyallii reaches its greatest importance in a band at the upper edge of the subalpine forest (Fig. 9). Abies lasiocarpa occurs with L. lyallii in the larch woodland, but is most important in the upper subalpine,

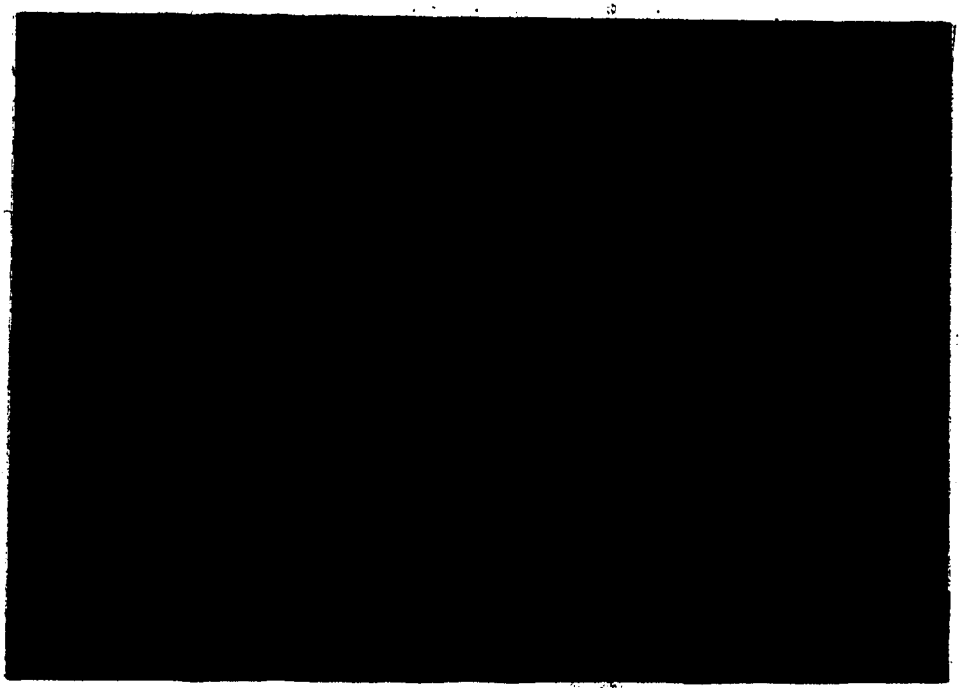

Figure 8. Location of elevational transect is shown in relation to study sites and the elevational banding of Larix lyallii. Photograph taken 17 September 1976.

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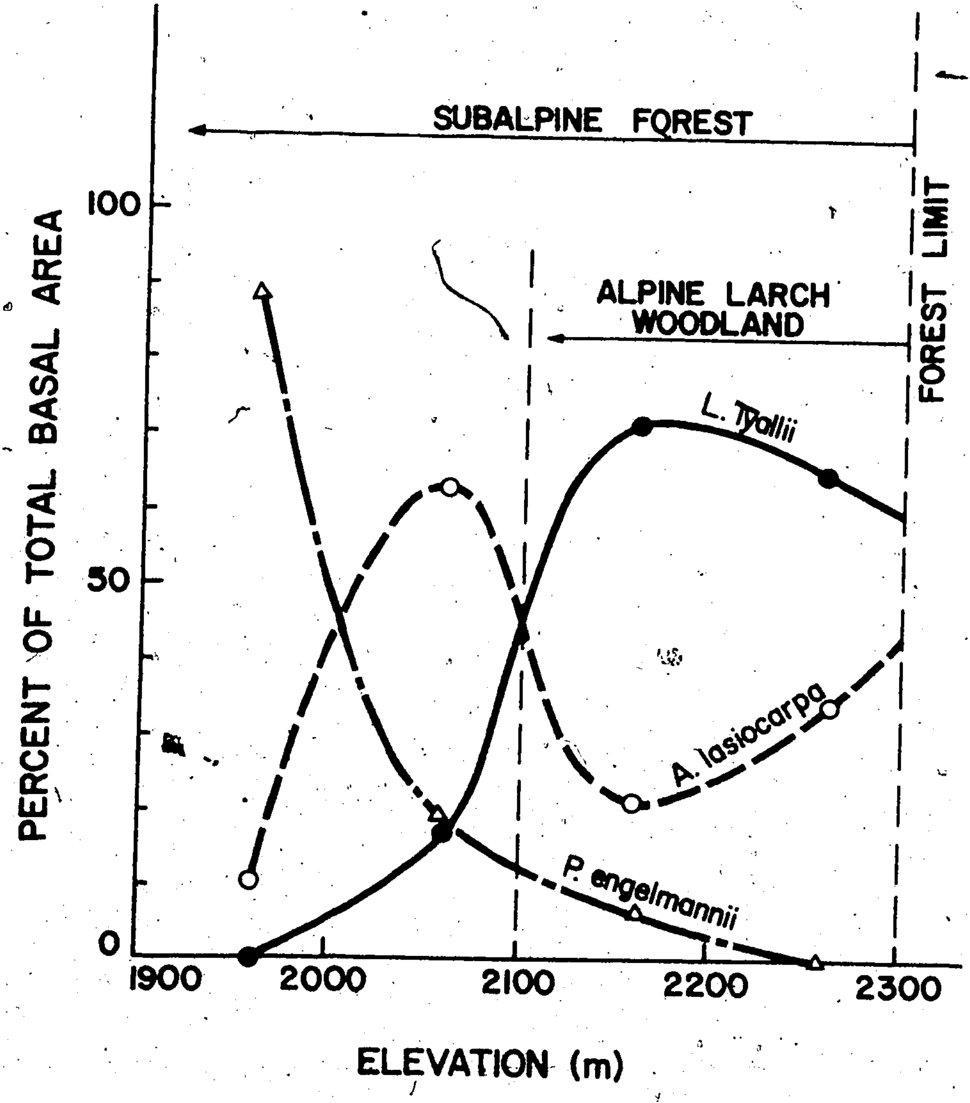

Figure 9. Basal area distribution among spruce, fir, and larch along an altitudinal transect in Marmot Creek Basin.

spruce-fir forest. The spruce found along the elevational transect vary from hybrids indeterminant between *Picea engelmannii* and *P. glauca* to individuals closely resembling *P. engelmannii* (Daubenmire 1974, Jacques et al. 1974). La Roi and Dugle (1968) have described the correlation of both morphological and chemical characteristics attributable to Engelmann spruce with elevation. Because of the high elevation, association with *A. lasiocarpa*, and morphological resemblance to *P. engelmannii*, the spruce on the transect and study sites are called *P. engelmannii* in this report. However, they are more properly considered hybrids. *Pinus contorta* was not encountered in the sampled stands, but it does occur as scattered individuals over the complete elevational range of the transect.

The understory vegetation and number of small (< 1.4 m) individuals of the three conifers changes along the altitudinal transect (Table 2). The stand at the lowest end of the transect is in the *Picea-Abies/Menziezia-Lycopodium* association (Kirby and Ogilvie 1969, Jacques et al. 1974). This association is the most widespread subalpine forest type in Marmot Creek Basin and the Kananaskis Valley. It occurs from 1675 to 2050 m on well-developed podzolic soils and has a dense tall shrub layer of *Menziezia ferruginea*, *Rhododendron albiflorum*, and *Sorbus* species. The *Vaccinium* species form a diffuse but constant low shrub layer. The herb-bryophyte layer is dominated by *Lycopodium annotinum*, *Pyrola* spp., *Arnica cordifolia*, and the feather mosses (*Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis*) and foliose lichens. Both the spruce and fir reproduce well in this forest type, but no young spruce were found in the stand sampled for the transect.

At slightly higher elevations (2000 - 2200 m) the *Picea-Abies Vaccinium scoparium* association is distinguishable. It covers 12% of the area of Marmot Creek Basin, compared with 24% for the

Table 2. Distribution of ten important vascular species and the feather mosses along an altitudinal transect in Marmot Creek Basin. Numbers of small trees of the three conifers in 90 m^2 plots are also given.

SPECIES	ELEVATION (m) 1960	2060	2160	2260
	COVER (%)			
Menziesia ferruginea	50	-	-	-
Lycopodium annotinum	5	-	-	-
Rhododendron albiflorum	5	1	-	-
Phyllodoce glanduliflora	+	11	1	5
Arnica cordifolia	+	2	4	+
Vaccinium myrtillus	-	1	7	1
Vaccinium scoparium	20	30	55	55
Feather mosses	80	20	-	-
	NUMBER OF TREES <1.4 m HIGH			
Picea engelmannii	0	27	3	0
Abies lasiocarpa	59	64	68	25
Larix lyallii	0	0	0	2

Picea-Abies/Menziesia-Lycopodium association. Here the tall shrub layer has deteriorated to only scattered individuals of Rhododendron albiflorum, but the low shrub layer of Vaccinium spp. and Phyllodoce spp. is much increased in importance. Similarly, mosses have much lower cover, but cover and diversity of forbs is increased. Alpine larch is present in this association, but shows no reproduction, even in openings. Both Engelmann spruce and subalpine fir are reproducing well, however.

The upper half of the transect is in the alpine larch woodland. Here L. lyallii is dominant, growing as evenly spaced, tall, straight individuals, and A. lasiocarpa is important, but grows in islands of upright trees, or krummholz at higher elevations. The canopy is open and the woodland floor has a low shrub layer with Vaccinium scoparium, Phyllodoce glanduliflora and many forbs, including Arnica latifolia, Antennaria lanata, and Valeriana sitchensis. Both A. lasiocarpa and L. lyallii are reproducing, with the fir seedlings more important in shaded sites and larch almost entirely restricted to openings. Baig (1972) classified this forest type as the Larix-Abies-Picea/Vaccinium scoparium association and gives a complete species list for stands of this type throughout southwestern Alberta. He also described the typical soils which develop under this vegetation.

Within the alpine larch woodland on Mt. Allan, stand structure and understory vegetation are quite variable, dependent on elevation, exposure, and disturbance history. Based on the understory species, the two study sites show large differences in moisture availability (Table 3). The understory on the mesic facing site is dominated by Carex pyrenaica, Phyllodoce glanduliflora, forbs, and graminoids. Vaccinium scoparium

Table 3. Importance values* and Arno's (1970) moisture index for species occurring on north- and south-facing *Larix lyallii* sites in Middle Creek cirque, Marmot Creek Basin.

SPECIES**	SITE		ARNO'S MOISTURE INDEX
	N-FACING	S-FACING	
Carex pyrenaica	19.7	-	
Erigeron perigrinus ssp. callianthemus	16.9	6.5	hydric = 3.0
Arnica latifolia var. latifolia	16.0	-	
Phyllodoce glanduliflora	14.4	-	mesic = 2.0
Senecio triangularis var. triangularis	13.7	-	mesic
Juncus drummondii var. drummondii	11.2	-	
Poa cusickii var. epilis	10.1	-	
Vaccinium scoparium	9.9	24.5	mesic
Pedicularis bracteosa var. bracteosa	9.0	-	
Stellaria umbellata	7.4	-	
Veronica wormskjoldii	6.5	-	
Antennaria lanata	6.0	-	mesic
Hieracium gracile	4.7	+	
Castilleja miniata var. miniata	4.7	-	
Sibbaldia procumbens	4.6	4.7	mesic
Valeriana sitchensis	4.5	-	mesic
Claytonia lanceolata	4.2	-	mesic
Trollius laxus var. albiflorus	3.8	-	
Oxyria digyna	3.2	-	
Luzula parviflora	3.1	-	
Potentilla diversifolia	2.8	11.1	mesic
Solidago multiradiata	2.7	13.6	
Agoseris sp.	2.7	-	
Salix glauca	2.7	-	
Phleum alpinum	2.1	-	
Ranunculus eschscholtzii var. eschscholtzii	2.0	-	
Poa alpina	2.0	2.5	
Dryas octopetala	-	17.5	
Juniperus communis var. montana	-	15.4	xeric = 1.0
Arenaria capillaris var. americana	-	13.6	xeric
Saxifraga bronchialis	-	12.5	xeric
Selaginella densa	-	11.1	
Sedum stenopetalum	-	7.2	
Hedysarum sulphurescens	-	5.4	
Pedicularis contorta var. contorta	-	5.4	xeric
Erigeron aureus	-	5.0	
Antennaria alpina var. media	-	4.7	
Arctostaphylos uva-ursi	-	4.6	
Anemone patens	-	4.3	
Epilobium angustifolium	-	4.3	
Campanula rotundifolia	+	3.9	
Achillea millefolium	-	3.3	xeric
Anemone multifida var. multifida	-	2.5	
Carex xerantica	-	2.1	
Total vascular cover (percent)	91	58	
Total moss cover (percent)	44	3	
Total lichen cover (percent)	3	5	

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*Importance Value (I.V.) = Relative cover + Relative frequency (Mueller-Dombois and Ellenberg 1974).

**Species with I.V. <2 are not included. See Carroll (1978) for a more complete species list for Middle Creek cirque. Nomenclature follows Hitchcock and Cronquist (1973).

is present, but much less important than it is on the meso-xeric south-facing site where it is dominant. On the south-facing site all other species with I.V. > 12 (Dryas octopetala, Juniperus communis, Arenaria capillaris, Saxifraga bronchialis, and Solidago multiradiata) are xerophytes. Total vascular cover (58% vs 91%) and moss cover (3% vs 44%) are much less on the south-facing than on the north-facing site. Forty vascular plant species occurred on each site.

Arno's (1970) moisture index indicators (Table 3) can be used to calculate a moisture index that will place the study site stands on the moisture gradient for alpine larch stands over its natural range given by Arno and Habeck (see their Fig. 17; 1972). The north-facing site has an index of 2.10 and the south-facing site has an index of 1.67 (see Arno 1970 for calculation procedure). The majority (117) of the 127 L. lyallii communities sampled by Arno fall from 1.25 (xeric) to 2.5 (meso-hydric) on the 1-3 moisture index gradient. Thus by this criterion, the two study site stands are representative of the moist and dry habitats occupied by alpine larch. They are not extreme or unrepresentative sites, however.

In agreement with the understory vegetation differences, the stand structure on the two study sites is quite different. Most of the north-facing slope is covered by a mature alpine larch woodland of ~ 15 m tall L. lyallii ranging in age from 223 to 402 yr ($\bar{x}$=285 yr, n=8). Islands of upright, smaller fir are scattered through this woodland. In the woodland are several openings of unknown origin, which have various densities of young L. lyallii (visible in Fig. 5). The north-facing study site stand is in one of these openings, and it is this stand that was sampled.

Larix lyallii and *A. lasiocarpa* both have large numbers of individuals of several sizes and high basal area on the site, but the fir are younger and much smaller (Table 4). Both species show abundant reproduction.

Many small fir trees on this site have been severely defoliated as a result of fungal infection, probably by *Herpotrichia nigra*. This may explain the greater decrease in number of fir as compared to larch from the ≤ 2 to the 3-7 cm DAB size class.

The alpine larch in the 3-7 cm DAB class were the main subject of the physiological and growth experiments. Their ages ranged from 31 - 62 yr ($\bar{x} = 41$ yr, n=14). Smaller trees ($\leq$ 2cm DAB) averaged 0.6 m tall and were 5 - 23 yr old ($\bar{x} = 14$ yr, n = 30). These small trees were also the subject of physiological and growth experimentation, most of which, however, was done on the south-facing site.

The south-facing study site was along the upper edge of the band of alpine larch woodland on that slope (see Fig. 4). The *L. lyallii* are both smaller (8-10 m) and younger (84 - 183 yr; $\bar{x} = 117$ yr, n=8) than the trees on the north-facing slope. They also are generally multi-stemmed on clustered sets of trunks, the lowest branches of an older, broken tree apparently having become upright main stems. Arno and Habeck (1972) note that this growth form is common on xeric and boggy sites. The nature of the disturbance that led to the younger trees on this site, and perhaps also to the multi-stemmed growth habit, is not known. No fire scars were found, although numerous scars are present on the trees. Charcoal fragments, and on the north-facing site a charcoal layer in the soil (Table 1), suggest that fire may have been the disturbing factor. It would be expected to be more frequent on the south-facing site (Tande pers. comm.).

Table 4. Stand structure on north- and south-facing study sites in Marmot Creek Basin.

SPECIES	DIAMETER AT BASE CLASSES (cm)							
	≤2*	3-7	8-12	13-17	18-22	23-27	30+	TOTAL
				SOUTH-FACING SITE				
Larix lyallii								
Density (n/ha)	1433	800	300	100	100	33	0	2766
Basal area (m^2/ha)	0.09	1.28	1.90	1.20	3.27	1.74	0	9.48
Mean height (m)	0.5	2.0	3.4	5.7	8.8	8.0	-	-
Abies lasiocarpa								
Density	15967	433	100	167	0	0	0	16667
Basal area	0.31	0.77	0.66	3.24	0	0	0	4.98
Mean height	0.3	1.5	3.1	4.8	-	-	-	-
Picea engelmannii								
Density	167	100	33	33	67	0	33	433
Basal area	0.01	0.20	0.39	0.55	2.07	0	3.01	6.23
Mean height	0.4	1.9	3.2	3.7	4.4	-	5.4	-
Pinus contorta								
Density	100	0	0	0	0	0	0	100
Basal area	0.18	0	0	0	0	0	0	0.18
Mean height	1.6	-	-	-	-	-	-	-
				NORTH-FACING SITE				
Larix lyallii								
Density	15533	4833	233	0	33	0	33	20665
Basal area	3.33	7.43	2.04	0	1.27	0	2.05	16.12
Mean height	0.9	2.4	4.6	-	7.2	-	8.2	-
Abies lasiocarpa								
Density	52067	1833	267	0	0	0	0	54167
Basal area	7.21	2.89	1.82	0	0	0	0	11.92
Mean height	0.5	1.6	3.0	-	-	-	-	-

*Values in ≤ 2 cm DAB size class are based on sampling 7 percent of the area.

Ungulate or rodent damage is the most probable cause of the numerous scars because they are not correlated in time, nor in orientation to the slope, and seem to occur with similar frequency on both the north and south slopes. A massive avalanche could have destroyed the stand on the south-facing site, but no down trunks, which would be expected to still be present, were found on the slope.

The sampled area along the upper edge of the woodland has a much less dense population of L. lyallii and more tightly clumped islands of A. lasiocarpa than on the north-facing site (Table 4). Picea engelmannii is as important as A. lasiocarpa here, resulting from a few large trees. It is reproducing poorly, however. The Pinus contorta growing on the south-facing study site are severely deformed krummholz stems, probably all derived from one parent plant.

The sapling-sized trees (3 - 7 cm DAB) used for physiological work ranged in age from 21 to 35 yr ($\bar{x}$ = 29 yr, n = 16). They were almost the same height as trees 12 yr older on the north-facing site. The ≤ 2 cm DAB trees, which were studied intensively on the south-facing site, averaged 0.5 m tall and ranged from 11 to 23 yr old ($\bar{x}$ = 16 yr, n = 28). Both larch and fir have fewer young individuals on this site than on the north-facing site, but fir shows a similar greater decrease in numbers from the ≤ 2 cm to the 3-7 cm DAB site classes. Larch has a more even size distribution. Direct comparisons of density or basal area to stand structures reported in the literature cannot be made because of the selective nature of the stand sampling on both sites.

In summary, both study sites have healthy, reproducing, multi-aged populations of L. lyallii. They have different densities and understory vegetation apparently in response to moisture conditions. The vegetation and stand structure of the sites are similar to that of other L. lyallii dominated communities found throughout its natural range. Additionally, the study sites provide a range of moisture, snow-melt, and insolation conditions representative of the range of L. lyallii stands.

CHAPTER III

BIOLOGY OF LARIX LYALLII

Arno (1970) and Arno and Habeck (1972) have reviewed the ecological life history of Larix lyallii and its relationship to other species in the genus. A summary is necessary to emphasize some of the characteristics of the species that suggested the present study, to show why this species is an excellent example of deciduous timberline trees, and as background for the physiological results. Growth rate, phenological patterns and some observations on reproduction are also presented.

RELATIONSHIPS WITHIN THE GENUS

Larix is a well-defined genus, bearing solitary needles on long terminal shoots and tufts of needles, and strobili, on secondary short shoots. It is very similar to the monotypic Pseudolarix, which has deciduous (vs. persistent) cone scales, much longer short shoots, and male strobili born in umbels of 20 - 25 (vs. singly). Cedrus is also very similar in branching pattern and leaf arrangement, but it is evergreen, rather than deciduous (Dallimore and Jackson 1967). Based on embryological characteristics, Larix is very closely allied to Picea and Pseudotsuga (Schopf 1943).

Larix is divided into two subgenera. One has bracts longer than the cone scales and includes the mountain species: L. griffithiana, L. mastersiana, L. potanini, L. lyallii, and L. occidentalis. The other subgenus has short cone scale bracts and includes the very widely distributed boreal species: *L. gmelini*, *L. sibirica*, and *L. laricina*, plus two mountain species: *L. decidua* and *L. kaempferi* (Ostenfeld and Larsen, 1930). For distribution maps, morphological descriptions and discussion of the basic ecology of the ten species (and several varieties) of *Larix* see Ostenfeld and Larsen (1930), Dallimore and Jackson (1967), and Arno (1970).

Members of the genus *Larix* are found only in the cool climatic regions of the Northern Hemisphere. They are very widely distributed in the boreal zone, especially in Eurasia, and must be considered second only to *Picea* species as botanically important boreal conifers. All species of *Larix*, except *L. occidentalis* and *L. mastersiana* are found at either arctic or alpine timberlines (Ostenfeld and Larsen 1930, Wang 1961, Tseplyaev 1965), and in many respects the ecology of all species in the genus is similar (Arno 1970, Arno and Habeck 1972).

Little is known about the migrations of *Larix*, although the probable origin of the genus is in eastern Asia, perhaps in the early Tertiary. This puts *Larix* among the most modern of coniferous genera (Arno 1970). The fossil evidence of *Larix* is meagre in pre-Miocene deposits, but fairly abundant in Europe and North America in post-Miocene strata. Arno (1970) has reviewed this evidence and discusses two possible migration processes that would have brought *Larix* to North America. He speculates on whether a mountain and a boreal species migrated from Asia to North America, or if a single ancestral line ~~made~~ the migration across the Bering land bridge, to later split into the mountain and boreal species found here. A third possibility, also speculative, is that there were two waves of migration. First, the ancestors of the long bracted species expanded across eastern Asia and western North America, were then forced south by glaciation at high latitudes and, in their isolation, differentiated into distinct species. Then a second expansion, and subsequent differentiation occurred, this time of the ancestors of the short-bracted species. Thorough study of the fossil evidence and systematic relationships within the genus could perhaps allow some of these hypotheses to be eliminated.

ECOLOGICAL CHARACTERISTICS OF *LARIX LYALLII*

The natural distributions of *L. lyallii* (Fig. 10) and *L. occidentalis* (see Arno 1970: Fig. 2) are correlated with the Pacific storm peninsula (Arno and Habeck 1972). Alpine larch only occurs east of the Cascade crest, and both there and in the Rocky Mountains its distribution is more patchy in the southern portions of its range (Fig. 10), where it is usually restricted to cool northern exposures. Throughout, it is found in timberline habitats, only rarely descending in avalanche tracks or on talus to the highest elevations at which *L. occidentalis* occurs. Natural hybrids between *L. lyallii* and *L. occidentalis*, although rare, are known from areas such as these (Carlson 1965, Arno 1970). Generally, *L. lyallii* forms a band of open woodland at the upper edge of the spruce-fir subalpine forest. It also often grows as upright trees high above the forest limit, even on exposed rocky sites. Krummholz forms are rarely found (Arno 1970). The occurrence of alpine larch in the subalpine forest, especially on ridges where the soils are rockier (see Fig. 8), is probably successional as no young larch trees can be found on the forest floor. Where alpine larch occurs at the upper edge of the subalpine forest, it is the climax dominant (Arno and Habeck 1972). Alpine larch in

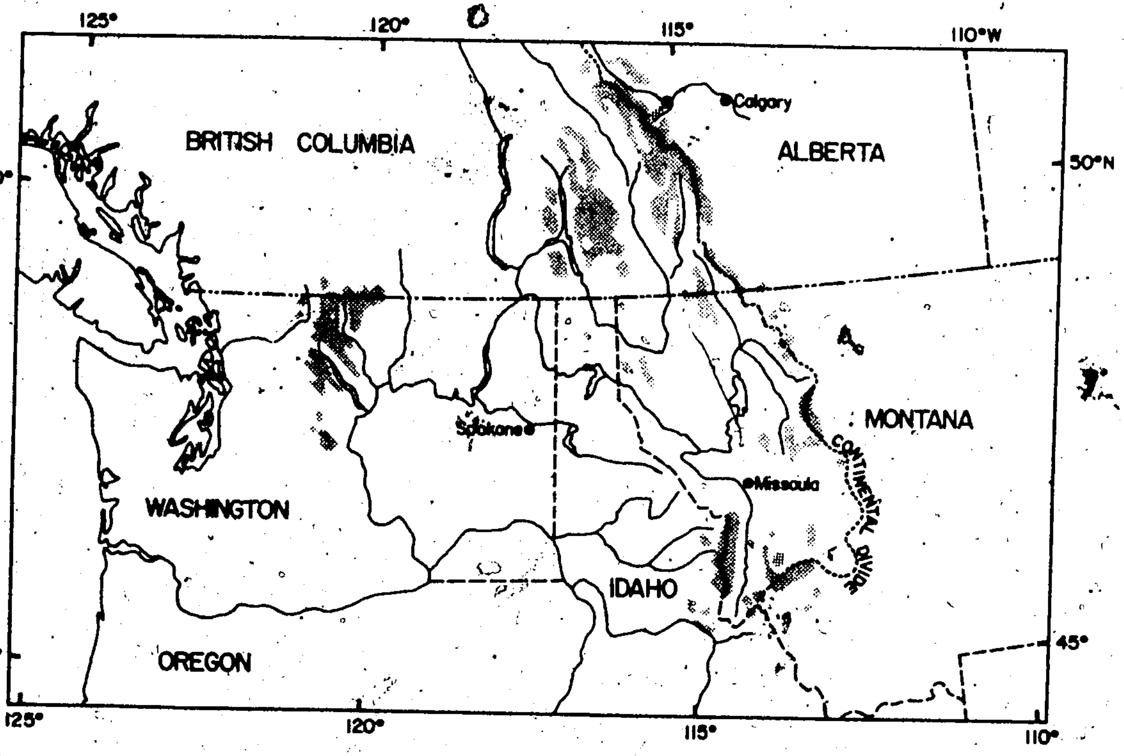


Figure 1[illegible] Natural distribution of *Larix lyalli* (from Arno and Habeck 1972). The study area location is shown by the solid circle.

Marmot Creek Basin and in the Kananaskis Valley fits these characteristics well.

Young trees have very flexible trunks, and this in combination with their deep rooting habit allows them to withstand avalanche and snow creep better than sympatric evergreen conifers. The branches of mature trees are tough and withy, withstanding well high wind and snow loads. In both cases mentioned above, the wood:foliage ratio is much less than that required by evergreen conifers because of less snow and wind catching area (Arno and Habeck 1972). Lack of needles in winter and early spring also prevents the snow fungus, Herpotrichia nigra, from damaging alpine larch in areas of late-lying snow. Blüthgen (1960) has reported a similar lack of damage to Betula pubescens ssp. tortuosa by the snow fungus, Lophodermium pinastri, while sympatric Pinus sylvestris is severly damaged.

In summary of this section, L. lyallii is a deciduous conifer that grows only in timberline habitats where it forms climax woodlands. It also often grows as upright trees well above the upper limit of even the krummholz of sympatric evergreen conifers. Because of these characteristics, it provides an excellent example of a dominant, deciduous, timberline tree, and it is for this reason that alpine larch was chosen as the subject of the present study. Also by virtue of its generic classification, it is closely related to many other deciduous timberline trees, making possible some generalization about the physiology of this group of relatively unstudied trees.

GROWTH, PHENOLOGY, AND REPRODUCTION

In this section a description of the timing and rates of needle expansion, shoot growth, flowering and senescence, and diameter growth of whole trees is presented. This information is necessary background for proper interpretation of the physiological data for several reasons: first, calculation of total photosynthate produced depends on leaf area, biomass, etc. and on the pattern of their change through the growing season; second, comparison of the timing and rates of growth processes on different sites gives a direct evaluation of the response of the species to different environmental conditions; finally, interpretations of the physiological results depend upon knowledge of the overall behavior of the species.

One unique, and most intriguing, aspect of the biology of the species is that it maintains green, functional needles year round when young. It becomes totally deciduous only after the lowermost branches have died. It has been suggested that the overwintering needles are evergreen (Arno and Habeck 1972), but in fact they are wintergreen, being functional for two seasons. Senescence and abscission, which is often incomplete, occur at the end of the second growing season.

Wintergreen needles are found on the lower branches of trees as old as 50 yr and up to 3 m tall, but are probably of little photosynthetic importance because of their low total area and shaded position. Also they are often partially covered by leaf litter (Arno and Habeck 1972). On smaller, younger trees, wintergreen needles appear to be much more important (Fig. 11).

Because of this difference, and the desire to study the physiology of the establishment and early growth phases of the life cycle of alpine larch, two groups of trees were sampled throughout this study. Well-established, sapling-sized trees 2 - 3 m high with > 99% deciduous needles were sampled on both of the intensive study sites and on the

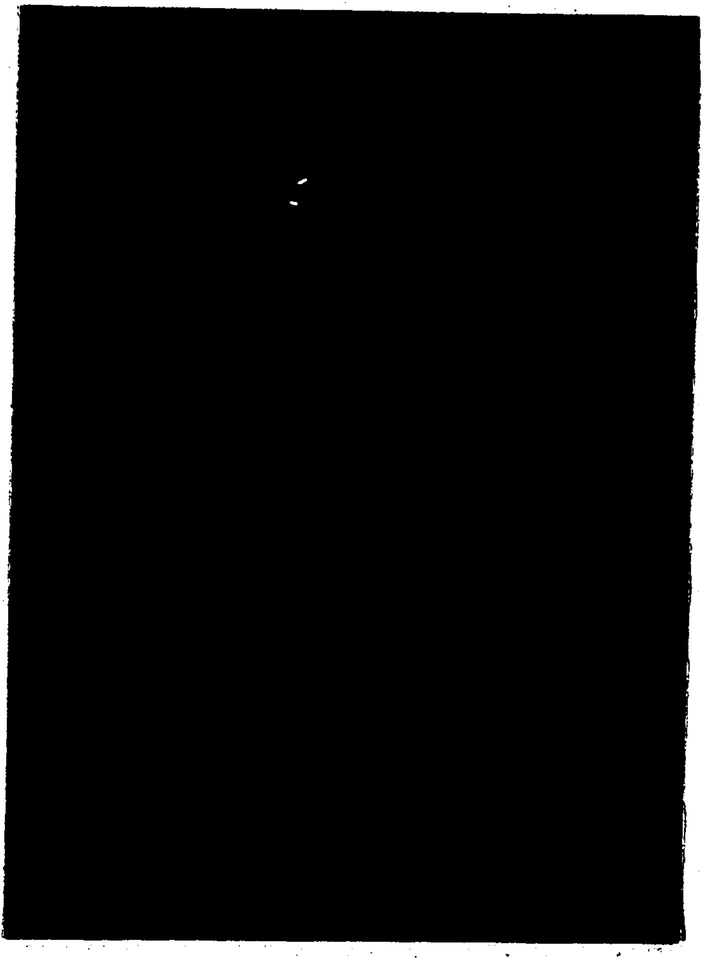


Figure 11. Wintergreen needles on a young alpine larch on the south-facing site. Photograph taken 14 June 1978.

COLOURED PICTURE

krummholz site. Small trees, 0.1 - 0.8 m high, had 33 - 67% of total needle dry weight as wintergreen needles. These were sampled almost exclusively on the south-facing site. Densities, ages, and diameters of both groups of trees are given in the preceding chapter (p.44-47, including Table 4).

Methods

Small trees

The small trees which were used for age determinations (see p.37) were collected on 18 September 1977 after the deciduous needles had begun to yellow. This made possible relatively accurate separation of the wintergreen and deciduous needles and their respective supporting branches. The dry weights (O.D.W.) of the biomass components were determined after oven drying at 45°C for 48 hr. Total height and terminal leader lengths were measured. Four small trees were carefully excavated by hand and rooting pattern observed and root/shoot ratios obtained. These data, with the ages of each individual, were used to calculate growth rates and relative allocation by age class.

Saplings

Terminal leader lengths for 1974, 1975, and 1976 were measured on 25 saplings on all three sites. Mean diameter growth rates of saplings were determined from measurements of increment cores (see p.37). Rooting patterns (roots > .5 mm dia.) of three saplings were examined by excavation to ≈ 1 m. Complete excavation was impossible with these trees, however, because of the great size of the root systems and the rocky soils. Aboveground biomass components (needle, branch, cone) were determined on three saplings at each intensive site by sampling 90° quadrants of 0.5 - 1 m high layers, along the whole height of the sapling.

The assumption that the saplings were symmetrical appeared to be justified. Thus, the biomass of each component at each layer was calculated by multiplying by four. The total component weight for each sapling was then determined. The means of the component weights from the three saplings on each site were considered as representative of the 'typical' sapling for that site.

Phenology and growth

Cone developmental stages were noted weekly, and short-shoot buds and subsequent needle lengths were measured with calipers at approximately weekly intervals. Five short shoots on each of three first-year, 10 cm long twigs were measured and averaged. Photographs, which included a plastic ruler, were taken biweekly of the same set of ten twigs on each site. They were used for supplemental measurements of the expansion of short shoots, needles and terminal buds, as they developed into long shoots. Measurements made for leaf area determinations during physiological sampling (see Ch. V) also supplemented these data.

Results and Discussion

Height growth

Height growth of small L. lyallii trees averages ∿1.5 $\mathrm{cm \cdot yr^{-1}}$ during the first 25 yr of their lives (Fig. 12). These growth rates are much lower than those of seedlings or young cuttings of Pinus cembra, L. decidua, and Picea abies at timberlines in Europe (Oswald 1963, Tranquillini and Unterholzner 1968, Oberarzbacher 1977). There were no detectable differences in height growth of small L. lyallii trees on the two intensive study sites, thus the data were combined for regression analysis (see Fig. 12). A linear boundary was also fitted to these data. This regression (Height(cm)=2.23·age(yr), r^2=.997, p<.01), which was

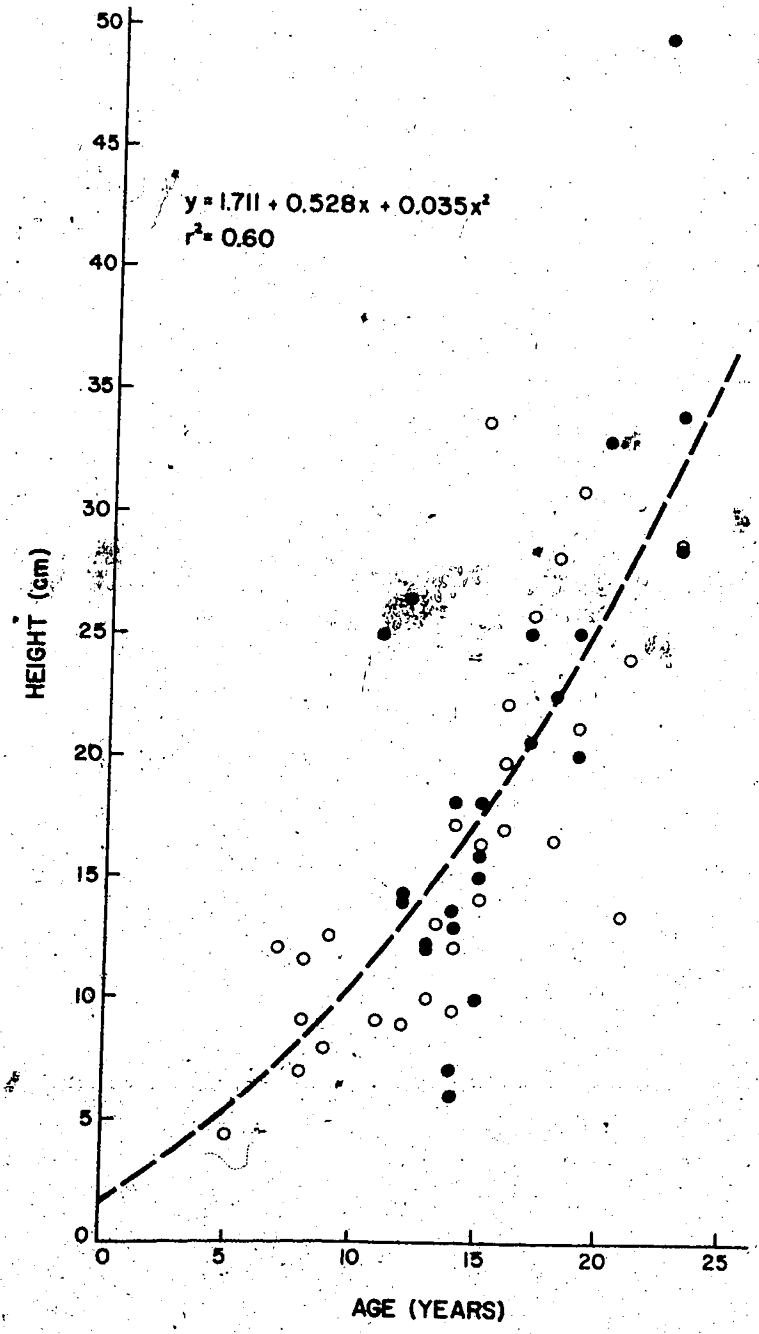


Figure 12. Polynomial regression of height on age for small *Larix lyallii* trees from both north-facing (o) and south-facing (•) sites. Data were combined when no differences between sites were found.

forced through the origin, defines the maximum growth of young *L. lyallii* under the site conditions prevailing in Marmot Basin. The large variability in height growth may be due to errors in aging these very small, slow-growing trees, or to compensating differences in site climate with large microsite diversity. Less intensive sampling and aging of *Picea engelmannii* and *Abies lasiocarpa* on the study sites showed that these two species also have very low height growth rates, similar to those of *L. lyallii*, when young.

After attaining 20-25 yr alpine larch saplings have a current annual increment of $>10\text{cm}\cdot\text{yr}^{-1}$ on the north-facing and krummholz sites, and $>16\text{cm}\cdot\text{yr}^{-1}$ on the south-facing site. Sapling terminal leader lengths from 1974, 1975, and 1976 show that the height growth rate on the south-facing site was consistently 1.5 - 1.6 times greater than on the other two sites (Table 5). These rates are comparable with the maximum height growth rates of *Pinus cembra*, L. decidua, and *Picea abies* at lower elevations within the subalpine forests in Europe (Oswald 1963, Tranquillini and Unterholzner 1968, and Oberarzbacher 1977).

The pattern of growth seen in *L. lyallii*, very slow growth when young followed by a period of very rapid growth, is similar to that found in some other conifer species, notably *Pinus palustris* (Chapman 1932). In contrast to *P. palustris*, where this pattern is an adaptation to frequent fires, this growth pattern in *L. lyallii* is probably an adaptation to allow adequate root system development for tapping a large and deep soil volume, which would dependably provide water late into the growing season, before a large leaf area is produced. This interpretation is supported by data and discussion in Chapter V. The extremely slow early growth also assures that young alpine larch, by remaining short, are rarely without the protection of the snowpack in winter. This minimizes winter mortality of shoots. When height growth accelerates

Table 5. Terminal leader growth of Larix lyallii saplings (>25 yr) on three sites in Marmot Creek Basin during 1974, 1975, and 1976 (Mean ± SE, n = 25).

SITE	TERMINAL LEADER GROWTH (cm·yr^{-1})			
	1976	1975	1974	MEAN
South-facing	14.6 ± 0.8	16.9 ± 0.8	16.8 ± 0.9	16.1
North-facing	10.0 ± 0.8	10.2 ± 0.8	11.3 ± 0.8	10.5
Kr[illegible]mholz	9.7 ± 0.5	12.2 ± 0.6	9.3 ± 0.7	10.4

at 20 - 25 yr the trees grow rapidly through the abrasion zone, which can be so destructive to the leading shoots of timberline trees (Marchand and Chabot 1978, Tranquillini 1979).

Diameter growth

Saplings on the south-facing site increased in diameter 1.5 times faster than similar trees on the north-facing site (Table 6). This difference agrees with the height growth difference for saplings on these two sites (Table 5). Older trees on all sites had lower diameter growth rates than saplings, as expected. Trees on the krummholz site had very slow diameter growth, 0.8 $\mathrm{mm\cdot yr^{-1}}$, compared to rates on north- and south-facing sites, 1.3 and 1.9 $\mathrm{mm\cdot yr^{-1}}$, respectively. Comparable slow growth rates have been found in other timberline trees (Mork 1960, Tranquillini and Unterholzner 1968, and Wardle 1970). Alpine larch can reach quite large diameter (>1.3 m) at timberline, despite very slow growth rates, by persisting for many centuries (Arno and Habeck 1972).

Diameter growth rates of alpine larch in Marmot Creek Basin agree with rates found by Arno and Habeck (1972:Fig. 9). They give three diameter growth rate classes: good growth (>1.6 $\mathrm{mm\cdot yr^{-1}}$), average growth (between 0.8 and 1.6 $\mathrm{mm\cdot yr^{-1}}$) and poor growth (<0.8 $\mathrm{mm\cdot yr^{-1}}$). Growth rates on the south-facing, north-facing and krummholz sites fall into the good, average, and poor classes, respectively.

This comparison again shows that the study sites in Marmot Creek Basin are representative of alpine larch sites over its natural range. Surprisingly, both diameter and height growth on the mesic (as determined by understory indicators, see p.44) north-facing site are less than on the meso-xeric south-facing site, but similar to the xeric krummholz site. This contrast suggests that the factors affecting the growth

Table 6. Diameter growth rates of young and old *Larix lyallii* on three sites in Marmot Creek Basin (Mean ± SE).

SITE	DIAMETER GROWTH ($mm \cdot yr^{-1}$)	AGE (yr)	n
South-facing	1.90 ± 0.08	29 ± 1	16
	1.47 ± 0.14	117 ± 13	8
North-facing	1.28 ± 0.12	41 ± 4	14
	1.19 ± 0.07	284 ± 21	8
Krummholz	0.77 ± 0.18	110 ± 19	6

of alpine larch, or its response to them, are different than those affecting the understory vegetation. Arno and Habeck (1972) noted the great variety of understory plants that grow in association with alpine larch. They suggested that individualistic responses of overstory and understory species to the complex of environmental factors at timberline prevented the formation of repeatedly occurring community types. The community analysis and growth rate data present the problem of how larch can respond differently than the understory species to moisture conditions.

Rooting pattern

One of the major differences between alpine larch and understory species, that causes a differential response to moisture, is in rooting patterns. Young trees of L. lyallii show impressive development of a taproot and sinking laterals. Small trees 16 - 25 yr old and 20 - 40 cm high have taproots penetrating 40 - 60 cm and laterals descending 20 - 60 cm at about 45°. Younger trees have taproots that are approximately twice as long as the trees are tall. Mycorrhizal development is evident on all trees, but shallow roots have a higher degree of infection than deep roots.

The root/shoot ratio of small alpine larch trees is 0.41 ± 0.05 (mean ± SE, n = 4). This value is slightly higher than, but comparable to the 0.33 and 0.38 reported by Benecke (1972) for timberline *Picea abies* and *Pinus mugo*, respectively. Both of these species have much higher root/shoot ratios at lower elevations. It appears that alpine larch does not allocate a greater percentage of resources to root growth than other timberline ecotone conifers, but differs simply in root morphology.

The deep rooting pattern of L. lyallii is maintained as the trees grow older, although the taproot loses its dominance. Root systems of saplings have many large sinking laterals as well as a taproot of about the same size. Deeply rooted saplings of larch are able to withstand great pressure from snow creep or avalanche without damage, and full grown trees are only rarely windthrown, despite their windy habitat (Arno 1970, Arno and Habeck 1972).

Most roots of alpine larch saplings are at depths greater than 20 cm, while roots of most subalpine and alpine plants that occur in the understory of larch stands remain above the 20 cm depth. Thus alpine larch is able to tap a soil moisture resource that is much more consistent in its availability throughout the growing season than that found in the upper soil layers and available to understory plants. Data supporting this conclusion are presented in Chapter V.

Biomass accumulation and allocation

Biomass accumulation and allocation in both small trees (<25 yr) and saplings (>25 yr) of L. lyallii show results that agree with the differential height growth of saplings on the two intensive study sites. Table 7 and Fig. 13a and b for saplings and small trees, respectively, show the much greater biomass accumulation of individuals on the south-facing site. The greater relative allocation to trunkwood on the north-facing site explains the maintenance of height similarity (equal for the first 20 - 25 yr), despite much lower overall biomass accumulation rates there (Table 7, Fig. 13a). This response is probably the result of differing radiational and competitive regimes. Although the mean total and mean needle biomass of small trees of each age class show a steady increase, the variability between individuals in the

Table 7. Biomass distribution among various plant parts of typical Larix lyallii saplings on north- and south-facing sites.

SITE	PLANT PART	DRY WEIGHT (g)	PERCENTAGE OF ABOVE-GROUND BIOMASS
North-facing 3.0 m tall 41 yr old	needles	200	5.3
	branches	2175	58.0
	1 yr twigs	8	0.2
	2 yr twigs	30	0.8
	trunk	1375	36.7
	cones	0	0.0
	Total shoot	3750	100.0
	root*	1850	49.3
	Total	5600	-
South-facing 2.5 m tall 29 yr old	needles	575	12.5
	branches	3100	67.4
	1 yr twigs	50	1.1
	2 yr twigs	80	1.7
	trunk	920	20.0
	cones	4	0.1
	Total shoot	4599	100.0
	root*	2090	45.4
	Total	6689	-

*Approximate amounts.

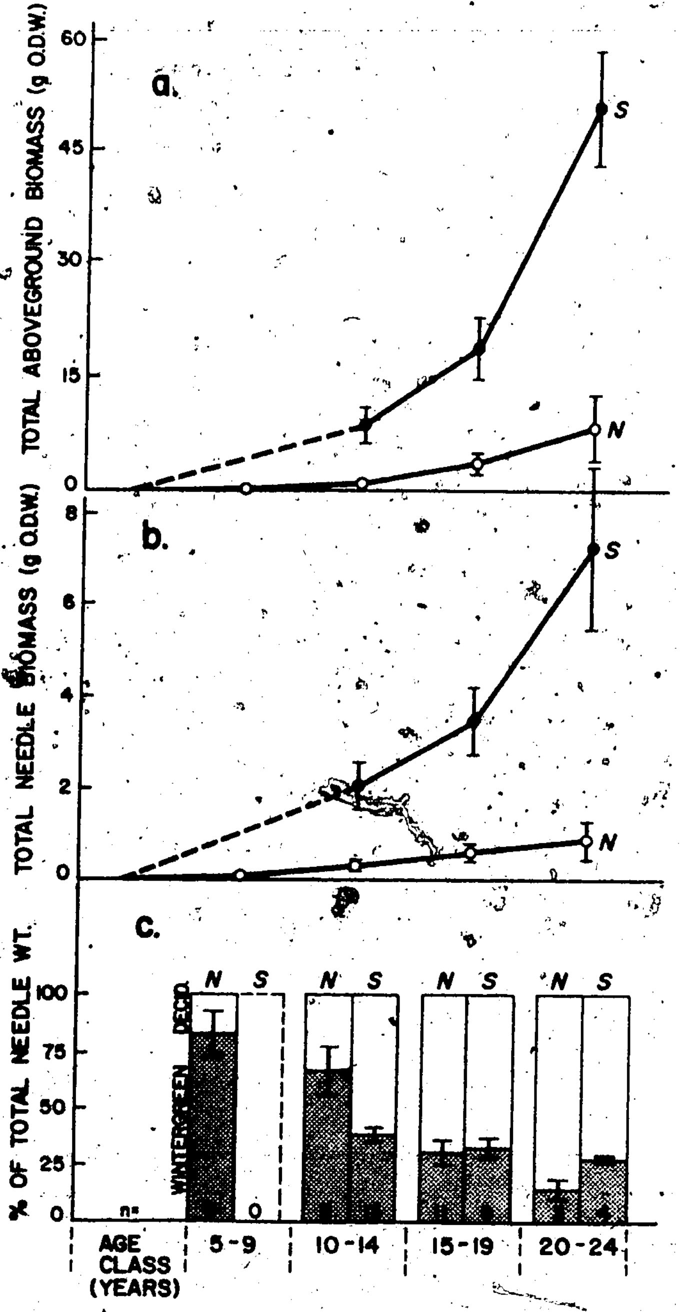


Figure 13. Total (a) and needle (b) biomass accumulation of Larix lyallii trees on north- (N) and south-facing (S) sites; and relative amounts of wintergreen and deciduous needles of those same trees (c). Means ± SE are shown, and n is indicated for each age class and site at the bottom of c.

same age class on the same site is large (Fig. 13a and b). This may be due to microsite differences, genetic variability, or errors in aging.

The relative amount of wintergreen needles decreases more rapidly with age on the north-facing site than on the south-facing site. On the latter site even the 20-25 yr old seedlings have a mean of 28% of needle biomass in wintergreen needles (Fig. 13c). As a function of total tree biomass, however, the relative amount of wintergreen needles declines rapidly on both sites until total biomass is >10 g (Fig. 14). Small trees larger than this have stable relative amounts of wintergreen needles, 28% on the south-facing site but only 7% on the north-facing site. This difference is significant at p = .01 (t = 5.8, df = 15). Discussion of the causes and significance of this difference is deferred until the physiological responses of the two needle types and the environmental conditions of the two sites have been presented.

Phenology

The phenological patterns of *L. lyallii* in Marmot Creek Basin (Fig. 15) are similar to those described by Arno and Habeck (1972) for larch in Montana. Senescence of needles, however, occurs two to three weeks earlier than in Montana. Also, observations of dissected short shoot buds, used for water relations studies (see Ch IV), indicate that expansion of the short shoot needles begins in April, when winter conditions still prevail. Owens and Molder (1979) have shown that short shoot meristems of *L. occidentalis*, which however were growing in a much milder clime, begin activity in mid-March or early April. Needle expansion in *L. lyallii* proceeds at a very slow rate until mid-May to mid-June (Fig. 15, 16a and b). There is great variability in time of flushing from year to year, site to site, and position on the tree. Short shoots

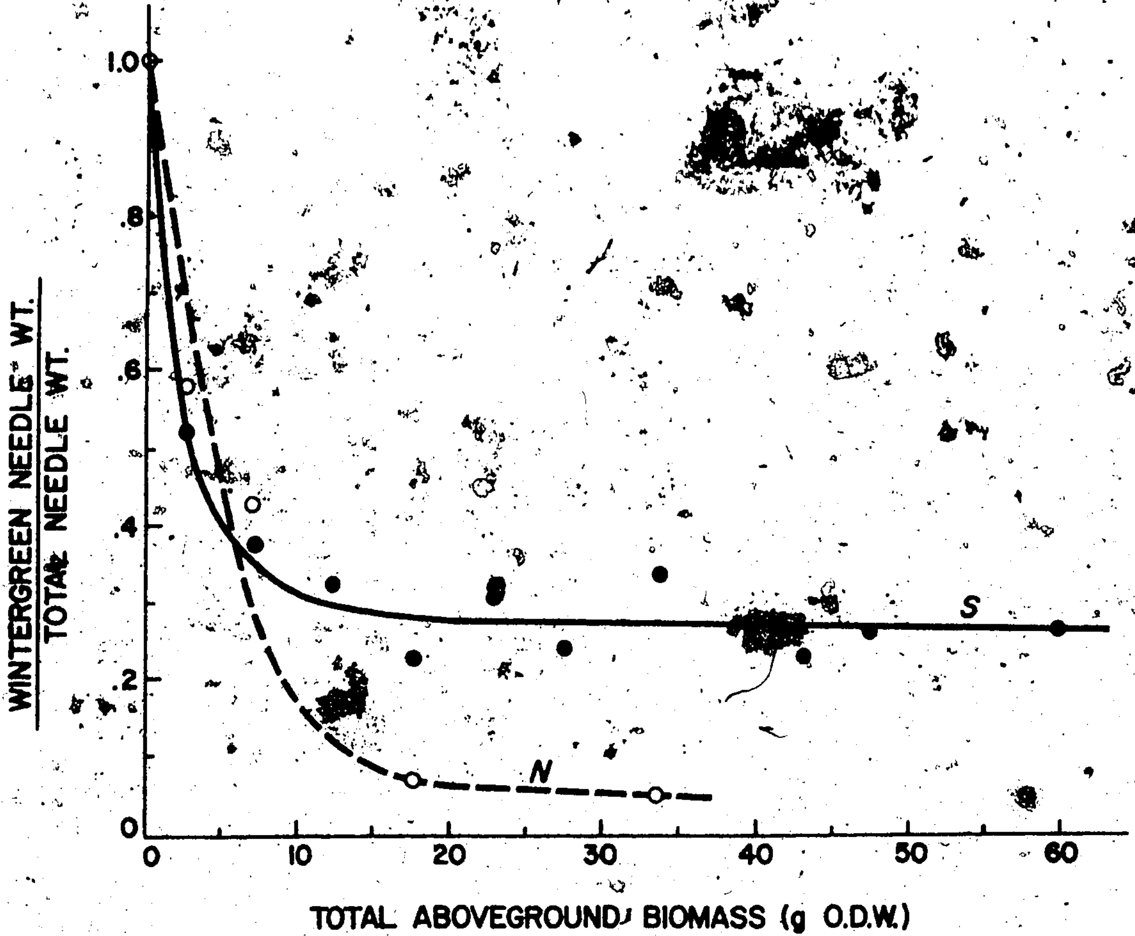


Figure 14. Relationship of relative amount of wintergreen needles to total biomass of small Larix lyallii trees on north-facing (o) and south-facing (•) sites. Means within 5 g size classes are shown.

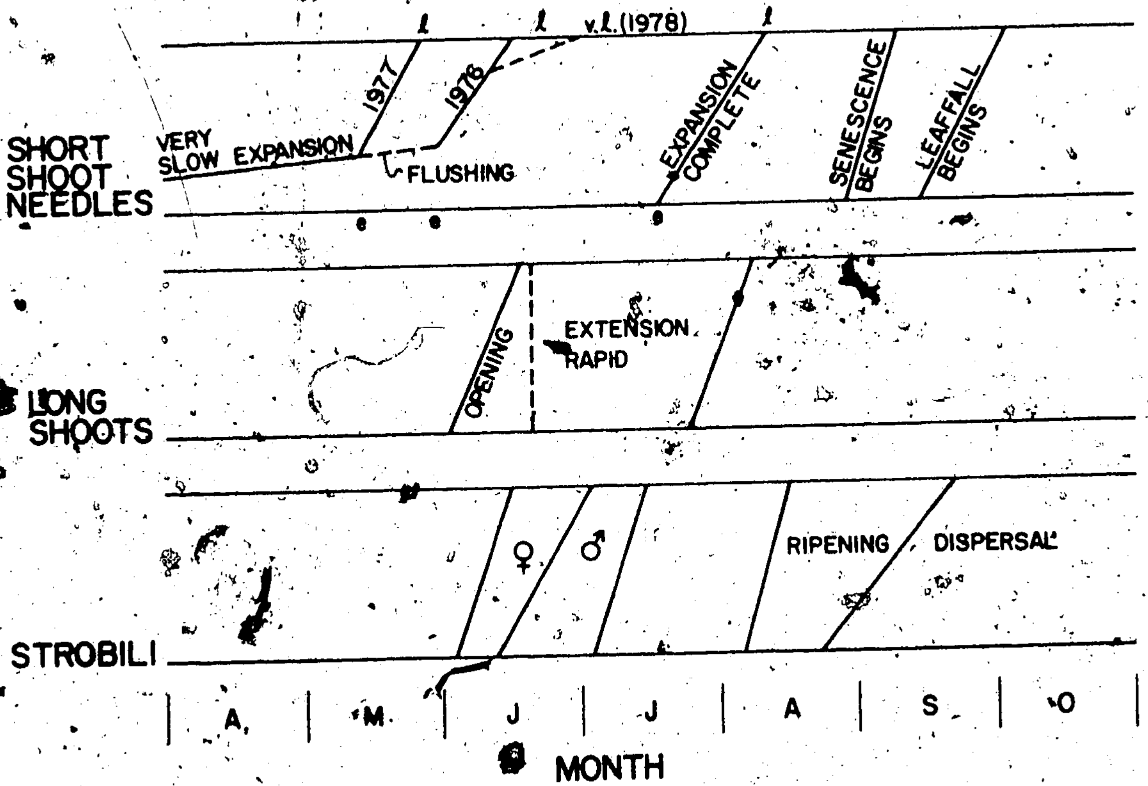


Figure 15. Phenology of *Larix lyallii* trees on south-facing, early melt-out (e) and north-facing, late meltout (l) sites in Marmot Creek Basin.

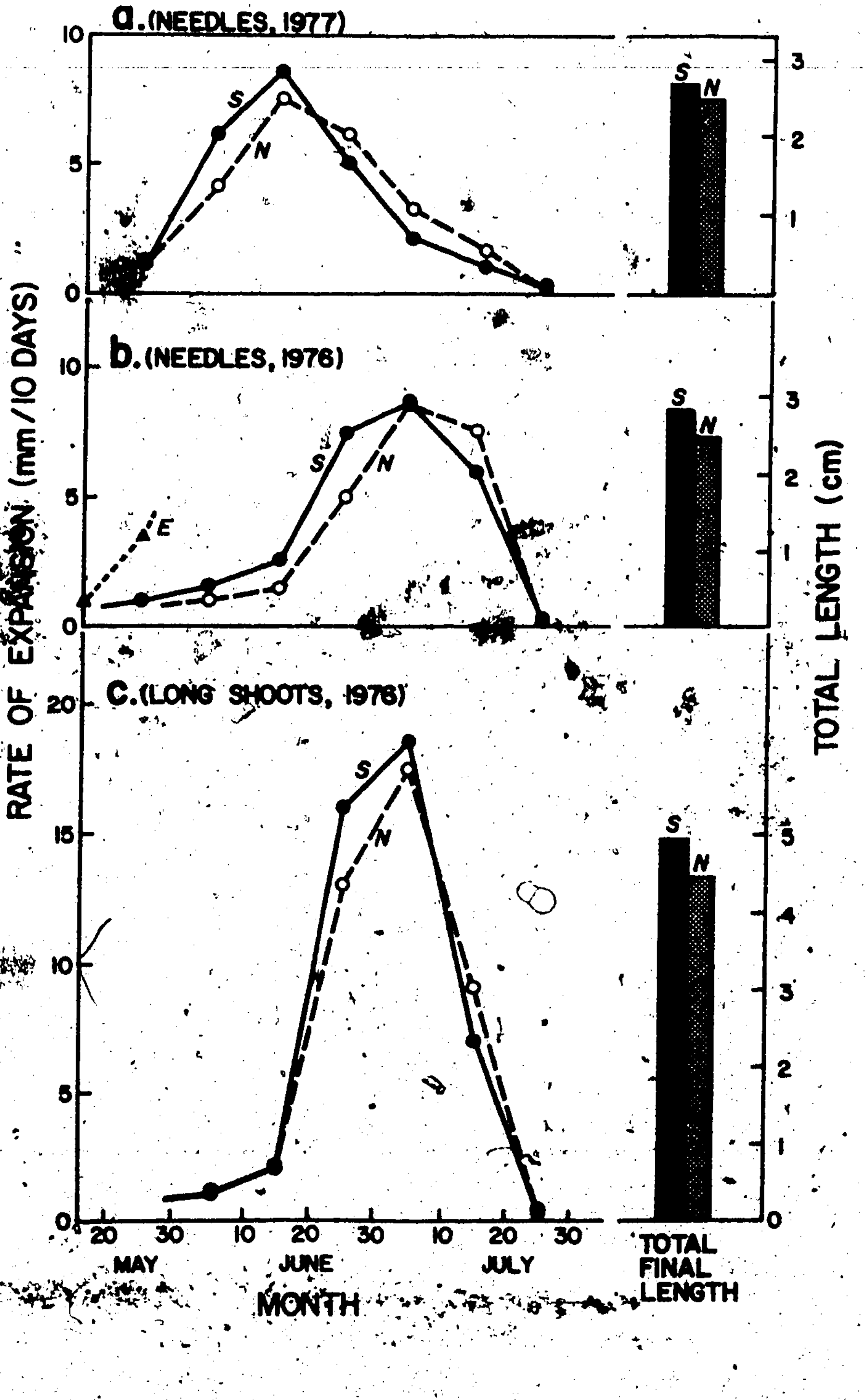


Figure 16. Seasonal growth pattern and final lengths of Larix lyallii needles (a and b) and long shoots (c) on north-facing (N), south-facing (S), and very early meltout (E) sites in Marmot Creek Basin.

on the trunk open earliest and can produce needles up to 2 cm long before the buds on the branch ends have burst. This gradient suggests a similar gradient in the concentration of an endogenous growth substance(s). Small trees and lower branches do not flush until about a week after snow release, which can be as late as mid-July in Marmot Creek Basin. On warm, early meltout sites, flushing may occur as early as the first week in May. In 1977, following a very low snow winter and when June mean temperature was about 8°C (4°C higher than in 1976), flushing occurred three weeks before it had in 1976 (Fig. 15, 16a and b). Also, in 1977, there was only about one week difference between the north- and south-facing sites, in contrast to the normal two week difference. Needles and long shoots on the south-facing site are consistently longer than those on the north-facing site (Fig. 16). This difference may be due to the earlier flushing on the south-facing site.

Expansion of needles and long shoots, which occurs almost simultaneously (Fig. 15 and 16), appears to be strongly controlled by warming, but its initiation occurs well before mean temperatures reach 4°C. This temperature was suggested by Arno and Habeck (1972) as the trigger for flushing. Long shoot growth of L. lyallii occurs much earlier in the season and proceeds more rapidly than that of L. decidua in timberline habitats (Oberarzbacher 1977, Benecke and Havranek 1980). Picea engelmannii and Abies lasiocarpa expand shoots in July, only a little later than L. lyallii. The early and rapid expansion of needles and long shoots seen in alpine larch allows this deciduous tree to make maximum use of the short timberline growing season for photosynthsis, growth, and maturation of new twigs. This may partially explain its greater success than L. decidua in timberline habitats. Further discussion of the importance of this feature of alpine larch biology will be found in Ch. VI.

Reproduction

Good reproduction of L. lyallii is apparent in the field (see Table 4). Often apparently even-aged groves of alpine larch are found in the openings common along the forest limit (Arno and Habeck 1972). The sapling stand on the north-facing study site is one such grove. Such stands are probably not even-aged; however, accurate aging of a[illegible]h by increment cores is difficult because of the great var-[illegible] height and slow growth when young.

[illegible]everal cotyledon stage alpine larch seedlings were discovered on the north-facing study site in 1977. A good seed crop was produced in 1976, but germination studies with some of this seed confirmed the low germination rates found by Shearer (1961) and others. Out of 5000 seeds, treated in numerous ways, only two living seedlings were obtained. Viability by a tetrazolium test was 40 - 60%, but the seed may nevertheless have been of poor quality, as has been previously reported (Shearer 1961, Carlson 1965). The low establishment success prevented use of seedlings for physiological experiments; thus, potted trees had to be relied upon despite the root damage problem. Field reproduction and establishment may only occasionally be good. Because of the longevity of the species, however, this is adequate for alpine larch to remain an important timberline tree.

Summary

The description given of the characteristics of the early stages of the life cycle of L. lyallii provides valuable insight into the ecology of this species, and suggests that study of the wintergreen needles may provide the best understanding of the establishment ecology of this species. Seedlings grow extremely slowly for their first 15 - 20 yr, and on some sites wintergreen needles are important throughout this period. Following this relatively long period of slow growth, height increases rapidly and the saplings begin to rely totally on deciduous needles for photosynthesis. Diameter growth is slow throughout the lifespan of alpine larch, but it can grow to large size for a timberline tree because of its longevity. Its phenology allows it to expand and mature shoots within the short growing season, and to take the fullest advantage of the time available for photosynthesis. Reproduction in the open, is at least occasionally good and, th[illegible]e, adequate for maintenance of the species importance at timberline.

CHAPTER IV

WINTER WATER RELATIONS OF LARIX LYALLII

INTRODUCTION

Winter desiccation is the most important determinant of the alpine timberline (Wardle 1971, Tranquillini 1979). Studies on timberline species in Europe and North America have shown that desiccation proceeds through the winter, causing the greatest stress to develop in late winter and early spring (Goldsmith and Smith 1926; Michaelis 1934a, b; Steiner 1935; Müller-Stoll 1954; Tranquillini 1957; Wardle 1968; Lindsay 1971; Hansen and Klikoff 1972; van Zinderen Bakker 1974). This drought stress often reaches experimentally determined lethal levels (Pisek and Larcher 1954, Platter 1976 in Tranquillini 1979), and even casual observation at timberline confirms that shoot mortality occurs often and is widespread. Death of foliage, and especially the terminal shoots, severely restricts the growth of timberline trees. The degree of desiccation and subsequent damage increases dramatically at the forest limit and in the krummholz zone (Wardle 1968, Holtmeier 1971, Lindsay 1971, Baig et al. 1974). This results from the decreased resistance of the trees to water loss, rather than from rapidly deteriorating environmental conditions (see Tranquillini 1979 for a review). The developmental processes which confer desiccation resistance, cuticle thickening and tissue maturation, proceed slowly in, and are often prematurely terminated by, the cool, short growing seasons at timberlines (Baig and Tranquillini 1976, Platter 1976 in Tranquillini 1979).

Although most studies confirm this general pattern as the cause of timberline, some important exceptions have been reported. Black spruce (Picea mariana) shoots apparently are not killed by desiccation at either alpine timberline on Mt. Washington, N. H. (Marchand and Chabot 1978) or at arctic timberline in the Mackenzie Valley, N. W. T. (Black and Bliss 1980). Black (1977) and Black and Bliss (1980), however, have documented the role of summer environmental conditions as controls of germination and establishment. These, in combination with periodic disturbance, determine the northern black spruce timberline. Slatyer (1976), also, has shown that winter desiccation is not a major factor limiting the snow gum (Eucalyptus pauciflora) at timberline in Australia. Rather, spring radiation frosts cause [illegible] damage.

These exceptions throw some doubt on the generality of susceptibility to winter desiccation as the major determinant of timberline. Also, most of the studies cited above have been on evergreen trees, which have exposed foliage all winter. Deciduous trees, because of their woodiness and less exposed area, would be expected to resist desiccation more than even the most resistant evergreen trees. Thus, they should be at an advantage in winter, timberline environments.

The winter water relations of Larix lyallii were studied in detail to determine if this species does have such an advantage over sympatric evergreen trees, and how that advantage is gained. The specific objectives were: 1) to determine the seasonal progression and ultimate degree of winter desiccation of twigs and buds of alpine larch; 2) to relate these to environmental conditions; 3) to determine the limits of tolerance of larch trees and compare these to the actual stress experienced; 4) to observe any damage and relate it to environmental conditions and previously determined physiological parameters; and 5) to compare damage to sympatric evergreen conifers.

Because of the importance of deciduous trees at timberlines, the results of this study will allow better evaluation of the role of winter desiccation as a timberline determinant. The results also will provide an understanding of how L. lyallii is adapted to its timberline habitat.

METHODS AND MATERIALS

Descriptive Field Studies

Sampling dates and sites

Snow depths and xylem pressure potentials ($\Psi_{p_{xylem}}$) of twigs above and below the snowpack were sampled during the winters of 1975-76 and 1976-77 at several timberline sites in the Kananaskis Valley, Alberta. From September 1977 to May 1978, environmental and water relations parameters were sampled monthly on the north- and south-facing study sites in Marmot Creek Basin. Sampling was done between 1100 and 1300 hr standard time.

The north-facing site is well protected from wind and direct radiation in winter and has deep snow accumulation. The south-facing site is exposed to the prevailing winds and direct solar radiation in winter. It is blown free of snow in patches.

Environmental measurements

Absolute monthly maximum and minimum air temperatures; soil temperature profiles, and snow depths were recorded on the sites. These were supplemented by data from various governmental agencies and published by Environment Canada in the Compilation of the Hydrometeorological Record, Marmot Creek Basin, Vol. 4 - 14, 1968 - 1978.

Maximum and minimum temperatures

Max - Min Thermometers (Taylor Instrument Co., Arden, NC; Model 5458) were mounted in small aluminum shelters attached to the north sides of large trees at 1.5 m. An additional aluminum foil wrapping prevented snow accumulation, radiational heating and wind buffetting. Approximate accuracy of these thermometers, as installed, was ± 1.5°C.

Soil temperature profiles

Copper-constantan (Cu-Con) thermocouples (0.8 mm dia.) were installed at 0, -10, and -50 cm in two soil pits at each site. The two temperature readings from each depth were averaged. Thermocouples were read with a digital voltmeter (DVM) (Fluke Co., Mountlake Terrace, WA; Model 8030A) using a 1000 gain low level amplifier (Tech. Services, University of Alberta) to increase resolution. The reference junction was a Cu-Con thermocouple taped to the bulb of a Hg-glass thermometer (Brooklyn Thermometer Co., Farmingdale, NY; 0.2°C/division). The reference junction and thermometer, imbedded in an aluminum block, the DVM, and the amplifier were all enclosed in a wooden box and heavily insulated to minimize temperature gradients. On extremely cold days (<-15°C) the instrument was carried in the front pouch pocket of an anorak so that a temperature adequate for operation could be maintained. Tests on this instrumentation, carried out in laboratory controlled-environment facilities, showed that rapid cooling (25° to 0°C) or heating (0° to 25°C) did not influence the ± 0.2°C accuracy.

Snow accumulation

Snow depths were measured with a marked pole at ten positions along a contour transect. Averages and ranges are given.

Water relations parameters

The 1977-78 winter sampling pattern for xylem pressure potential ($\Psi_{P_{xylem}}$), total water potential (Ψ), osmotic plus matric potential ($\Psi_{\pi+\tau}$), and water content (% O.D.W.) is shown in Table 8. See Eq. 1 and 2 (p. 80) for definitions. Needleless twigs of L. lyallii had 15 - 25 short shoot buds and were one or two years old. These, wintergreen needled shoots from the base of small L. lyallii, and branch tips of the evergreen conifers were clipped, immediately sealed in plastic bags and kept cold during transport to the laboratory for reading. Relative shrink-swell of the bole was recorded in the field.

Xylem pressure potential

$\Psi_{P_{xylem}}$ determinations were made with a pressure chamber (Scholander et al. 1965) manufactured by PMS Instrument, Co., Corvallis, OR. Pressure was increased at about 0.03 MPa·s^{-1}. To avoid exclusion errors (Millar and Hansen 1975) only 2 mm of the stem, from which the bark had been stripped, was allowed to extend out of the sealing cork. [illegible]nd lens or binocular microscope was used to view the return of the [illegible] sap to the cut surface.

Preliminary determinations of $\Psi_{P_{xylem}}$ made in the field and after the 10 - 16 hr transport time were not significantly different, and variability increased only slightly. Thus, it was concluded that in winter condition twigs and branch tips could be transported to the laboratory for determination of water relations parameters.

Water potential and components

Measurements of Ψ and $\Psi_{\pi+\tau}$ were made with Spanner (1951) type psychrometers constructed after Mayo (1974). In the laboratory, wintergreen needles were cut into 5 mm segments, and buds were dissected out

Table 6. Sampling pattern for water relations parameters from September 1977 to May 1978. All parameters were sampled monthly, except for those enclosed in parentheses. Wintergreen needled shoots were collected near the ground, regardless of the presence or absence of snow.

SPECIES	AGE AND HEIGHT OF TREES	SAMPLE SIZE, n, FROM N TREES*		PARAMETERS SAMPLED, TYPE OF PLANT MATERIAL, AND POSITION (i.e. above or below the snow)	
		n	N	North-facing site	South-facing site
Larix lyallii				Saplings	
	30–40 yr 3–4 m	7	7	$\Psi_{p_{xylem}}$; twigs; above and below	$\Psi_{p_{xylem}}$; twigs; above and below
		4 (2, 3)	7	Ψ, $\Psi_{\pi+\tau}$, % O.D.W.; dissected buds; above (below)	Ψ, $\Psi_{\pi+\tau}$, % O.D.W.; dissected buds; above (below)
				Small Trees	
	10–15 yr 0.2–0.7 m	7	7	Snowpack too deep to allow access to these small trees	$\Psi_{p_{xylem}}$; twigs; above and below
		4	7		Ψ, $\Psi_{\pi+\tau}$, % O.D.W.; dissected buds; above (below)
		7	7		$\Psi_{p_{xylem}}$; wintergreen needled shoots
		4	7		Ψ, $\Psi_{\pi+\tau}$, % O.D.W.; wintergreen needles
Abies lasiocarpa	30–50 yr 3–6 m	7	7	$\Psi_{p_{xylem}}$; branch tips; above	$\Psi_{p_{xylem}}$; branch tips; above
Picea engelmannii	40–70 yr 3–6 m	7	5	Does not occur on this site	$\Psi_{p_{xylem}}$; branch tips; above
Pinus contorta	50+ yr 1–3 m	7	2	Does [illegible] occur on this site	$\Psi_{p_{xylem}}$; branch tips; above

*When n < N composite samples were loaded into n psychrometer chambers, and when n > N several branch tips were taken from each tree.

of the short shoots with fine forceps, before being placed in the chambers. The chambers were entirely filled with tissue. Equilibration required 24 hr for wintergreen needles and up to 60 hr for the dissected buds during mid-winter. These long equilibration times are extraordinary, yet they were repeatedly verified. Typical time courses of equilibration are given in Appendix A. Equilibration time for buds decreased to 40 hr in April and to 20 hr by the end of May. The slow equilibration and its change with the season probably relates to the state of cold-hardiness or dormancy of this tissue, and to the effectiveness of the cuticle.

Filled psychrometers were suspended in a large, well-stirred, room temperature water bath during equilibration and reading. Readings were taken with a microvoltmeter (Wescor, Inc., Logan, UT; Model MJ55) after application of a 7 mA cooling current for 10 s. Two readings (within 0.3 µv of each other) were corrected to 25°C (Weibe et al. 1970) and averaged.

After determination of Ψ, each chamber was wrapped in aluminum foil and submerged in liquid nitrogen (-196°C) to rupture cell membranes. After warming to room temperature, the chambers were reequilibrated (2 hr) and a second set of readings taken to determine $\Psi_{\pi+\tau}$.

The psychrometers were individually calibrated using standardized KCl solutions (Slavik 1974) (see Appendix A). Turgor (Ψ_p) was estimated by Eq. 1 (Slatyer 1967).

$$\Psi_p = \Psi - (\Psi_{\pi+\tau}) \qquad (1)$$

Water content

Water content, as percent of oven-dry weight (% O.D.W.), was determined for the samples from the chambers after the psychrometric determinations. Fresh weight (W_f) and dry weight (W_d), after drying for 48 hr at 45°C, allowed calculation of % O.D.W. by Eq. 2 (Slavik 1974).

$$\%\ \text{O.D.W.} = \frac{W_f - W_d}{W_d} \cdot 100 \qquad (2)$$

Relative shrink-swell of bole reading

Dendrometer positioning screws (10 cm long) were installed in two *L. lyallii* trees on each site. A precision dial micrometer mounted on an aluminum base, with positioning cutouts (Daubenmire 1945), was used to measure changes in bole radius. Repeatability of this measurement was better than ± 25 μm. Readings, taken monthly, from the two trees on each site were averaged.

Estimation of Damage

Exposure tolerance of small larch trees

Growth chamber experiment

Thirty-six small larch trees, 15-20 yr old, were carefully dug and potted in 23 cm diameter plastic pots during the summer of 1976. Field soil was used and the soil around the base of the tree was disturbed as little as possible. Many of the roots of even these small trees extend beyond the volume contained by a 23 cm dia. x 20 cm deep pot, so root damage could not be avoided. These potted trees were maintained in the field until leaf abscission.

Twenty-four of these trees were subjected to increasingly winter-like conditions in a controlled environment chamber (EGC Inc., Chagrin Falls, OH.). Conditions in the chamber (Table 9) were changed at two week intervals. $\Psi_{P_{xylem}}$ was monitored weekly as the trees dried. Most trees had $\Psi_{P_{xylem}} \leq -6.5$ MPa after 8-9 wk.

Table 9. Conditions in controlled environment chamber during exposure tolerance experiment on small larch trees.

WEEK	DURATION (hr): LIGHT	DURATION (hr): DARK	LIGHT TYPE	TEMP. (°C) LIGHT	TEMP. (°C) DARK	REL. HUM. (%) LIGHT	REL. HUM. (%) DARK
1, 2	12	12	Full incandescent and fluorescent	5	0	65	90
3, 4	10	14	Full fluorescent	0	-1	70	90
5-10	0	24	-	-	-3	-	75

As controls, the remaining twelve trees were kept outside in Edmonton, Alberta during this period and were often, although not continuously, covered with snow. Their $\Psi_{p_{xylem}}$ was also monitored.

At the end of the experimental period both sets of trees were moved into a greenhouse with spring-like conditions (12 hr/12 hr, light/dark, 16°/ 8 °C) and recovery observed. Trees were considered recovered if $\Psi_{p_{xylem}}$ was similar to that of controls and a full set of needles, which lasted one growing season, was produced.

Snow fence experiment

To avoid the artificial conditions of potted trees and growth chambers, a field experiment kept several small larch trees on the south-facing site exposed during the 1977-78 winter. One meter square snow fences with small larch trees at each lower corner (Fig. 17) were installed perpendicular to the prevailing wind direction. Wind deflected around these barriers prevented snow accumulation over the experimental trees.

Water relations parameters, as in the other field studies, and visible damage (reddening of needles and needle cast) were monitored monthly. These data were contrasted to similar data obtained on snow covered trees during the normal monthly sampling. In addition, survival, needle production, and growth of the exposed trees were followed through the next growing season.

Field comparisons of damage to larch and fir

To assess the amount of winter damage suffered by *L. lyallii* in comparison to *A. lasiocarpa*, paired trees were sampled for foliage and apical and lateral bud mortality following the low snow, high damage winter of 1976-77. The sampled trees were growing side by side

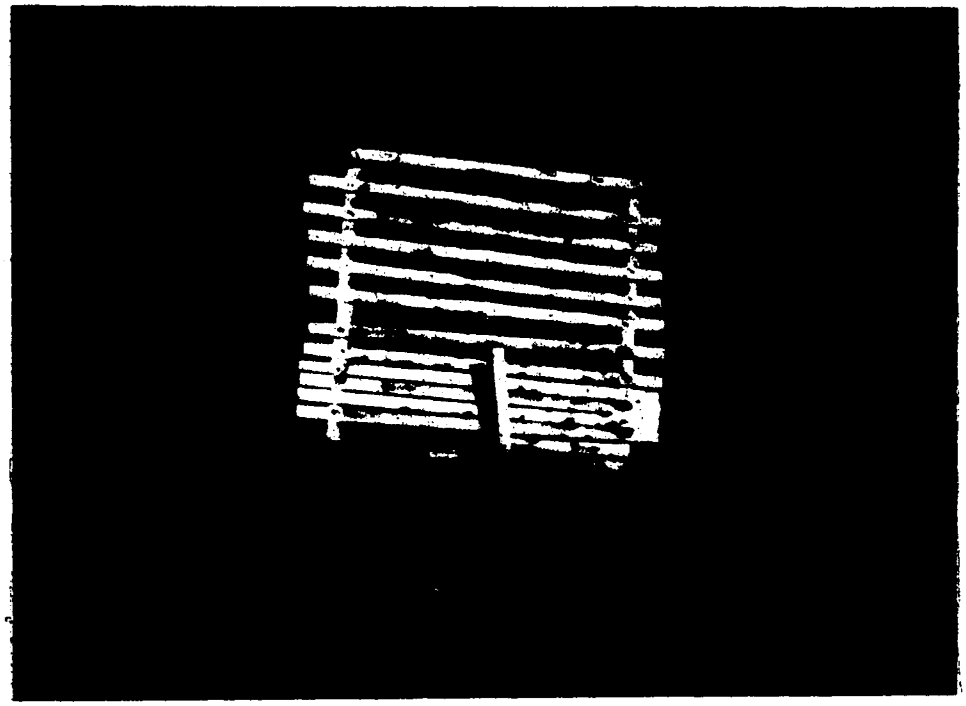


Figure 17. Mini-snow fence to maintain snow-free conditions around small alpine larch tr~~ees at~~ the lower corners. Photograph taken 7 September 1977.

COLOURED PICTURE

on the south-facing and krummholz sites. Trees were paired for similar height and exposure. Sampling was done in mid-summer so that live and dead shoots could easily be distinguished. Live and dead short shoots and buds were counted, and percent of total foliage that was dead was determined for evergreen and wintergreen needles. Wilcoxon's signed ranks test, one-tailed, was used for statistical comparison (Sokal and Rohlf 1969).

Winter Water Loss Rates and Role of Young Twig Tomentum

Effect of tomentum on twig temperature

To determine if the tomentum on 1 yr old *L. lyallii* twigs influences radiational heating, measurements were made of the air-twig temperature differential for tomentose 1 yr twigs and non-tomentose 3-4 yr old twigs. Measurements were made on a clear October day (16th) when air temperature at twig level (1 m) was 5.8 ± 0.2°C. Two pairs of thermocouple networks, each consisting of three fine wire Cu-Con thermocouples (0.076 mm diameter) connected in parallel, were read alternately 15 times with the equipment previously described (p.77). Thermocouples were attached to twigs with fine spring-steel wire clips. One network pair gave air-tomentose twig difference and the other gave air-non-tomentose twig difference. The unpaired t-test was used for statistical comparison.

Rates of water loss and effect of tomentum

The rates of water loss were determined on alpine larch twigs collected on 19 February 1978. Branch twigs, including 3-4 yr of growth were sealed in plastic bags, clipped, and kept frozen until the rate determination could begin. In the laboratory the 3-4 yr and 1 yr sections of branch were clipped and the cut ends sealed with 5 min. epoxy. Paired new growth twigs were chosen for evaluation of the effect of tomentum on the rate of water loss. Using a scalpel, the tomentum was carefully removed from one twig in each pair. Five twigs of each type (1 yr tomentose, 1 yr stripped, 3-4 yr non-tomentose) were arranged randomly in styrofoam supports, which held them upright. One set of 15 twigs was prepared for each of four environmental treatments.

Four vapor pressure deficit (VPD) treatments were obtained by using high and low humidity desiccators (85 and 8% at 25°C) under high and low radiation (200 and 50 Wm^{-2}). Constant humidities within the desiccation chambers were maintained by saturated solutions of KCl and KOH, respectively (Winston and Bates 1960). A fan inside each chamber maintained adequate mixing and high air speeds. Air and twig temperatures were monitored with fine wire Cu-Con thermocouples (0.076 mm diameter) read with a digital thermometer (Fluke Co., Mountlake Terrace, WA; Model 2100A). The experiments were conducted inside a controlled environment chamber (EGC, Chagrin Falls, OH), which maintained air temperatures of 26.2 ±2.0°C under low light and 34.8 ±1.0°C under high light.

At approximately two hour intervals the twigs were removed from the desiccators and quickly weighed on an analytical balance. After eight hours the twigs were dried at 80°C to constant weight and measured with calipers. Surface area was calculated using a cylindrical model. The glass bead technique for determining surface area (Thompson and Leyton 1971) was ineffective because the tomentum and waxy bark prevented uniform glass bead adherence.

RESULTS

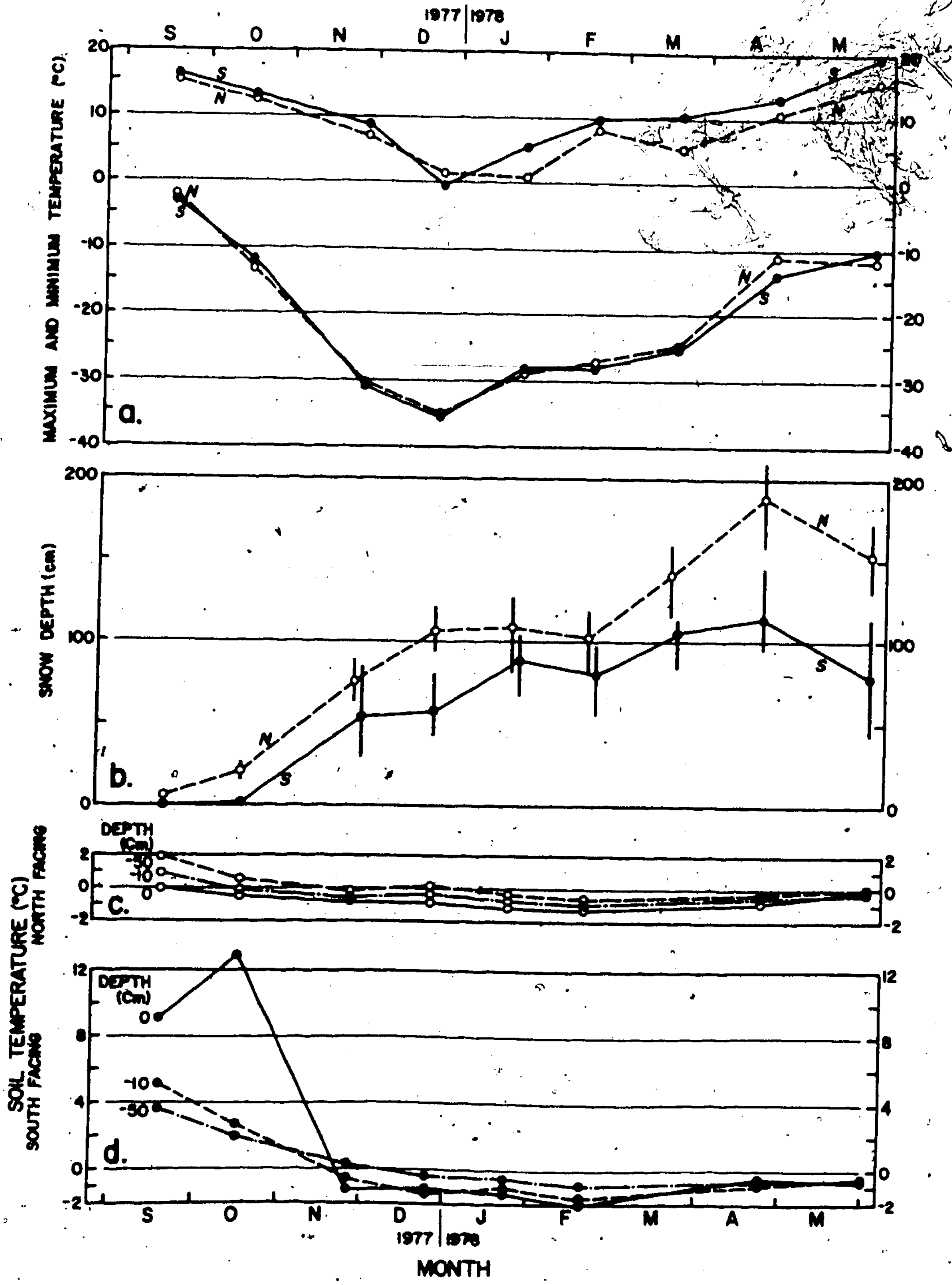
The Winter Environment

The north- and south-facing sites did not show any differences in monthly minimum temperatures during the 1977-78 winter (Fig. 18a). Monthly maximum temperatures were also similar from September through December 1977, despite the major exposure difference. From January to June 1978, however, the south-facing site was consistently 1 - 4°C warmer on the warmest days. On the south-facing site, at least one day per month was above freezing, except during December when the maximum temperature was -1°C. On the north-facing site, the maximum temperature was only slightly above the freezing point (1.0 and 0.5°C) in December and January. Because of these low monthly maximum temperatures, there was probably little or no thawing of exposed plant tissues during December on the south-facing site and during December and January on the north-facing site.

Figure 18b shows the much greater snow accumulation on the north-facing site, a result of earlier snowpack development, less consolidattion by wind and solar heating, and protection from the prevailing winds. The great range of snow depths on the south-facing site in November is the result of snow redistribution on this exposed site during a particularly windy month (Environment Canada, 1977). Differential accumulation on the two sites was noticeable in December and January, but wind data are missing. Accumulation was also different on the two sites during March and April, a result of higher maximum temperatures on the south-facing site.

The difference in snow cover during September and October, in combination with the different exposure results in very large differences

Figure 18. Environmental data from the north-facing (N) and south-facing (S) study sites for the 1977-78 winter season; a) absolute monthly maximum and minimum temperatures; b) mean and range of snow depths along 10-point, contour transects; c and d) soil temperatures at 0, 10, and 50 cm depths on north- and south-facing sites, respectively. (The average of two measurements at each depth is plotted).


1977 | 1978
S O N D J F M A M
MAXIMUM AND MINIMUM TEMPERATURE (°C)
20
10
0
-10
-20
-30
-40
S
N
a.
SNOW DEPTH (cm)
200
100
0
b.
SOIL TEMPERATURE (°C)
NORTH FACING
DEPTH (Cm)
-50
-10
0
2
-2
c.
SOUTH FACING
DEPTH (Cm)
0
-10
-50
12
8
4
d.
S O N D J F M A M
1977 | 1978
MONTH

in soil temperatures on the two sites (Fig. 18c and d). In late August and early September, frost often remained on the ground until mid-day on the north-facing site. At the same time, soil surface temperatures on the south-facing site were as high as 20 - 25°C. After an insulating mantle of snow (~ 50 cm) had developed, the soils maintained a fairly constant temperature profile. They were not < -1.0°C at 50 cm and only a little cooler above. The soils became isothermal at -0.5°C in late April (south-facing) or mid-May (north-facing), probably because of snowpack meltwater influx.

Meteorological data (Environment Canada 1968 to 1978) from Marmot Creek Basin allow comparison of long-term mean conditions with those of the 1977-78 winter when the intensive sampling was done. At a station only 0.5 km west of the north-facing study site, mean monthly temperatures throughout the 1977-78 winter were very close to the 10 yr monthly means (Fig. 19). Interpretation of winter-time absolute maximum and minimum temperatures is difficult because of their wide range and great daily fluctuation (Janz and Storr 1977). To aid in interpreting the absolute maxima and minima given in Fig. 18a, similar values, based on the 10 yr record, are compared to the mean maximum and minimum temperatures in Fig. 19.

Snow accumulation during 1977-78 was also very close to the 10 yr mean (Table 10). Other environmental variables (humidity, wind speed, radiation) show greater deviation from the 10 yr mean. Although humidities were higher than normal, at the low winter temperatures this makes little difference in vapor pressure deficit. Wind speeds were greater than normal in the fall and early winter (1977), but below normal in the late winter and early spring (1978). Incoming short-wave radiation

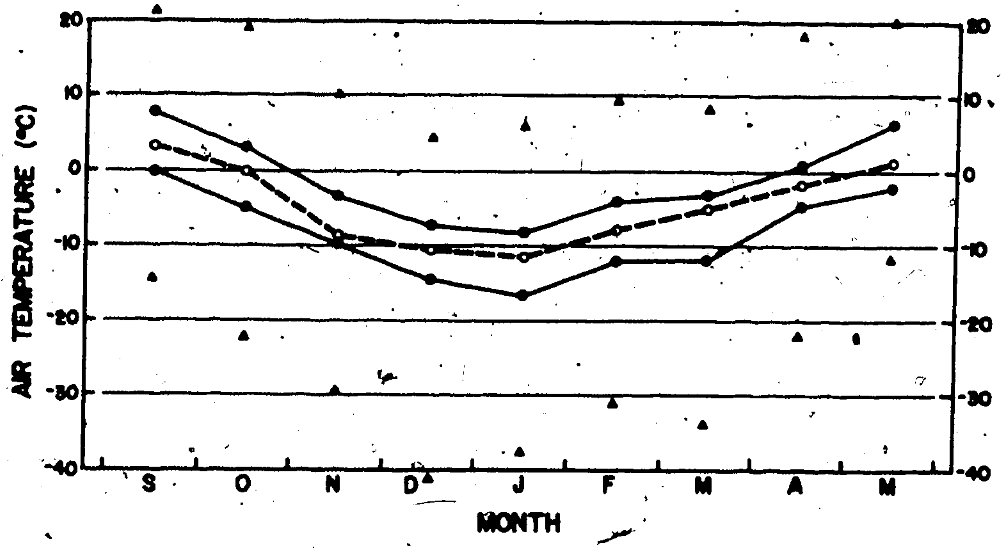


Figure 19. Ten year mean (●) and absolute (▲) maximum and minimum temperatures, and mean temperatures for the 1977-78 winter (o) at Twin 1, (2285 m). This station is 0.5 km west of the north-facing study site in Marmot Creek Basin. Data from Environment Canada (1968-1978).

Table 10. Winter environmental data, 10 (9) yr means and 1977-78, from meteorological stations in Marmot Creek Basin. Humidity, vapor pressure deficit (VPD)* and wind are from Twin 1 (see Fig. 19). Radiation data are 9 yr means from Twin 12 (1750 m) in the subalpine forest ~ 3 km east of the study sites. Snow water-equivalents are from a permanent snow course (#19) in Middle Creek cirque between the two study sites.

PARAMETER	MONTH	1977-78	10 (9) YR MEAN
Mean humidity (%)	October	61	61
	December	76	72
	February	76	67
	April	76	67
Mean maximum VPD* (kPa)	October	0.50	0.43
	December	0.14	0.15
	February	0.18	0.22
	April	0.29	0.34
Mean wind speed ($m \cdot s^{-1}$)	October	4.5	3.9
	November (Dec. missing)	6.0	4.3
	February	3.6	3.9
	April	2.3	3.5
Mean daily global radiation ($MJ \cdot m^{-2}$)	October	11.1	8.6
	December	2.1	2.2
	February	7.3	6.3
	April	12.1	15.8
Mean snow water-equivalent (cm)	February	12.7	13.0
	March	14.7	15.5
	April	24.6	21.6
	May	32.3	24.4
	June	-	6.9

*VPD calculated from mean monthly temperature and humidity according to Williams and Brochu (1969).

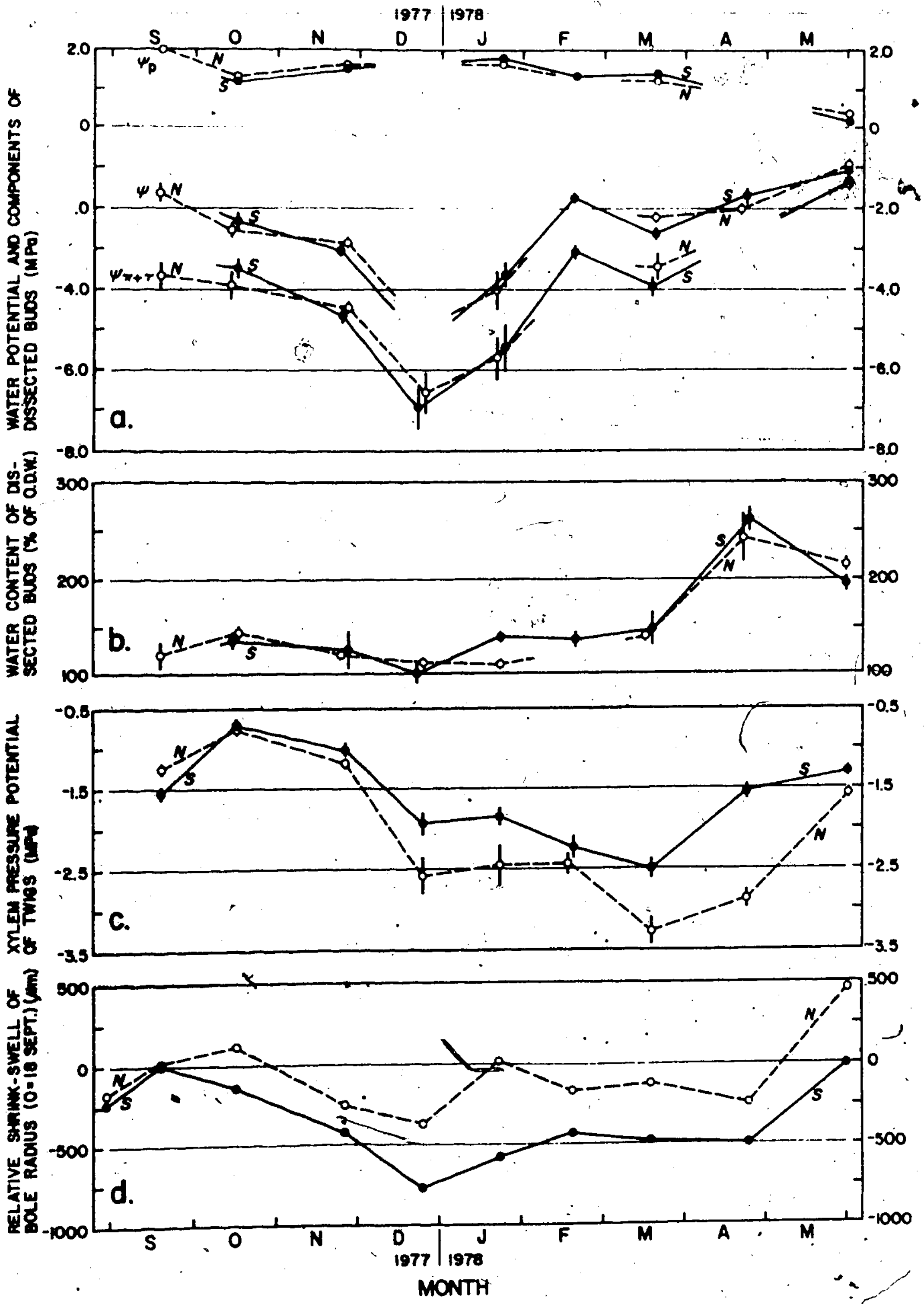
also varied from above to below mean on a month-to-month basis. Although some parameters deviated slightly from the mean, in Marmot Creek Basin the 1977-78 winter was very close to average in the important parameters: temperature, VPD, and snow accumulation.

Seasonal Variation in Water Relations Parameters

Winter water relations parameters of L. lyallii saplings on both sites are shown in Fig. 20. $\Psi_{\pi+\tau}$ of dissected buds drops to very low values (-6.6 and -7.0 MPa, north- and south-facing, respectively) in December but rises in late winter (Fig. 20a). Estimates for Ψ based on $\Psi_{\pi+\tau}$ and November and January Ψ_p are also very low (-5.0 and -5.3 MPa, respectively). Seasonal variation in both Ψ and $\Psi_{\pi+\tau}$ is similar to the variation in air temperatures. The correlation of $\Psi_{\pi+\tau}$ is better with maximum temperatures ($r=0.89$) than with minimum temperatures ($r=0.73$), but both are significant at $p<0.01$. The extremely low values of $\Psi_{\pi+\tau}$ recorded for December are near the limits of measurement by thermocouple psychrometry (Van Haveren and Brown 1972) and should be regarded as estimates. The large standard errors of the December and January measurements reflect this uncertainty. Nevertheless, these measurements are indicative of very low potentials.

As with Ψ and $\Psi_{\pi+\tau}$, there were no significant differences in Ψ_p of dissected buds from the two sites. Ψ_p remained quite high (mean of 1.5 MPa) and constant throughout the winter (Fig. 20a). The first visually observable changes in the buds occurred in March, when during dissection the immature leaves were more fragile than usual. Initial expansion was not apparent until April and was proceeding rapidly by the 1 June sampling. Ψ_p declined significantly ($p<.05$) during expansion.

Figure 20. Water relations parameters of Larix lyallii saplings on north-facing (N) and south-facing (S) study sites during the 1977-78 winter: a) total (Ψ), osmotic plus matric ($\Psi_{\pi+\tau}$), and turgor (Ψ_p) potentials of dissected buds (mean ± SE, n = 4(5)); b) water content (% O.D.W.) of dissected buds (mean ± SE, n = 4(5)); c) xylem pressure potential ($\Psi_{p_{xylem}}$) of twigs (mean ± SE, n = 7); d) shrink-swell of bole radius relative to the value on 18 September 1977 (mean, n = 2). All samples were collected above the snowpack.


1977 | 1978
S O N D J F M A M
WATER POTENTIAL AND COMPONENTS OF DISSECTED BUDS (MPa)
2.0
0
-2.0
-4.0
-6.0
-8.0
ψ_p
ψ
$\psi_{\pi+\tau}$
N
S
a.
WATER CONTENT OF DISSECTED BUDS (% OF O.D.W.)
300
200
100
b.
XYLEM PRESSURE POTENTIAL OF TWIGS (MPa)
-0.5
-1.5
-2.5
-3.5
c.
RELATIVE SHRINK-SWELL OF BOLE RADIUS (0=18 SEPT.) (μm)
500
0
-500
-1000
d.
MONTH

Bud expansion is indicated by the 100 - 120% O.D.W. increase in water content from March to April (Fig. 20b). Throughout the winter there were no significant differences between the two sites, except in January, when the buds on the south-facing site showed a 34% O.D.W. increase in water content. At the same time, water content of buds on the north-facing site remained almost unchanged from December. Buds on this site had rehydrated to pre-December values by March. These differences parallel the pattern of maximum temperatures on the two sites (see Fig. 18a). It appears that when temperatures of +5 to 10°C occur, the tissues thaw sufficiently to allow bud rehydration consistent with their hardened state.

Notwithstanding the exceptions just mentioned, water content of the dissected buds remained relatively constant throughout the winter months. On both sites, buds show a trend of water loss from October through December or January decreasing from 142 - 136% to 108 - 100% O.D.W. In the late winter (March) buds from trees at both sites rehydrate to 137 - 143% O.D.W. before rapid expansion and water uptake begins in early spring (April) (Fig. 20b). While these small changes in water content are proceeding, Ψ and $\Psi_{\pi+\tau}$ are undergoing large changes. Using the Van't Hoff relation (Eq. 3), an approximation of the expected osmotic pressure (Π_s) change due to the concentration effect of the measured dehydration can be calculated (Nobel 1974).

$$\Pi_s = RT\, c_s \tag{3}$$

where R = gas constant (8.3141×10^{-3} l·MPa·mole^{-1}·°K^{-1}

T = temperature (°K)

c_s = total solute concentration (moles·kg^{-1}).

From Eq. 3 it can be seen that the osmotic pressures of states i and j, Π_{s_i} and Π_{s_j}, respectively, are related to the concentrations, c_{s_i} and c_{s_j}, by Eq. 4 (assuming constant temperature):

$$\frac{\Pi_{s_i}}{\Pi_{s_j}} = \frac{c_{s_i}}{c_{s_j}} . \tag{4}$$

The ratio of solute concentrations can be calculated from water content data by making an assumption about the portion of dry matter that is osmotically active. Assuming 100%, which will overestimate the difference,

$$\frac{c_{s_i}}{c_{s_j}} = \frac{\%\ \text{O.D.W.}_j}{\%\ \text{O.D.W.}_i} . \tag{5}$$

Substituting,

$$\frac{\Pi_{s_i}}{\Pi_{s_j}} = \frac{\%\ \text{O.D.W.}_j}{\%\ \text{O.D.W.}_i} \tag{6}$$

Bud water content declined from 142 to 110% O.D.W. on the north-facing site and from 136 to 100% O.D.W. on the south-facing site from October to December. Using these values, October $\Psi_{\pi+\tau}$ values as estimates of Π_{s_i} (-3.87 MPa and -3.45 MPa, north- and south-facing, respectively) and Eq. 6, predicted December Π_{s_j} values can be calculated. Thus, estimated December $\Psi_{\pi+\tau}$ values for the north- and south-facing sites are -4.98 MPa and -4.69 MPa, respectively. These estimates would be ~ 0.60 MPa less negative if only 50% of the dry matter was osmotically inactive. Matric potential effects and solute interactions are not included in the estimates (see Nobel 1974). Nevertheless, the estimated values are much less negative than measured December $\Psi_{\pi+\tau}$ for the north- and south-facing sites, -6.61 MPa and -7.00 MPa, respectively.

These differences and the parallel rise in $\Psi_{\pi+\tau}$ on both sites in January, when water contents fell slightly on the north-facing site, but rose on the south-facing site, support the conclusion that the observed changes in water potential are not due entirely to dehydration of the buds. The pattern of water potential changes is probably related to the cold hardiness and dormancy of the tissue. It thus may be under physiological rather than direct environmental control.

Total and osmotic plus matric potentials and water contents were determined for buds of small L. lyallii trees in the same manner as for the saplings, and in all cases the values obtained were not different ($p=0.05$) than the corresponding values for sapling buds. This correspondence further supports the conclusion that the buds of larch are relatively indifferent to environmental conditions during winter.

Xylem pressure potential of the needleless twigs of larch showed a pattern very different from that of the bud water potentials. The lowest $\Psi_{P_{xylem}}$ was reached in March and was much higher than the lowest potentials obtained from the buds (Fig. 20c). Data from 1975-76 and 1976-77 confirm this pattern of xylem pressure potential through the winter season. The lowest $\Psi_{P_{xylem}}$ measured for well extablished trees was -3.60 MPa in 1976-77 on a very exposed, north-facing site at Highwood Pass, Alberta.

Xylem pressure potential was consistently lower on the north-facing site, although only statistically so in September, March, April and May. A possible explanation for the lower potentials is shown by the lower shrinkage of the bole on that site (Fig. 20d). Perhaps due to less thawing of exposed branches and twigs, water stored in the bole above the snowpack and 'available' (Larcher 1963; Jarvis 1975; Waring and Running 1976, 1978) could not move to the branch tips. Thus $\Psi_{p_{xylem}}$ fell to lower levels there. A simple diagrammatic model relating bole storage, $\Psi_{p_{xylem}}$ and bud Ψ will be given in the discussion (see Fig. 24).

The low xylem pressure potentials seen in late winter or early spring, and differences between sites suggest that this parameter is an indicator of cumulative, winter season, net water losses. It appears to be influenced directly by environmental rather than physiological conditions. Also, $\Psi_{p_{xylem}}$, is not closely linked to bud water potential.

The ratio of bud water potential to twig xylem pressure potential (from the same samples) is shown in Fig 21. This indicates clearly the very high resistance that must exist between the short shoot buds and the xylem. The resistance forms rapidly in early October and probably remains quite high until February or March, by which time the two potentials are again in equilibrium. Small variations around the 1/1 ratio in June, July, and August (included for comparison) and in February through May are probably the result of experimental errors, diurnal variations and non-equilibrium conditions.

On the north-facing site twigs below the snowpack have the same or higher xylem pressure potential than twigs on the same trees, but above the snowpack (Fig. 22a). On the south-facing site, however, twigs below the snowpack have lower $\Psi_{p_{xylem}}$ than twigs above the snow. Although these trends are apparent, statistically there are no differences ($p=0.05$) between $\Psi_{p_{xylem}}$ above and below the snowpack. Xylem pressure potentials from 1975-76 and 1976-77 follow the same trends. These

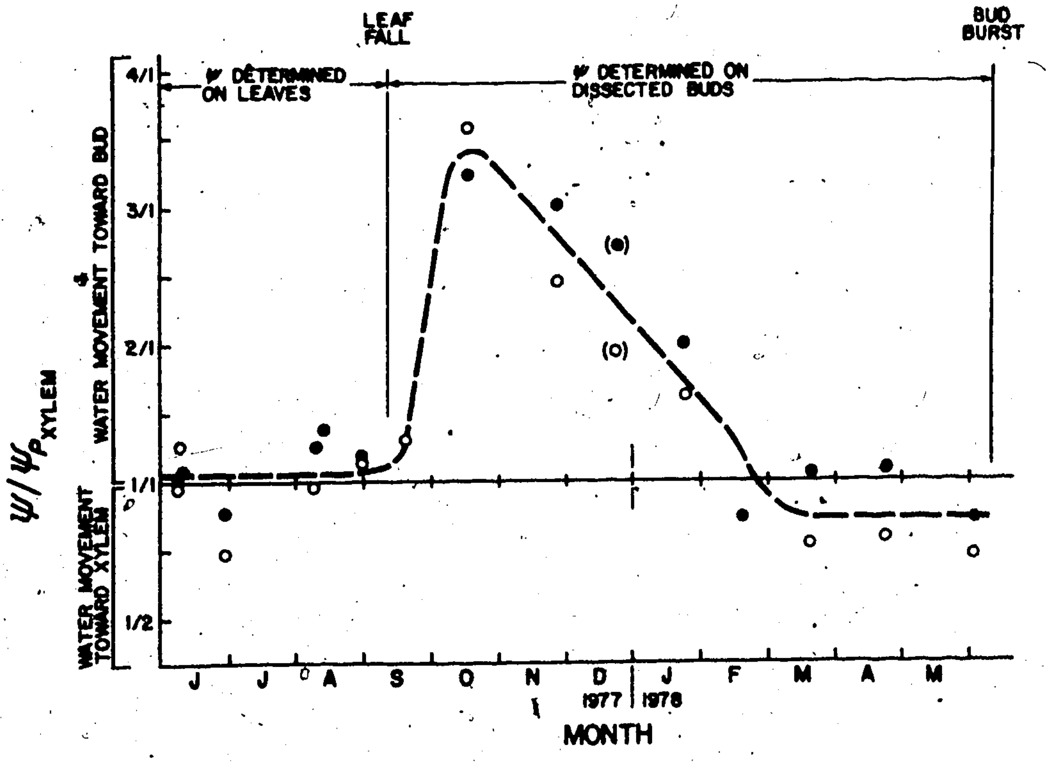
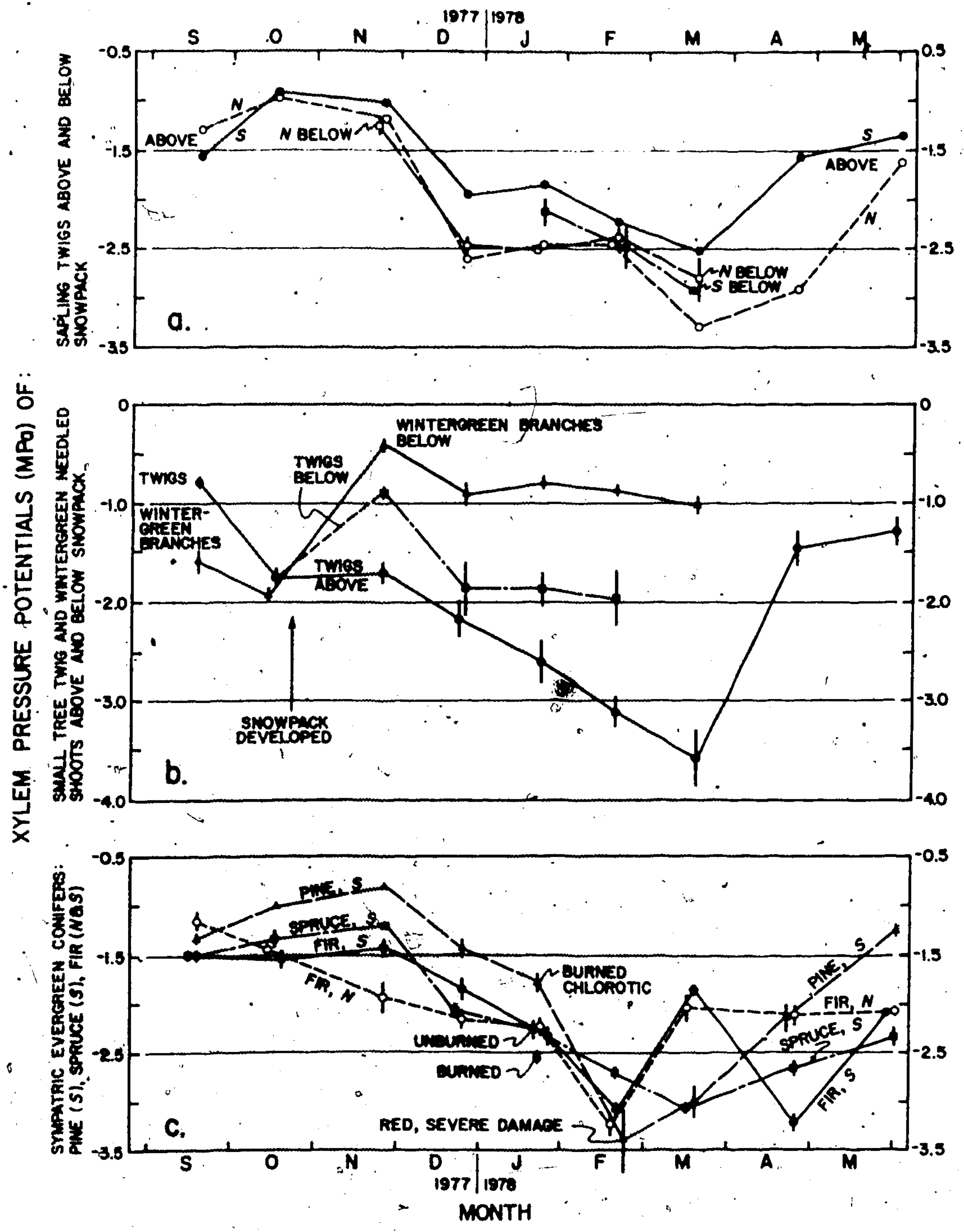


Figure 21. The ratio of leaf or dissected bud total water potential (Ψ), as determined by chamber psychrometry, to the xylem pressure potential ($\Psi_{P_{xylem}}$), as determined by the pressure chamber technique, varies similarly in trees from both the north-facing (o) and the south-facing sites (●). Ψ values for December were estimated by subtracting the average of November and January turgor (Ψ_p) from $\Psi_{\pi+\tau}$ determined in December (See Eq. 1).

Figure 22. Monthly, midday (1100-1300) xylem pressure potentials of: a) twigs of sapling Larix lyallii on both north-facing (N) and south-facing (S) sites, and collected either above (SE given in Fig. 20c) or below the snowpack; b) twigs from above and below the snowpack and wintergreen needled branch tips from below the snowpack, of small L. lyallii on the south-facing site; c) branch tips of Abies lasiocarpa (fir,s), Picea engelmannii (spruce,s) and Pinus contorta (pine,s) on the south-facing site, and A. lasiocarpa (fir,s) on the north-facing site, all collected above the snowpack. Mean ± SE, n = 7.


XYLEM PRESSURE POTENTIALS (MPa) OF:
1977 | 1978
S O N D J F M A M
-0.5
-1.5
-2.5
-3.5
0.5
SAPLING TWIGS ABOVE AND BELOW SNOWPACK
ABOVE
N
S
N BELOW
N BELOW
S BELOW
S
ABOVE
N
a.
0
-1.0
-2.0
-3.0
-4.0
SMALL TREE TWIG AND WINTERGREEN NEEDLED SHOOTS ABOVE AND BELOW SNOWPACK
WINTERGREEN BRANCHES BELOW
TWIGS
TWIGS BELOW
WINTER-GREEN BRANCHES
TWIGS ABOVE
SNOWPACK DEVELOPED
b.
SYMPATRIC EVERGREEN CONIFERS: PINE (S), SPRUCE (S), FIR (N & S)
PINE, S
SPRUCE, S
FIR, S
FIR, N
BURNED CHLOROTIC
UNBURNED
BURNED
RED, SEVERE DAMAGE
PINE, S
FIR, N
SPRUCE, S
FIR, S
c.
MONTH

data also show that there was no detectable diurnal change in sapling twig $\Psi_{p_{xylem}}$.

The water potentials and water content of L. lyallii sapling buds from above and below the snowpack (Table 11) also show no statistical differences ($p=0.05$). These data (except the January water contents) show the same trends as the $\Psi_{p_{xylem}}$ measurements from above and below the snowpack on the two sites.

Small larch tree twigs on the south-facing slope show much lower xylem pressure potentials, -3.5 MPa, than do twigs from larger trees, -2.5 MPa, on the same site (Fig. 22a and b). Twigs and wintergreen needled shoots protected by the snow have much higher $\Psi_{p_{xylem}}$ than exposed twigs (Fig. 22b). This again contrasts with the results from saplings, where there are no above - below snow pack differences.

Only a small volume of water can be stored in the stems of these small trees. Therefore, even with thawing, little water can be supplied to the twigs. Continued water loss causes the $\Psi_{p_{xylem}}$ of exposed twigs to fall, while snow protected twigs lose little water. Thus, they have higher $\Psi_{p_{xylem}}$ values.

Figure 22c shows the xylem pressure ~~potentials~~ potentia of the evergreen conifers sympatric with L. lyallii on both study sites. Abies lasiocarpa, Picea engelmannii and a few Pinus contorta occur on the south-facing site, while only A. lasiocarpa occurs on the north-facing site. Pinus contorta showed apparent visible damage, and appeared chlorotic in January when at only -1.80 MPa. After this initial damage had occurred, $\Psi_{p_{xylem}}$ dropped sharply and severe damage was apparent. A number of exposed branch tips were killed, while on others 50 - 80% of the needles were killed. Windward shoots of Picea engelmannii were

Table 11. Water potential (Ψ) and water content of buds of *Larix lyallii* saplings collected from above and below the snowpack. No above-below comparisons are significant ($p > .05$). t-statistic and df are given in parentheses.

MONTH (1978) AND SITE	Ψ (MPa)				WATER CONTENT (%O.D.W.)			
	ABOVE	BELOW	(t	df)	ABOVE	BELOW	(t	df)
January North-facing	-4.0	-3.4	(1.3	3)	108	100	(0.8	3)
February South-facing	-1.7	-2.0	(2.0	6)	130	120	(2.2	6)
March South-facing	-2.6	-2.6	(0.2	4)	143	127	(0.7	4)

damaged in January and had $\Psi_{p_{xylem}} = -2.50$ MPa. Leeward branches showed no visible damage when examined with a hand lens and had $\Psi_{p_{xylem}} = -2.30$ MPa. The $\Psi_{p_{xylem}}$ values were not statistically different ($t=1.69$, $df=6$). There continued to be both damaged and undamaged shoots (and needles) on P. engelmannii for the rest of the winter, but no significant differences were found in $\Psi_{p_{xylem}}$ of the two types. Of the evergreen conifers, the seasonal pattern of spruce $\Psi_{p_{xylem}}$ was most similar to that of L. lyallii (Fig. 22a and c).

The sampled A. lasiocarpa showed no apparent damage on either site during the 1977-78 winter even though $\Psi_{p_{xylem}}$ fell to -3.00 or -3.20 MPa in February (Fig. 22c).

The $\Psi_{p_{xylem}}$ of subalpine fir was nearly identical on both sites from December to March. In April, however, when the needles were noticeably greener and more flexible than previously, the south-facing site fir trees dropped to their lowest seasonal potentials. Trees on the north-facing site remained at their March levels. This difference is probably due to the more severe radiational conditions on the south-facing site, causing needle over temperatures and increased water loss rates. Uptake rates on both sites were probably similar since soil temperatures were nearly identical and the snow-insulated boles were probably at least partially frozen. It is also possible that some stomatal activity was involved in the rapid $\Psi_{p_{xylem}}$ decline of fir since neither pine nor spruce on the same site showed a corresponding drop.

From September to November, fir $\Psi_{p_{xylem}}$ changed little on the south-facing site. During this period 50 cm soil temperatures on the south-facing site declined from 4° to 0°C. Soil moisture was probably high because of melted fall snows. These conditions allowed fir on the south-facing site to replace water losses, thus preventing any decline in $\Psi_{p_{xylem}}$. On the north-facing site, however, less water uptake occurred because of the colder, drier soil and $\Psi_{p_{xylem}}$ dropped. In December and January water losses of fir were greater on the south-facing site than on the north-facing site due to differing radiational climates, but similar soil temperatures.

The water uptake and loss patterns of fir shown by $\Psi_{p_{xylem}}$, and in many ways those of spruce and pine, parallel the patterns of larch. This supports the conclusion that the water status of the tissues, as measured by the Scholander pressure chamber, is controlled by environmental conditions. In contrast, the water status of the larch buds, which behave as a relatively isolated system, is cued by environmental conditions, but is under physiological control.

Limits of Tolerance to Desiccation

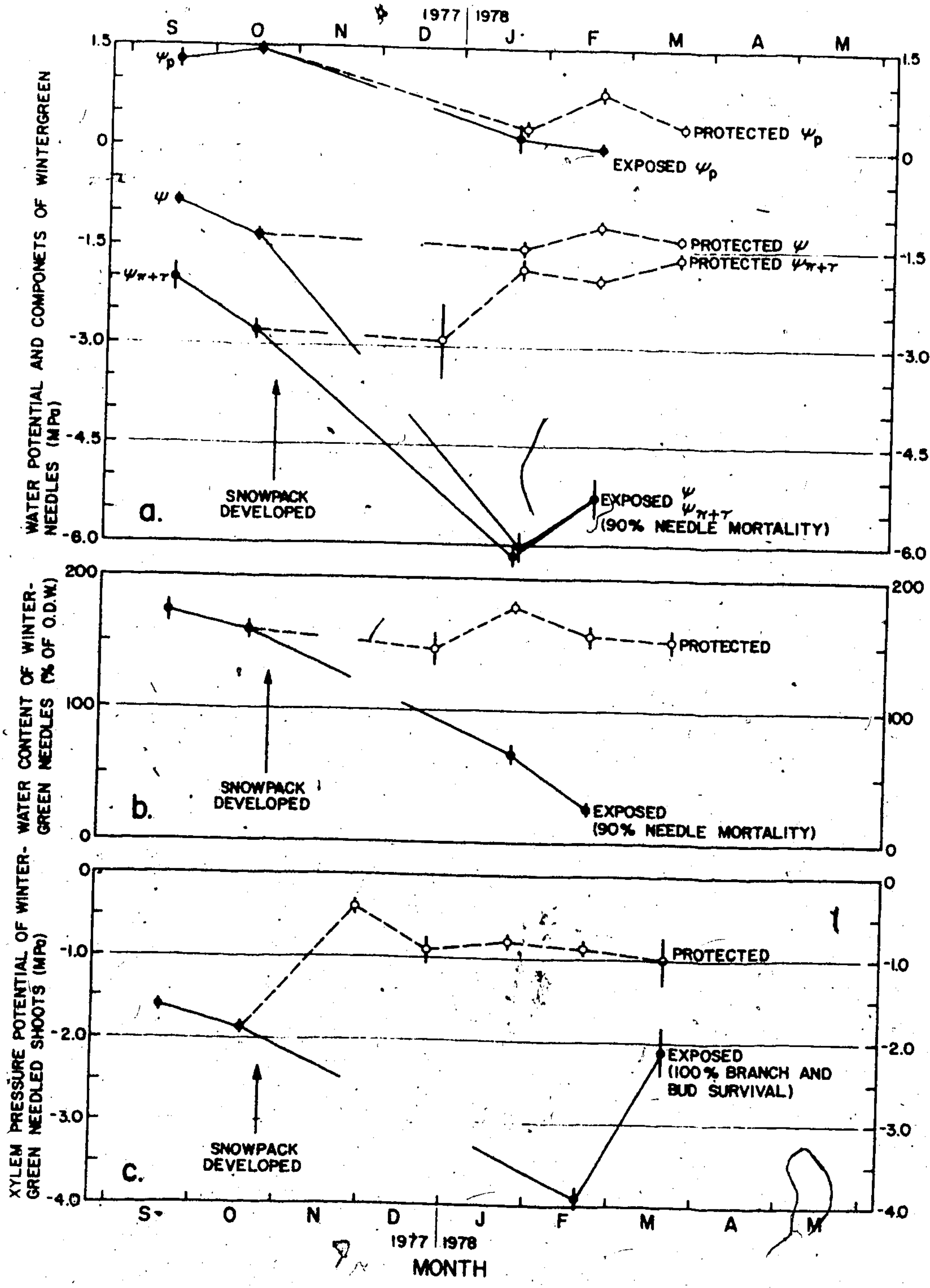
When small L. lyallii trees in pots were dried to low xylem pressure potentials (<-6.50 MPa) in a growth chamber, all wintergreen needles were cast. The trees recovered, after watering and warming, at the same pace as that of the control trees, and bud burst and needle elongation were similar. After one season's growth in a greenhouse, twenty (85%) of the stressed trees had produced full sets of needles, showed high $\Psi_{p_{xylem}}$ and appeared healthy. Eleven (92%) of the control trees had survived. Survival was independent (X_0^2=0.46, df=1) of the drying treatment, even after the damage to roots caused by potting. This experiment shows that small alpine larch trees are tolerant of $\Psi_{p_{xylem}}$ lower than any measured in naturally growing trees, whether protected or exposed. The wintergreen needles, however, do not tolerate such drying, and if killed represent a major carbon loss, and replacemant cost for these trees.

Results of the snow fence experiment are given in Fig. 23. Osmotic plus matric potential of protected (control) wintergreen needles reached a minimum of -2.90 MPa in December, while that of the exposed needles fell to ~-6.20 MPa in January (Fig. 23a). The wintergreen needles appeared burned, but were not cast until February. Only those needles (~10%) closest to the main stem and protected by the numerous short branches survived. Water content declined significantly (Fig. 23b) and turgor fell to zero (Fig. 23a) as the needles suffered damage and died. The snow protected needles remained hydrated (Fig. 23b), maintained turgor (Fig. 23a), and were healthy through the following (1978) growing season.

Although most wintergreen needles on the exposed trees were killed, the short shoot buds on those same branches were undamaged. After rehydration in spring, 1978, as shown by the recovery of branch $\Psi_{P_{xylem}}$ (Fig. 23c), they produced a full complement of new needles. The $\Psi_{P_{xylem}}$ of wintergreen needled shoots on control trees rose sharply to -0.40 MPa in November, after the development of a protective snowpack. Water uptake from the soil probably accounts for this rise as soil temperatures at 50 cm and below were >0°C. Protected shoot $\Psi_{P_{xylem}}$ then remained above -1.0 MPa throughout the winter (Fig. 23c).

These data support the conclusions reached from the growth chamber experiment. Wintergreen needles of young larch are not tolerant of exposure to winter conditions, and suffer severe dehydration and eventual mortality when not protected by snow. This damage apparently can occur after only one month's exposure. The buds and branches, however do survive undamaged after prolonged exposure and dehydration to low (-4.00 to -6.50 MPa) $\Psi_{P_{xylem}}$. This level of dehydration or exposure is not common

Figure 23. Water relations parameters of small *Larix lyallii* trees which were *protected* by the snow pack (controls) or experimentally maintained in an *exposed* condition. a) total (Ψ), osmotic plus matric ($\Psi_{\pi+\tau}$) and turgor (Ψ_p) potentials of wintergreen needles (mean ± SE, n=4); b) water content of wintergreen needles (mean ± SE, n=4); c) xylem pressure potential ($\Psi_{p_{xylem}}$) of wintergreen needled shoots (mean ± SE, n=7(5)).


1977 | 1978
S O N D J F M A M
1.5
0
-1.5
-3.0
-4.5
-6.0
WATER POTENTIAL AND COMPONETS OF WINTERGREEN NEEDLES (MPa)
ψ_p
PROTECTED ψ_p
EXPOSED ψ_p
ψ
PROTECTED ψ
$\psi_{\pi+\tau}$
PROTECTED $\psi_{\pi+\tau}$
SNOWPACK DEVELOPED
a.
EXPOSED ψ $\psi_{\pi+\tau}$
(90% NEEDLE MORTALITY)
200
100
0
WATER CONTENT OF WINTER-GREEN NEEDLES (% OF O.D.W.)
PROTECTED
SNOWPACK DEVELOPED
b.
EXPOSED
(90% NEEDLE MORTALITY)
0
-1.0
-2.0
-3.0
-4.0
XYLEM PRESSURE POTENTIAL OF WINTER-GREEN NEEDLED SHOOTS (MPa)
PROTECTED
EXPOSED
(100% BRANCH AND BUD SURVIVAL)
SNOWPACK DEVELOPED
c.
S O N D J F M A M
1977 | 1978
MONTH

under field conditions.

It is also apparent that Ψ of wintergreen needles is not equivalent to the $\Psi_{P_{xylem}}$ of the branches which bear them (Fig. 23a and c). This is true over a wide range of potentials when the branches and needles are in winter condition. These data imply that a large resistance to water movement forms between the xylem and the wintergreen needle in a manner analagous to that seen with the overwintering buds (see Fig. 21). The result of this is that the needles behave as a system relatively independent of the xylem. When protected by snow, little if any water is lost, and Ψ and $\Psi_{\pi+\tau}$ vary in relation to the state of hardiness or dormancy on the needles. Without snow cover protection needle loss is much more rapid than uptake from the xylem, and both water content and potential fall. Lethal levels of desiccation are rapidly reached. This suggests that the stomate-cuticle system of wintergreen larch needles is less effective than that of the evergreen conifers. The importance of snow cover for establishment is also suggested, and will be discussed in the context of the carbon cost of loosing overwintering needles, and concommitant reduction in carbon gain the following season (see Ch. VI).

Comparison of Damage to Larch and Fir

Comparison of the amount of damage caused by winter desiccation and/or abrasion to fir and larch gives some indication of the relative advantages of being evergreen or deciduous under winter conditions at timberline. The apical and lateral buds of larch suffered one third as much damage as those of paired subalpine fir during the 1976-77 winter. Also, the foliage-producing short shoot buds of larch were damaged one-half as much as the foliage of fir (Table 12). These data show that the high tolerance

Table 12. Winter damage to subalpine larch and fir on two exposed sites during the low snow winter of 1976-77. Paired trees, 0.35 - 2.00 m tall, were sampled during the 1977 growing season. Mean percent dead is given.

SITE	SPECIES	APICAL & LATERAL BUDS AND / OR BRANCHES (% dead)	FOLIAGE OR SHORT SHOOTS (% dead)
South-facing	Larch	13.2	16.6
	Fir	40.3	34.8
	(One-tailed, Wilcoxon's signed ranks test)	T=-2 p=.005	T=-3.5 p = .01
Krummholz band	Larch	33.8	16.8
	Fir	50.5	40.8
		(n = 4; too small for Wilcoxon's test)	

of alpine larch to desiccation, shown previously, results in less damage to not only its foliage producing buds, but also to its growing points. This is especially important in allowing L. lyallii to maintain an upright growth form under more rigorous conditions than fir, and probably accounts for its occurrence in a band above the subalpine fir-spruce forest. Much reduced damage to apical, lateral, and short shoot buds is a major advantage L. lyallii obtains by being deciduous.

Role of Tomentum and Water Loss Rates

The growing shoots of L. lyallii are covered by a dense, white tomentum which usually lasts through one winter. Two hypotheses that explain its presence can be tested during the winter. The first suggests that tomentum can alter the radiation balance of the twig surface, hence reducing twig temperatures. The second hypothesis states that the tomentum decreases the rate of water loss by increasing the thickness of the boundary layer.

According to the first hypothesis, lowered twig temperatures would reduce the water vapor pressure gradient, effectively reducing water loss. Measurement of tomentose 1 yr twig temperatures, simultaneously with measurement of non-tomentose 3-4 yr twig temperatures was done to test this hypothesis. Results showed tomentose twigs to be $0.4 \pm 0.2^{\circ}C$ to $1.0 \pm 0.3^{\circ}C$ lower in temperature than non-tomentose twigs. Is this small reduction in twig temperature ecologically significant?

The change in the vapor pressure gradient (due to twig temperature reduction) is directly proportional to the change in the rate of water loss by Ohm's law analogy (Slatyer 1967). Conditions similar to late winter or early spring were assumed and the vapor pressure gradients calculated for twig temperatures 1°C over or equal to air temperature. Assuming: twig saturation (100% relative humidity), air temperature of 5°C, and relative humidity of 40%; a 1°C reduction in twig temperature would only reduce evaporative losses by 10%. It is problematic whether such a reduction would substantially decrease shoot mortality, and thus be considered ecologically significant. Considering the great tolerance of alpine larch to winter dehydration due to the isolation of the buds from the main volume of twig tissue, as shown above, it is doubtful whether this is the case.

Measurement of actual rates of water loss under controlled environmental conditions allowed calculation of the conductivity to water vapor, and an estimation of the effect of the tomentum on it. This approach was taken to test the second hypothesis for tomentum presence.

The flux of water vapor from the twigs (J) was calculated from the weight loss rates and twig areas. Then, assumming a constant vapor density gradient ($\rho_{\text{twig surface}} - \rho_{\text{air}}$), the conductivity (K) to water vapor loss was calculated from the integrated form of Fick's law (Eq. 7):

$$J = \frac{(\rho_{\text{twig surface}} - \rho_{\text{air}})}{r} \qquad (7)$$

where r = resistance = $\frac{1}{K}$.

Mean conductivity for tomentose 1 yr twigs was 0.0046 $\text{cm}\cdot\text{s}^{-1}$, for stripped 1 yr twigs was 0.0059 $\text{cm}\cdot\text{s}^{-1}$, and for non-tomentose 3 - 4 yr twigs was 0.0051 $\text{cm}\cdot\text{s}^{-1}$. Resistances were 217, 169, and 196 $\text{s}\cdot\text{cm}^{-1}$, respectively.

Analysis of variance of the conductivity data (Table 13) showed that there were no significant differences in the conductivity to water vapor between the three twig types. The tomentum did not affect the water vapor loss rate enough to be detected in this experiment.

Table 13. Nested ANOVA for differences in conductance to water vapor of three twig types under four vapor density gradient treatments.

SOURCE	df	MS	F	p
Replicates	4	4.007×10^{-6}	1.88	n.s.
Vapor density gradients	3	59.535×10^{-6}	25.87	0.01
Error	12	2.136×10^{-6}	-	-
Subtotal	19			
Twig type	2	7.989×10^{-6}	1.44	n.s.
Twig type X Vapor density gradients	6	5.561×10^{-6}	4.99	0.01
Error	32	1.113×10^{-6}	-	-
Total	59			

Conductivities were significantly different at different vapor density gradients (Table 13). Mean conductivities of all twig types were higher in the low vapor density gradient treatments than in the high gradient treatments (Table 14). This difference is caused by the up to ten times greater amount of water lost by the twigs in the higher vapor density gradient treatments. The amount of water in the twigs affects the vapor density there ($\rho_{\text{twig surface}}$) and thus affects the vapor density gradient. Xylem pressure potentials of all twigs were -2.35 ± .25 MPa at the beginning of the experiment, and, based on other twig drying experiments, had fallen to ~-6.50 MPa after eight hours in the driest treatment. This change, although large biologically, is not great enough to explain the 50% reduction in rate of water loss.

The amount of water in the twigs probably also affects the physical properties of the bark, causing the conductance to decrease as the twigs become drier. This may be the cause of the difference shown in Table 14. It may also explain the significant interaction between twig type and vapor pressure gradient (Table 13). The interaction suggests that the physical changes in the bark are not identical in the three twig types.

DISCUSSION

Well established L. lyallii suffered far less winter desiccation damage than the dominant, sympatric, evergreen conifer, Abies lasiocarpa. Relatively light damage to apical and lateral buds (Table 12) explains how alpine larch maintains an upright growth form, while nearby evergreens are forced into krummholz forms (Arno and Habeck 1972). Greater damage at the krummholz site than on the south-facing site agrees with

Table 14. Non-significant ranges ($p = 0.01$) by Duncan's Multiple Range Test for mean conductance of all twig types at four vapor density gradients.

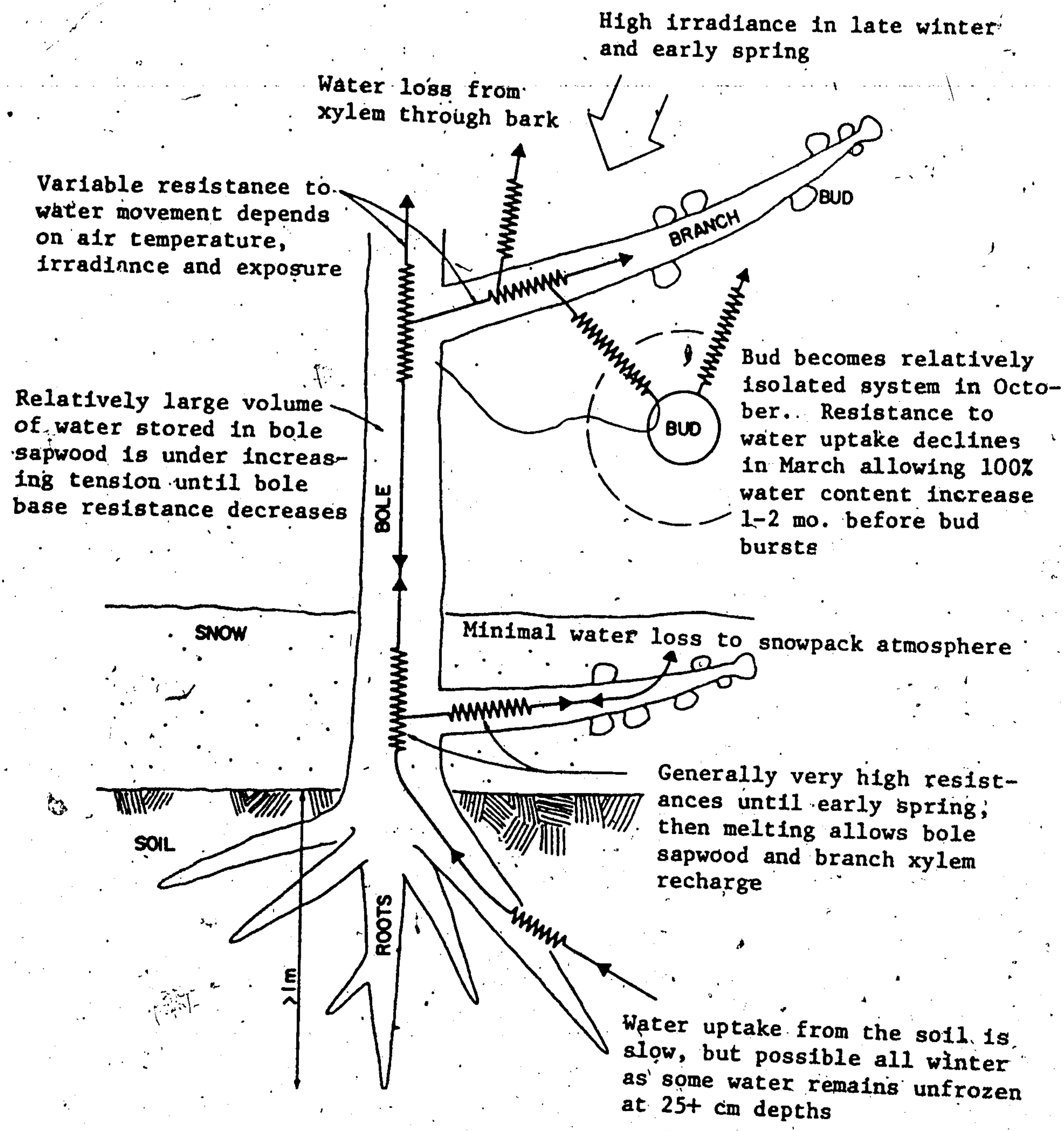
Vapor density gradient ($\mu g \cdot cm^{-3}$)	37.4	22.5	7.1	3.9
$\bar{K}$ ($cm \cdot s^{-1}$)	0.0036	0.0035	0.0074	0.0063

the results of Michaelis (1936a), Wardle (1968), Holtmeier (1971), Lindsay (1971), Baig et al. (1974) and Platter (1976, in Tranquillini 1979). However, even at this same site L. lyallii generally maintains upright growth and isolated individuals occur at higher elevations. The occurrence of upright trees of the damage-resistant L. lyallii above sympatric evergreens is common throughout its range (Arno and Habeck 1972). Drought-resistance pines, Pinus flexilis and Pinus aristata, can also occur, upright, above krummholz of other sympatric evergreens (Wardle 1965).

The damage data for L. lyallii do not contradict the hypothesis of Wardle (1971) and Tranquillini (1979) that winter desiccation damage determines the upper limit of timberline trees. These data show, however, that this deciduous species is at a considerable advantage over sympatric evergreens, and must reach its limit at a higher elevation.

Alpine larch obtains the advantage of superior winter desiccation stress tolerance by a combination of physiological-developmental and anatomical features. A simplified model of water movement in the soil-larch-atmosphere system in winter is illustrated in Figure 24.

The most striking result, and the one that differs most from previous winter water relations studies, is the apparent isolation of the bud from the xylem (Fig. 21 and 24). Romberger (1963) ~~reviews~~ the occurrence of a "peculiar anatomical feature — the crown" in eight genera of gymnosperms, including Larix. In L. occidentalis this structure, a plate of thick walled, pectic cells, begins to form between the bud and stem pith in late August. Development is completed just before dormancy in mid-October (Owens and Molder 1977). This sequence corres-



High irradiance in late winter and early spring

Water loss from xylem through bark

Variable resistance to water movement depends on air temperature, irradiance and exposure

Relatively large volume of water stored in bole sapwood is under increasing tension until bole base resistance decreases

Bud becomes relatively isolated system in October. Resistance to water uptake declines in March allowing 100% water content increase 1-2 mo. before bud bursts

Minimal water loss to snowpack atmosphere

Generally very high resistances until early spring, then melting allows bole sapwood and branch xylem recharge

Water uptake from the soil is slow, but possible all winter as some water remains unfrozen at 25+ cm depths

Figure 24. Simplified diagramatic model of <u>Larix lyallii</u> in winter showing pathways for and resistances to water movement.

ponds with what would be expected for L. lyallii. Senescence begins in late August (Fig. 15) and a very large bud-xylem water potential gradient develops by mid-October (Fig. 21).

The crown could serve as the isolating structure. It is, however, penetrated by procambial strands (Owens, pers. comm.; Romberger 1963). These may conduct water, even though experiments have shown that dye does not move past the base of the crown (Lewis and Dowding 1924, Romberger 1963). The present study suggests that in L. lyallii there is a very high resistance to water movement between the bud and the xylem, as a very substantial water potential gradient is maintained from October through January (Fig. 21).

The isolation of the bud from the xylem has several consequences which contribute to the great stress tolerance of alpine larch. Water lost directly from the xylem through the bark (Fig. 24) does not affect the water content of the buds. Even in the absence of desiccation tolerant buds, this would explain the tolerance of young, potted larch trees to very low xylem pressure potentials (see p. 106).

The bud tissues are, however, tolerant of very low (-6.6 to -7.0 MPa) water potentials (Fig. 20). Picea abies showed damage when osmotic potentials ranged from -4.2 to -6.4 MPa (Michaelis 1934b, Muller-Stoll 1954). Minimum osmotic potentials for a variety of species, compiled by Wilkinson (1977), range from -1.6 to -6.1 MPa.

The low water potentials of the immature, non-vacuolate bud cells may be more closely related to freezing tolerance (Levitt 1972) than to actual desiccation. The seasonal pattern of water potential of Ledum groenlandicum (Wilkinson 1977) and of Picea engelmanii and Abies lasiocarpa (Lindsay 1971) show minima in mid-winter (December or Janurary) when temperatures are lowest. This is similar to the pattern shown by L. Lyallii buds.

A final consequence of the high xylem-bud resistance is that low water potentials can be maintained in the buds, without water influx from the xylem. Xylem pressure potentials in December and January were only -1.8 to -2.6 MPa in the presumably non-cavitating stems of L. lyallii, while bud potentials were ~-5.0 MPa.

In the buds high turgor potentials (> 1.0 MPa) are maintained throughout the winter. This is quite surprising and contrasts sharply with the near zero to negative wintertime turgor potentials of Ledum groenlandicum (Wilkinson 1977). The buds also had quite high water contents, higher than the wintergreen needles (Fig. 21 and 23) and as high or higher than water contents reported through winter by Platter (1976 in Tranquillini 1979) for Pinus cembra (needles), Picea abies (needles and shoots), and Larix decidua (shoots).

The winter seasonal pattern of xylem pressure potential is very different than that of bud water potential. It follows the pattern reported for many timberline trees (Goldsmith and Smith 1926, Michaelis 1934b, Tranquillini 1957, Platter 1976 in Tranquillini 1979) and other conifers (van Zinderen Bakker 1974).

Referring again to Fig. 24, it can be seen that the portion of the tree above the snowpack is isolated from the snow covered branches and belowground system by the frozen, well-insulated, bole base. Water losses from the xylem through the bark are dependent on surface temperatures, which affect the water vapor density gradient to the air. When branches thaw due to above freezing air temperatures or high irradiance, water movement from the bole sapwood to branch xylem can occur. This phenomenon appears to occur more often on the south- than on the north-facing site, where xylem pressure potentials are lower and bole shrinkage less (Fig. 20). In small trees very low xylem pressure potentials develop in branches above the snowpack (Fig. 22), because bole water storage is much less. Similar data and interpretation are given by Tranquillini (1957, 1979) and Larcher (1963) for small individuals of timberline evergreens.

The seasonal pattern of xylem pressure potential, and the site and tree type differences just mentioned, all support the interpretation of cumumlative water loss through the winter. It will reach lower values where any recharge of branch tips is prevented by lack of thawing of bole and branch xylem, or by lack of stored, "available", water, as in small trees. Soil temperatures and snowpack depth will also be very important in determining the level of stress developed by late winter (Tranquillini, 1979).

The data presented in this study suggest that <u>L. lyallii</u> does not experience xylem pressure potentials that would be damaging, even on the most severe sites. This results from a combination of very great tolerance limits (< -6.5 MPa) and only moderately low field xylem pressure potentials (see p. 98).

Xylem pressure potentials of sympatric evergreens correspond well with those of larch saplings, and with the previously cited studies of evergreen timberline trees. Damage to <u>Pinus contorta</u> (see p. 103) at -1.8 MPa is somewhat surprising as damage to <u>Pinus banksiana</u> occurs only at < -3.0 to -3.5 MPa (Mayo, pers. comm.).

Also the sympatric spruce and fir, which are generally less desiccation resistant, were either not apparently damaged (fir) or did not show any visibly reddened needles until xylem pressure potentials were -2.3 to -2.5 MPa. The damage to the pine can probably be understood by considering the size and growth form of the sampled trees. Both were severely deformed krummholz type "trees", and only 1 - 1.5 m high. Their resistance to desiccation might be expected to be very low because of poor overall vigor and repeated losses of foliage in winter. This would support the general timberline hypothesis (Wardle 1971, Tranquillini 1979), in that these individuals are unable to develop their maximum potential desiccation resistance because of poor growing season conditions.

All of the tree species showed large increases in xylem pressure potential, and larch buds increased significantly in water content, in March or April (Fig. 20 and 22). Small L. lyallii trees on the south-facing site had a very large increase of xylem pressure potential from February to March (Fig. 23). These increases all occur as the snowpack begins to melt, and the bole base resistance declines (Fig. 24). On the south-facing site where the small trees were sampled the snow was not as deep as in other areas. Thus it is conceivable that additional soil water (from melted snow) became available and was taken up by the roots during March. It must be remembered that because of the leaflessness of the larch branches the volume of water required to increase the xylem pressure potential a certain amount would be much less than the volume required for a similar increase in an evergreen tree.

The snow-fence experiment (p. 107) demonstrates clearly that the wintergreen needles of young alpine larch are not tolerant of exposure to winter conditions. It suggests that maximum leaf resistances are far less than those of needles of evergreen trees. It also implies that alpine larch requires snow cover protection for establishment. Because the wintergreen needles are always born near the ground, this condition is not difficult to satisfy, in the habitats where alpine larch is found. These needles provide small larch trees with a potentially much longer growing season as they could be photosynthetically active immediately after snowmelt in the spring and could continue to fix CO_2 late into the fall. This will be discussed further in Ch. VI.

Measurements of the rate of water loss from winter twigs under controlled environmental conditions provided estimates of 169 - 217 $s \cdot cm^{-1}$ (p. 113) for diffusive resistance. Marchand and Chabot (1978) report calculated wintertime leaf resistances of 316 - 346 $s \cdot cm^{-1}$ for <u>Picea mariana</u> in the dark. The slightly lower resistances of <u>L. lyallii</u> bark as compared to spruce needles agree with the transpiration data of Ivanoff (1924 a,b) (see p. 14). Apparently <u>L. lyallii</u> does not obtain its wintertime advantage by having greater resistance to desiccation, but by superior tolerance, as discussed above. Also, since the tomentum was shown to have no detectable effect on the diffusive conductance, it must be concluded that an explanation other than that based on winter conditions (see p. 112) must be sought. The tomentum may effectively protect the young long shoot twigs from herbivory by small, sucking insects, such as aphids.

In summary it is apparent that L. lyallii obtains a signficant advantage over sympatric evergreens because of its growth habit and physiological tolerance. Although alpine larch desiccates during the winter, often to potentials lower than those of the evergreens, its limits of tolerance are so great in winter that it suffers less damage. The great tolerance of the species results from anatomical and physiological features that might also be found in other deciduous, timberline species. This advantage should be greatest where winter conditions are most desiccating.

The low levels of winter desiccation damage to L. lyallii explain how it maintains an upright growth form and how it is able to grow up into the alpine in sites where summer conditions are favorable. These sites must also be snow covered in winter since exposure of wintergreen needles rapidly causes damage or death. The leafless winter condition also reduces wind and snowload damage, snow creep and avalance damage and susceptibility to attack by snow fungi in deep snowpack areas.

CHAPTER V

THE SUMMER ENVIRONMENT, PHOTOSYNTHETIC CAPACITY AND WATER RELATIONS OF LARIX LYALLII

INTRODUCTION

Comparative studies of evergreen and deciduous trees have shown that high CO_2 fixation rates allow deciduous trees to at least partially compensate for their shorter growing period (Tranquillini 1962, 1964; Sweet and Waring 1968; Schulze et al. 1977). Climatic conditions at timberline make this prospect particularly difficult. Cool air and soil temperatures, increased cloudiness, wind, and drought all could further limit the total amount of carbon fixed in the short timberline growing season (Tranquillini and Turner 1961; Tranquillini 1963, 1969; Maruyama 1971; Vowinckel et al. 1973; Auger 1974; Havranek and Benecke 1978).

Although evergreen trees seldom suffer either atmospheric or soil drought stress (Tranquillini 1979), these factors could be more important limits for deciduous trees at timberlines. For C_3 plants, including deciduous trees, high net photosynthetic rates are closely linked to low leaf diffusion resistances. Any increase in leaf resistance due to atmospheric or soil drought, especially during midday periods when temperature and light conditions are most favorable, would be expected to cause large reductions in total carbon uptake. This might limit growth and maturation of new shoots and overwintering buds, or constitute a limit in itself.

The prediction that drought is an important limiting factor for deciduous trees at timberline appears to apply especially to *Larix lyallii*. This is because its distribution, only at timberline areas affected by

Pacific summer storms (see Ch. III), correlates well with moist, rainy environments.

The general objective of this section was to evaluate the hypothesis that there is a summer disadvantage to being deciduous in timberline habitats. The degree of this disadvantage in relation to sympatric evergreens, and its causes, was also sought. This was approached by simultaneously: studying the photosynthetic capacity of alpine larch, characterizing its environment, and intensively studying its water relations.

Objectives of the photosynthetic studies, which were carried out in the laboratory, were: 1) to determine the maximum rates of net assimilation at several phenological stages; 2) to determine light and temperature response curves of net assimilation over the range of conditions found in the field; 3) and to determine the effects of atmospheric and soil drought on photosynthetic capacity.

Quantitative description of the environment on the study sites provided the data necessary to integrate the photosynthetic measurements over a growing season. Such an integration works well with factors such as light and temperature, but does not provide accurate results for the responses to atmospheric and soil drought, especially when these are complicated by low soil temperatures. To better understand these responses under field conditions and because of the predicted importance of drought, the water relations of alpine larch were studied intensively in the field.

Specific objectives were: 1) to describe the seasonal and diurnal variation of a suite of water relations parameters; 2) to correlate the responses of these parameters, with a functional model, to the prevailing environmental conditions; 3) to experimentally determine the effects of both atmospheric and soil moisture stress on alpine larch and; 4) to use these and the descriptive data to evaluate the degree of drought stress experienced by this deciduous tree and the limitation this causes.

METHODS AND MATERIALS

Environmental Measurements

During the summer months of 1976 and 1977 meteorological stations recording temperature, humidity, short-wave irradiance (350 - 3500 nm), precipitation, and total wind run were maintained on both the north- and south-facing study sites. During periods of intensive physiological sampling the following parameters were also recorded: short-wave irradiance (280 - 2800 nm); photon flux density of photosynthetically active radiation (400 - 700 nm, PhAR); leaf, air and soil temperatures; humidity of free and canopy air; and soil moisture. Observations of cloud cover, type and height were made each day the site was visited.

Extensive meteorological data, including temperature, humidity, several radiation fluxes, precipitation, and wind, from nearby stations were available in the Compilation of the Hydrometeorological Record, Marmot Creek Basin, Vol. 4 - 14 (Environment Canada 1968 - 1978). One station, Twin 1, was only 40 m east of the krummholz study site. In 1978 temperature and humidity data were provided by Dan Ludwig, Biology Department, University of Calgary. His hygrothermograph was enclosed in a standard Stevenson screen about 100 m northwest of the north-facing study site, and calibration was by procedures similar to those outlined below.

Instrumentation

Hygrothermographs (Belfort Instrument Co., Baltimore, MD: Model 5-594) continuously recorded air temperature and humidity. The instruments were enclosed in aluminum louvered shelters (Vogel and Johnson 1965) placed 15 cm above the ground (or snow) surface during 1976, or in standard Stevenson screens 1.5 m above the ground in 1977.

An aspirated psychrometer (Bendix-Frieze, Baltimore, MD: Psychron Model 566) and psychrometer tables appropriate for ambient barometric pressure (Marvin 1941) were used to obtain temperature and humidity calibration points twice weekly. Temperature and humidity indicated by the hygrothermograph at the time of calibration were recorded, but no adjustment was made. Rather, regression of the indicated versus calibration values was used to correct hourly values determined from the continuous recording.

Maximum-minimum thermometers (Taylor Instrument Co., Arden, NC; Model 5458) mounted in hygrothermograph shelters provided a check on the maximum and minimum temperatures determined from the hourly values. An accurate Hg-glass thermometer was used to calibrate the maximum-minimum thermometers.

Two cross-calibrated thermographs (C.F. Casella and Co. Ltd., London, England; Model M-760) were used to determine regressions between temperature measured in the small aluminum shelters and temperature at screen height. Hourly temperatures from 1976 were corrected to screen height temperature using these regressions before calculation of daily mean, daytime mean, nightime mean, and maximum and minimum temperatures. The thermographs were also used to determine how much air temperature was increased under experimental drought shelters (described on p. 114).

Daily short-wave irradiance (350 - 3500 nm) was recorded on both the north- and south-facing sites in 1976 with Robitzch-type pyranographs (Belfort Instrument Co., Baltimore, MD: Model 51850) mounted horizontally on top of the hygrothermograph shelters. In 1977 only the south-facing site had a pyranograph. These instruments were calibrated side-by-side for several days at the beginning of each season with a Kipp pyranometer (Kipp and Zonen, Delft, The Netherlands; Model CM-5).

Precipitation was measured with cylindrical rain gauges (Taylor Instrument Co., Arden, NC: "Clear-Vu") mounted in the open, with the orifice at 35 cm. A little mineral oil in each one prevented evaporation between readings.

Totalizing anemometers (R.W. Munro Lt[illegible], London, England; Cup-counter MK II) mounted at 1.25 m measured winds above 0.25 $m \cdot s^{-1}$ and allowed calculation of average wind speed between readings.

During intensive physiological sampling short-wave irradiance (280 - 2800 nm) and PhAR were recorded on a portable strip chart recorder (Esterline-Angus Instrument Co., Indianapolis, IN; Model T-171-B) alternately connected to the Kipp pyranometer or to a cosine quantum sensor (Li-Cor Inc., Lincoln, NE; Model LI-190S). Leaf, air and soil temperatures were measured with Cu-Con thermocouples (0.076, 0.076, and 0.800 mm dia, respectively) read on the DVM-reference junction system described previously (see p. 77). The DVM was also used to read the voltage output from a Brady array humidity sensor (Thunder Scientific Corp., Albuquerque, NM: Model PC-2000) held either in free air or within the tree canopy.

The Brady array sensor, although responding rapidly and accurately to humidity changes, is temperature sensitive and subject to contamination. Thus it was calibrated at 5, 15, and 25° C over saturated salt solutions which provided humidities of: 12, 23, 33, 45, 55, 72, 80, and 85% (Winston and Bates 1960). Regression of relative humidity on log transformed output at each calibration temperature and linear regression of the slopes and intercepts against temperature allowed calculation of humidity from voltage output and sensor temperature. Calibration checks at 25° C at the beginning and end of each season showed that no significant sensor deterioration or drift had occurred. Also, vapor pressure deficits determined with a dew point hygrometer (EG&G International Inc., Waltham, MA: Model 880) were in close agreement with those determined from humidities calculated from the Brady array output.

Soil moisture was determined gravimetrically on samples (n=5) taken with a hand corer from 5-15 cm depth.

Wind, temperature, and humidity profiles (0.10, 0.25, 0.50, 1.00, 2.00 m) within the canopy and in free air were measured with the psychrometer and with a hot-wire anemometer with omni-directional probe (Teledyne Inc., Hastings-Raydist Div., Hampton, VA; Model AB-27). Wind readings were taken every 10 sec up and down the profile for 10 min; all readings at each height were averaged. Three to five readings of temperature and humidity were taken at each height and averaged.

During meltout in 1976 soil, snow-soil interface, and air temperature were recorded hourly on both study sites with multipoint recorders (Grant Inst., (Cambridge) Ltd., England; Model D). When aboveground the thermistor sensors were individually shielded by self-aspirating aluminum shields.

Photosynthetic Measurements

Plant materials

Nearly all photosynthesis measurements were made on excised branches, which had been clipped under water in the field and immediately covered with plastic bags for transport to the laboratory. This took about 1 1/2 hr. In the laboratory the branches were kept in a controlled environment chamber (Sherer Div., Marshall, MI; Model CEC 37-14) at 10° C with standard fluorescent and incandescent lighting. During a 7 hr dark period the temperature was 5° C. Photosynthetic measurements were made on the first and second days following collection. Before enclosing the branch in the cuvette, it was recut under water and the cut end attached to a distilled water-filled potometer. The potometer consisted of a serum stopper, a short length of tygon tubing, and a 1 ml pipette. No air bubbles were allowed to enter the potometer when the branch was attached. Terostat VIII (Terosan, Heidelberg) sealed the branch and serum stopper into a cutout in the cuvette base.

Attached branches of potted small trees were used in a drying experiment. The four healthiest small trees which had been used as controls in the winter drying experiments (see p. 81) were grown in the greenhouse until the needles were fully expanded. They were then placed in a controlled environment chamber (Environmental Growth Chambers, Chagrin Falls, OH) with 16 hr, 12±0.5°C, 85±5% relative humidity days. Lighting was by standard fluorescent and incandescent lamps, 10% of the wattage being incandescent. Air temperature was

6±0.5°C and humidity 90±5% at night. The potted trees were watered with distilled water and covered with plastic bags for three days, after which the bags were removed and water withheld.

Gas-exchange systems

Two separate open-type gas-exchange systems were used for net assimilation measurements. The system used during the 1976 and 1977 summers employed an URAS II (Hartman and Braun, Federal Republic of Germany) infra-red gas analyzer (IRGA) and a Koch-Siemens (Koch et al. 1971) cuvette with the water vapor control bypass loop removed. The cuvette was enclosed in a high light intensity controlled environment chamber (Environmental Growth Chambers, Chagrin Falls, OH). In this chamber Lucolux and Multivapor lamps provided nearly full sun intensities. Spectra taken within the cuvette are given in Appendix B.. A mass flow meter (Matheson Gas Products, Fort Rutherford, NJ; Model 8116) measured flow, while dew point hygrometers (E.G. and G. International Inc., Waltham, MA; Model 880) measured the dew point of cuvette inlet and outlet air. Outputs of these instruments, the IRGA, a PhAR sensor inside the cuvette, and a leaf temperature thermocouple were recorded on a six-channel Rikadenki, KA series strip chart recorder (supplied by Soltec Corp., Encino CA). This gas-exchange system is described in detail by Amundson (1978), and was used unmodified except that the SO_2 generation and detection subsystems were bypassed.

The other gas-exchange system was used during the summer of 1978 and for the drying experiment on potted small trees. A flow diagram is given in Appendix C. It employed a Beckman 865 IRGA (Fullerton, CA) and a simple mini-cuvette. The cuvette was a plexiglass cylinder, 5 cm dia and 15 cm long, capped with plexiglass on one end and with inlet and outlet tubes on opposite sides (see Appendix C). Smoke tests showed that adequate mixing occurred without a fan, and the flow rates used assured high "wind" speeds within the cuvette. This cuvette just fit over the branch to be measured and was sealed with Terostat VIII and a slit rubber stopper fitted around the branch base.

Leaf temperature was controlled by adjusting the temperature in the controlled environment chamber in which the cuvette was mounted. A 1000 W quartz-halogen lamp filtered through 5 cm of water supplemented the the chamber lights. Spectral analyses of these lamp types are given by Wilkinson (1977).

Humidity was controlled by manually adjusting the fraction of the air stream passing through a bubbler at chamber temperature. Humidity of the cuvette outlet air was determined with the Brady array sensor and DVM described previously or with an EG&G dew point hygrometer, or both.

A blank chamber in the reference air stream with volume equal to that of the cuvette and humidity sensor chamber in the sample stream removed the effects of short-term fluctuations in the CO_2 concentration of the outside air. Ambient CO_2 concentration was monitored by comparison to standard gases, and CO_2 depletion in the cuvette was adjusted so that in the cuvette the concentration was in the 305 to 320 $\mu l \cdot l^{-1}$ range. Response of net assimilation of larch to different CO_2 concentrations is shown in Appendix D.

Flow rates were measured with dual range rotameters (Matheson Gas Products, East Rutherford, NJ; Model 602) with the needle valves removed to reduce back pressure. Once installed in the gas-exchange system these were calibrated with a bubble calibrator (Levy 1964) and the readings corrected to standard temperature and pressure (STP).

A multi-channel strip chart recorder (Honeywell Inc., Fort Washington, PA; Eleckrtonik 16) was used to record output from: the IRGA; a Li-Cor quantum sensor; and air, leaf, Brady array sensor, and sample flow meter temperatures. Flow rates, dew point, Brady array output, and potometer readings were written on the strip chart.

Both the URAS II and the Beckman 865 IRGAs were spanned at 45 µl·1-1 full scale and calibrated twice daily with standard gases. The CO_2 concentration in these gases had been previously determined by comparing them to gases of known CO_2 concentration produced by Wöstoff pumps (Bate et al. 1969).

Calculation of net assimilation rates followed Sestak et al. (1971) and included corrections for temperature and barometric pressure at the time of the observation when the flow rate had been measured by the rotameter rather than the mass flow meter. Dry weight of leaf tissue was used in these calculations, and no corrections were made for the amount of branch included in the cuvette.

Leaf dry weight was chosen as the basis for expressing net assimilation because of the uncertainty of the leaf area determinations. The glass bead technique (Thompson and Leyton 1971) could not be used with larch because: 1) when left on the branch the flexible needles stuck together preventing complete coverage by glass beads, and 2) individual needles proved too fragile to be handled by forceps in the coating, weighing, coating, reweighing process. For these reasons a geometric technique was used to determine leaf area. It is described under water relations procedures below, while approximate dry weight to leaf area conversion factors are given in Results.

Experiments

Excised branches were used in 1976 to determine: light response curves of deciduous needles at 4.0, 9.5, 17.5 and 24.0° C and of wintergreen needles at 15° C. Temperature responses of expanding and mature deciduous needles and of wintergreen needles were determined under high light conditions ($\sim$1400 $\mu E \cdot m^{-2} \cdot s^{-1}$ PhAR). These data were supplemented with data from 1977 and 1978 when measurement conditions and plant materials were similar.

In 1977 net assimilation and dark respiration of branches from saplings and small trees that had been subjected to shade and drought stress treatments (described under water relations experiments, below) were measured at 18.0° C, 1400 $\mu E \cdot m^{-2} \cdot s^{-1}$PhAR or dark, and water vapor concentration difference ($\Delta c_{wv} \approx 6\ \mu g \cdot cm^{-3}$). The response of net assimilation to humidity at 17.5° C and 500$\mu E \cdot m^{-2} \cdot s^{-1}$PhAR was determined in 1978.

Attached branches were used for gas-exchange measurements during the drying experiment in February 1977. The potted small trees were allowed to dehydrate. Net assimilation, dark respiration, leaf water potential and components, and water content were measured simultaneously and repeatedly at dawn and midday until net assimilation fell to 5% of maximum. Measurement conditions were: 18.0° C, 1100$\mu E \cdot m^{-2} \cdot s^{-1}$PhAR, and $\Delta c_{wv} \approx 8.5\ \mu g \cdot cm^{-3}$.

Water Relations Measurements

Sampling schedule and parameters

In both 1976 and 1977 water relations parameters were sampled before dawn approximately every two weeks, except during periods of very bad weather. Xylem pressure potentials were sampled most intensively, but leaf water content, water potential and components, and change in bole radius (1977 only) were also measured. Plant materials, numbers of replicates, and procedures are given under Procedures, below. Midday sampling was occasional on clear, warm days. This supplemented midday readings obtained during the diurnal sampling periods.

Intensive, diurnal samplings were completed in June, July, and August in 1976 and 1977. The duration of these sampling periods ranged from 24-48 hr, except when they had to be aborted because of: rain or snow, instrument breakdown or operator failure. During an intensive sampling period water relations and environmental parameters were recorded at each site at intervals ranging from 1-4 hr. The schedule was: to sample at the south-facing site, move the portable equipment to the north-facing site, sample, and then move to the krummholz site. Sampling at the krummholz site was completed less often than at the other two sites because of the long travel time required.

Environmental parameters recorded included: irradiance, PhAR, air and leaf temperatures, canopy and free air humidities, and soil temperatures and moisture. Instrumentation is described on p. 129. Samples for determination of: xylem pressure potential, leaf water content, water potential and components, and diffusive conductance were taken. Bole shrink-swell and transpiration readings were recorded. Plant materials, number of replicates and procedures, are given below.

A sampling schedule similar to that of the diurnal runs was used to monitor the responses of both saplings and small trees to experimentally induced drought. Sampling was initiated in August 1977, but most was done in 1978.

Procedures

The techniques used to obtain xylem pressure potentials, water potential and components, leaf water content and change in bole radius are described on pp. 78-81. Differences caused by the use of deciduous leaves are described below.

Xylem pressure potential

Twigs of uniform size (10-12 cm) were clipped from each of seven saplings, immediately sealed in plastic bags, and kept cool until readings could be made. For intensive sampling periods the Scholander pressure chamber and half-size nitrogen cylinders were carried into Middle Creek cirque so readings could be made within 1/2 - 1 hr. For pre-dawn and midday sampling the samples were carrried to the laboratory for reading; this took 3-6 hr.

Repeated trials, where the same twigs were read several times, from a few minutes after clipping until up to 12 hr later, showed no significant differences in the $\psi_{P_{xylem}}$ determined immediately, or later. It was thus concluded that for this species, samples could, if kept cool, be held in plastic bags for several hours before making

$\psi_{P_{xylem}}$ determinations.

Additionally, comparisons were made between extensive samples (one twig from seven saplings) and intensive samples (seven twigs from one sapling). No differences in mean values were found, and variance was only slightly higher in the extensive samples.. Because of the need for repeatedly sampling these relatively small trees, $\psi_{P_{xylem}}$ was determined from extensive samples. Evergreens were also sampled extensively.

Water potential and components

At selected sampling times, four chamber psychrometers were filled with needles, deciduous or wintergreen, cut into 5 mm lengths. The needles all came from an individual sapling. The chambers were immediately sealed and kept cool until they could be transported to the laboratory. Equilibration began from the moment they were sealed, and for summer condition leaves took 4-6 hr. Because of the constraints of psychrometer numbers (20-25 were available) and time from loading to first reading, ψ and $\psi_{\pi + \tau}$ could not be obtained at each sampling time.

Leaf water content

When water contents of the psychrometer samples were determined, high variability was found, and each sampling period was not represented. Thus, extensive samples of 0.5-1 g (O.D.W.) of deciduous needles were collected at each sampling time. These were immediately sealed into screw cap vials. The fresh weight, dry weight, and vial weight allowed calculation of %O.D.W. by Eq. 2 (p. 81).

Diffusive conductance

Two diffusion resistance porometers, both of which were aspirated and used LiCl-gel sensors, were used in this study. In 1976 a Turner-Parlange type porometer was used. It was calibrated by Drs. R. Amundson and R. Walker, University of Washington, Seattle, WA according to the specifications of Turner and Parlange (1970). In 1977 and 1978 a porometer designed and calibrated according to the specifications of Gresham et al. (1975) was employed. These porometers were mounted on a tripod and fitted with a sun shade for field use.

Calculation of leaf resistance, and its inverse, conductance, followed Kanemasu et al. (1969), Turner and Parlange (1970), and Gresham et al. (1975). Means and variance were calculated only after conversion to conductance, as it is this value which is included in a linear manner in the calculations of flux rates (see Eq. 7).

Measurements were made on five excised needles, held in the porometer with Terostat VIII. Less than 30 s elapsed from excison to the beginning of the first reading and only sunlit needles were used. Needle area (both surfaces) was estimated from measurements of length (l), base width (w_1) and width at the widest point (w_2) using Eq. 8, which is based on a trapezoidal model.

$$A = n \cdot \bar{l}(\bar{w}_1 + \bar{w}_2) \qquad (8)$$

where A = total area of needles in the porometer

n = number of needles

$\bar{l}$, $\bar{w}_1$, $\bar{w}_2$ are mean length and widths.

Transpiration rates

Transpiration rates of cut branches were measured with potometers. Seven to nine were used on each site. Branches were cut under water and immediately attached to a small potometer (see p. 131 and Appendix C). The potometers and their branches were hung in alpine larch saplings so that the branches were oriented naturally. This, however, contributed to the variability of the results because of differences in shading.

Calculation of transpiration rates was straightforward from ml of H_2O lost between two readings at known times, and leaf area. Leaf area was determined by the same technique as described above and Eq. 8. In this case, however, total number of needles was estimated by counting short shoots and subsampling to determine number per short shoot. Long shoot needles were counted and measured separately, and their area added to the area of short shoot needles. These procedures were also employed to determine the leaf areas of branches used for photosynthesis. Dry weight-leaf area ratio was determined for all branches used for photosynthesis and transpiration measurements. These data were combined for analysis.

Experiments

The descriptive study of water relations completed for this research was an attempt to use the experiments provided daily by nature. Analysis of the 1976 descriptive field data suggested that drought and shade stresses were important limits for alpine larch. For this reason several drought and shade stress shelters were installed at the field site in 1977. These shelters subjected alpine larch saplings and small trees to long term stress without inducing the artifacts caused by laboratory and growth chamber growing conditions, nor causing root damage.

Clear polyethylene sheets were mounted on wooden frames (2m x 2m for small trees and 3m x 3m for saplings). These frames were installed parallel to the ground surface and ∿60 cm above it. For saplings the frames were constructed so that the trunk of the tree passed through the sheet. Some branches were under the shelter, and others were above it.

Shade shelters were smaller (1m x 1m) and consisted of 3 layers of blackened cheesecloth supported by lath strips. Shade plus drought stress shelters were of hybrid design, with lath and cheesecloth over the polyethylene.

Five pairs of saplings were chosen and one of each assigned randomly to drought or control treatments. Saplings were not shade stressed. A split plot design was used for the small trees, with five in each of the four treatments: control, drought stressed, shade stressed, and shade plus drought stressed.

Branches or needles from these trees were removed as needed for water relations or photosynthetic measurements. With the saplings comparisons were also made between branches low and high in the canopy. During the final sampling period, a shelter removal experiment was done to examine the response of diffusive conductance to a reduced water vapor density gradient. During this sampling period a Campbell CR-5 Data Logger (Campbell Scientific Inc., Logan, UT, USA) was used for logging environmental data. With the exception of that sampling period all data, except the light parameters, were recorded by hand.

RESULTS

The Summer Environment

Summer environmental data are given in Figs. 25 and 26 for 1976 and 1977, respectively. In both years mean daily irradiance on the south-facing site for June-July was 21.5±.9 $MJ \cdot m^{-2}$, and for August-early September 14.9±.9 $MJ \cdot m^{-2}$. The north-facing site received 13% less radiation in June-July and 37% less in August-early September. This difference was mainly due to shading of the site by the large L. lyallii and Abies lasiocarpa trees on the slope above it. Differential growth rates between saplings on the two sites (Table 5 and 6) are partially explained by this difference in available light.

Air temperatures near the ground were much lower on the north-facing site in the spring, before meltout (Fig. 25b). When corrected to screen height, however, there is less difference, and the 1977 data confirm this. Indeed, at 1.5 m, the difference in air temperature at the two sites was less than the error of the hygrothermographs used. Thus, for saplings, growth processes would not be different. Small trees would be expected to grow more slowly in the cool, near-surface, environment on the north-facing site. This was shown in Fig. 13.

1976 and 1977 show contrasting seasonal patterns of air temperature (Figs.25b and 26b). 1977 was much warmer early in the growing season, (meltout occurred 2 1/2 - 3 weeks earlier), but generally cooler in August and September. The longest period between frosts was only 14 d,

Figure 25. Summer environmental data from the north- and south-facing study sites for 1976. Five day running means of: a.) daily irradiance, b.) air temperature at 15 cm (dotted lines, above and below the lines for the north- and south-facing sites, respectively, show temperature corrected to 1.5 m), and c.) vapor pressure deficit at 15 cm. The frost-free period is shown by the solid bar in b. Individual precipitation events (d.); mean snow depths (e.); and mean (± SE) soil moisture values (f.) are shown. Approximate ψ_{soil} levels, taken from Fig. 7, are also indicated in f.

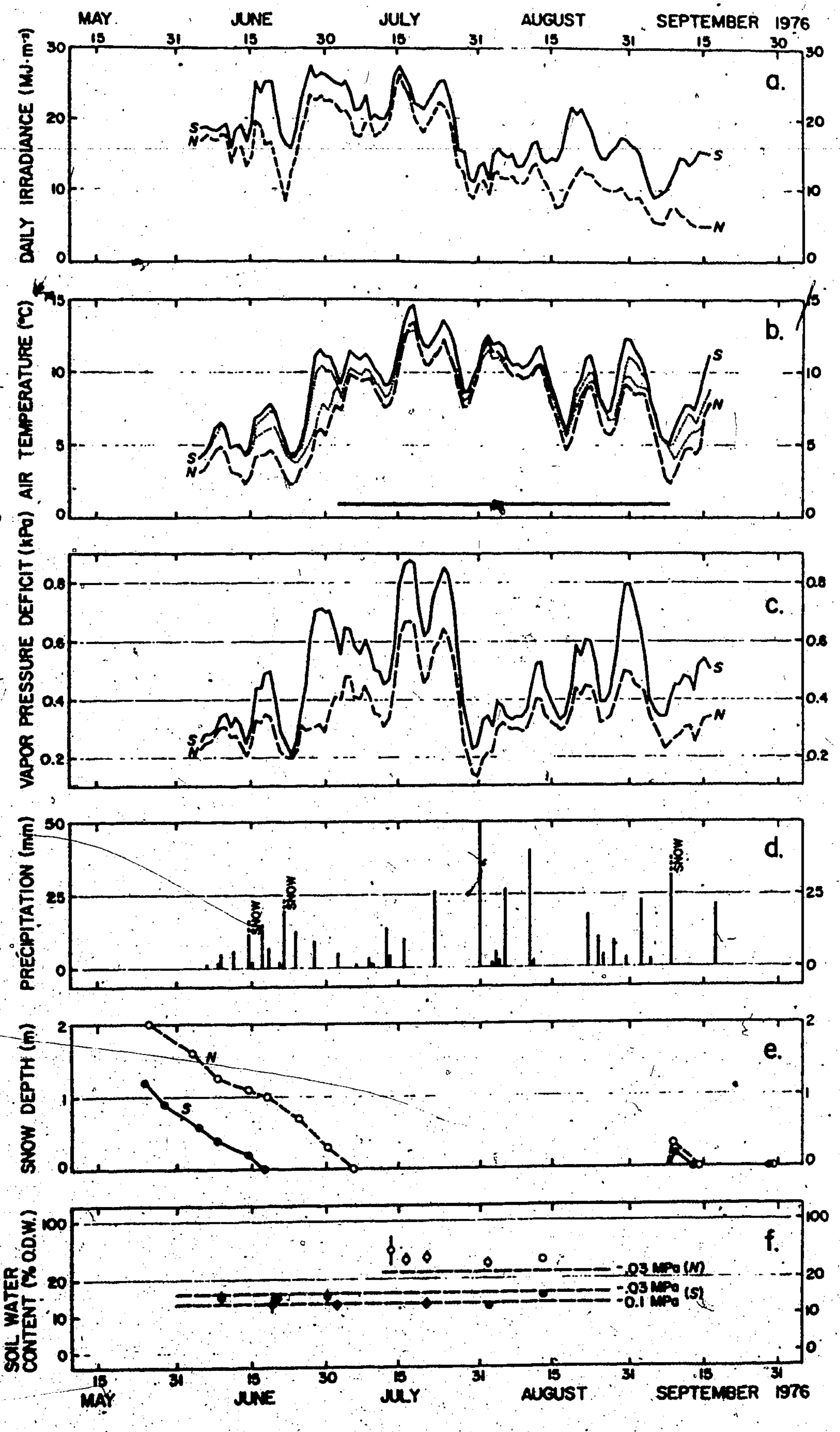
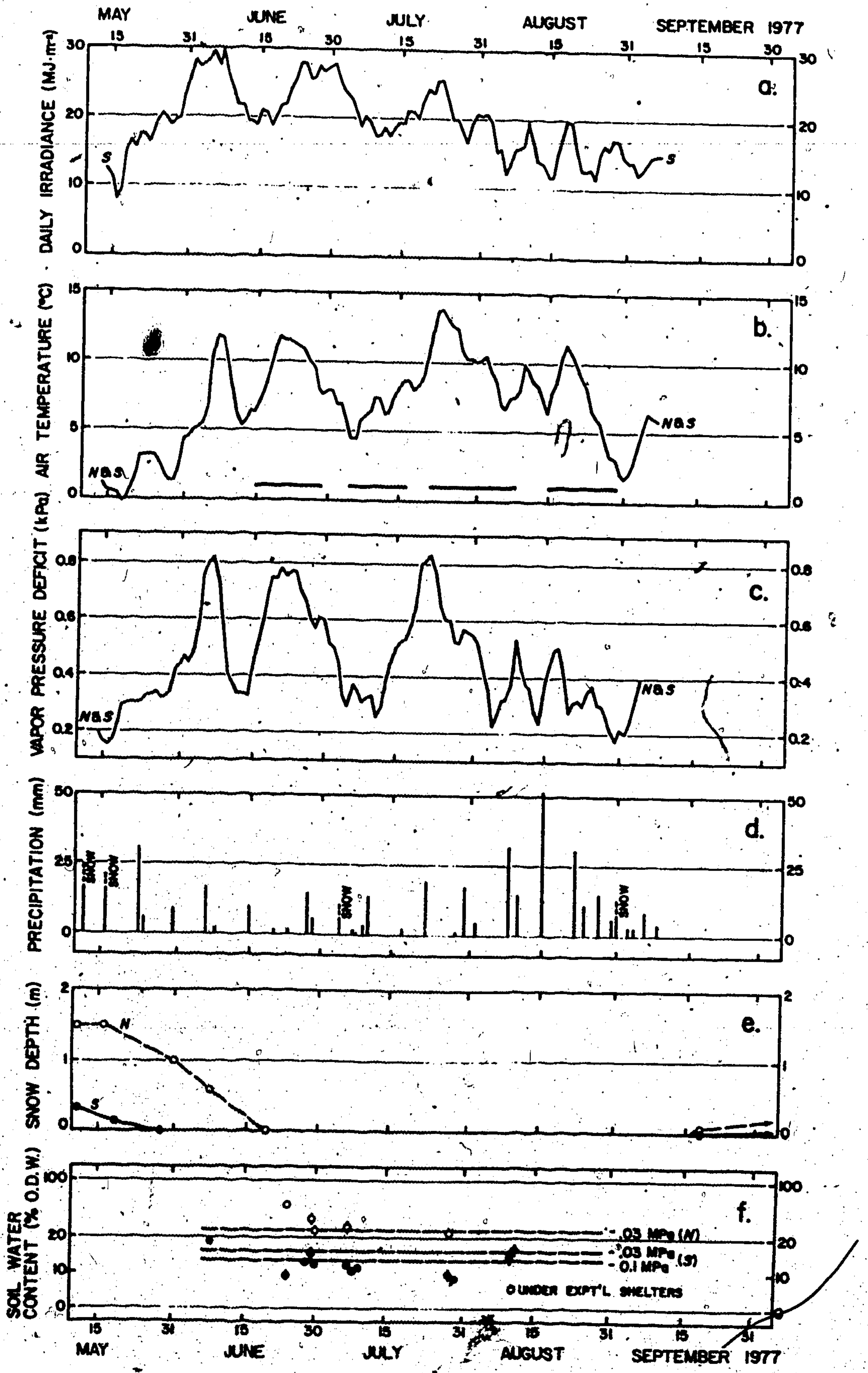

MAY
JUNE
JULY
AUGUST
SEPTEMBER 1976
15
31
15
30
15
31
15
31
15
30
DAILY IRRADIANCE (MJ·m⁻²)
a.
S
N
30
20
10
0
AIR TEMPERATURE (°C)
b.
15
10
5
0
VAPOR PRESSURE DEFICIT (kPa)
c.
0.8
0.6
0.4
0.2
PRECIPITATION (mm)
d.
SNOW
SNOW
SNOW
50
25
0
SNOW DEPTH (m)
e.
2
1
0
SOIL WATER CONTENT (% O.D.W.)
f.
.03 MPa (N)
.03 MPa (S)
0.1 MPa
100
20
10
0
15
31
15
30
15
31
15
31
15
31
MAY
JUNE
JULY
AUGUST
SEPTEMBER 1976

Figure 26. Summer environmental data from the north- and south-facing study sites for 1977. Five day running means of: a.) daily irradiance (south-facing only), b.) air temperature at 1.5 m (there were no differences greater than 1.0° C between the two sites), and c.) vapor pressure deficit at 1.5 m. Frost-free periods are shown by the solid bars in b. See Fig. 25 for descriptions of (d.), (e.), and (f.).


MAY
JUNE
JULY
AUGUST
SEPTEMBER 1977
15
31
15
30
15
31
15
31
15
30
DAILY IRRADIANCE (MJ·m⁻²)
0
10
20
30
a.
S
S
AIR TEMPERATURE (°C)
0
5
10
15
b.
N&S
N&S
VAPOR PRESSURE DEFICIT (kPa)
0.2
0.4
0.6
0.8
c.
N&S
N&S
PRECIPITATION (mm)
0
25
50
d.
SNOW
SNOW
SNOW
SNOW
SNOW DEPTH (m)
0
1
2
e.
N
S
SOIL WATER CONTENT (% O.D.W.)
0
10
20
100
f.
.03 MPa (N)
.03 MPa (S)
0.1 MPa
◇ UNDER EXPT'L. SHELTERS

which is in sharp contrast to the 68 d frost free period in 1976.

Vapor pressure deficits, which are generally quite low, parallel the temperature differences. When near-surface temperatures were used in the calculation, there were large differences between the two sites (Fig. 25c). When screen-height temperatures were used, however, no significant differences were found (Fig. 26c).

Total summer precipitation was slightly higher in 1976 than in 1977, but the pattern was quite different (Table 15). June 1977 was much drier than normal, and August 1977 much wetter. Both years, and 1978, had above average summer precipitation. The precipitation totals for 1976 and 1977 in Table 15, which are from Environment Canada (1968-78), agree almost exactly with the data gathered by the author on the study sites. It is important to note that during the summer it was a rare week in which less than 15 mm of precipitation fell (Figs. 25d and 26d).

On both sites soil water content remained high throughout the growing season, as a result of the regularly occurring precipitation (Figs. 25f and 26f). Soil water potential was: at or above -0.03 MPa on the north-facing site, both years; at or above -0.10 MPa on the south-facing site in 1976; but fell to a minimum of -0.30 MPa several times in 1977. Considering the shallow depth at which the soil water content samples were taken and the deep rooting habit of <u>L. lyallii</u>, it can be concluded that these trees experienced no soil moisture deficits in either growing season.

Mean wind speed was higher (1.4 $m \cdot s^{-1}$) on the south-facing than on the north-facing site (0.3 $m \cdot s^{-1}$), but both values are quite low,

Table 15. Summer environmental data for 1976, 1977 and 1978, and 10(9) yr means from meteorological stations in Marmot Creek Basin. Radiation data are from Twin 12 (1750 m) in the subalpine forest ~3 km east of the study sites. Temperature, humidity, VPD and precipitation are from Twin 1, 0.5 km west of the north-facing study site. Data are from Environment Canada (1968-1978).

PARAMETER	MONTH	1976	1977	1978	10(9) YR MEAN
Mean daily global radiation (MJ·m^{-2})	May	20.8	16.7	17.3	19.1
	June	19.8	22.5	21.6	21.2
	July	20.1	19.0	17.6	20.8
	August	14.7	14.1	15.5	17.0
	September	13.4	10.0	11.3	12.3
Mean temperature (°C)	May	2.9	2.0	1.[illegible]	2.0
	June	4.1	8.3	7.3	6.1
	July	9.3	9.0	9.6	9.5
	August	8.8	6.9	8.8	9.4
	September	8.5	3.1	5.9	4.1
Mean humidity (%)	May	59	64	69	63
	June	65	58	61	63
	July	62	64	70	63
	August	67	72	66	62
	September	59	74	67	64
Mean maximum VPD* (kPa)	May	0.62	0.50	0.44	0.50
	June	0.62	1.03	0.88	0.73
	July	0.98	0.94	0.82	0.95
	August	0.73	0.62	0.82	0.93
	September	0.73	0.44	0.66	0.60
Precipitation (mm)	June	87	45	94	83
	July	100	63	74	68
	August	112	168	89	93
	Total	299	276	257	244

*VPD was calculated from monthly mean maximum temperatures and mean minimum humidities according to Williams and Brochu (1969).

especially for a timberline site. Differential stress due to site wind exposure probably does not occur during the summer months.

Soil temperatures, at all depths >1 cm, were always higher on the south- than on the north-facing site (Fig. 27). The largest difference (∿10° C) occurred just before the north-facing site melted out. Of course, there were larger differences when comparing soil surface temperatures, but these do not affect the roots of L. lyallii. Seasonal maximum soil temperatures in the rooting zone of this species (see p. 63) is not much greater than 12° C.

For most of the growing season tree roots on the north-facing site are in a very cool (i.e. <10° C) environment. They may penetrate less deeply, however, because of adequate water availability and better thermal regime at shallow depths. Some evidence for this was found while examining soil profiles (see p. 30). This rooting pattern lessens the otherwise large difference in root environment temperature between the two sites.

Soil temperature, nevertheless, is one of the major differences between the two sites. Irradiance, and length of the growing season also showed quite large differences. L. lyallii flushes while still completely snowed in. This habit considerably reduces the difference in length of the growing season, for trees projecting above the snow surface. Differences in the atmospheric environment (temperature and humidity) were less than expected. Indeed, the sites are nearly identical in this respect.

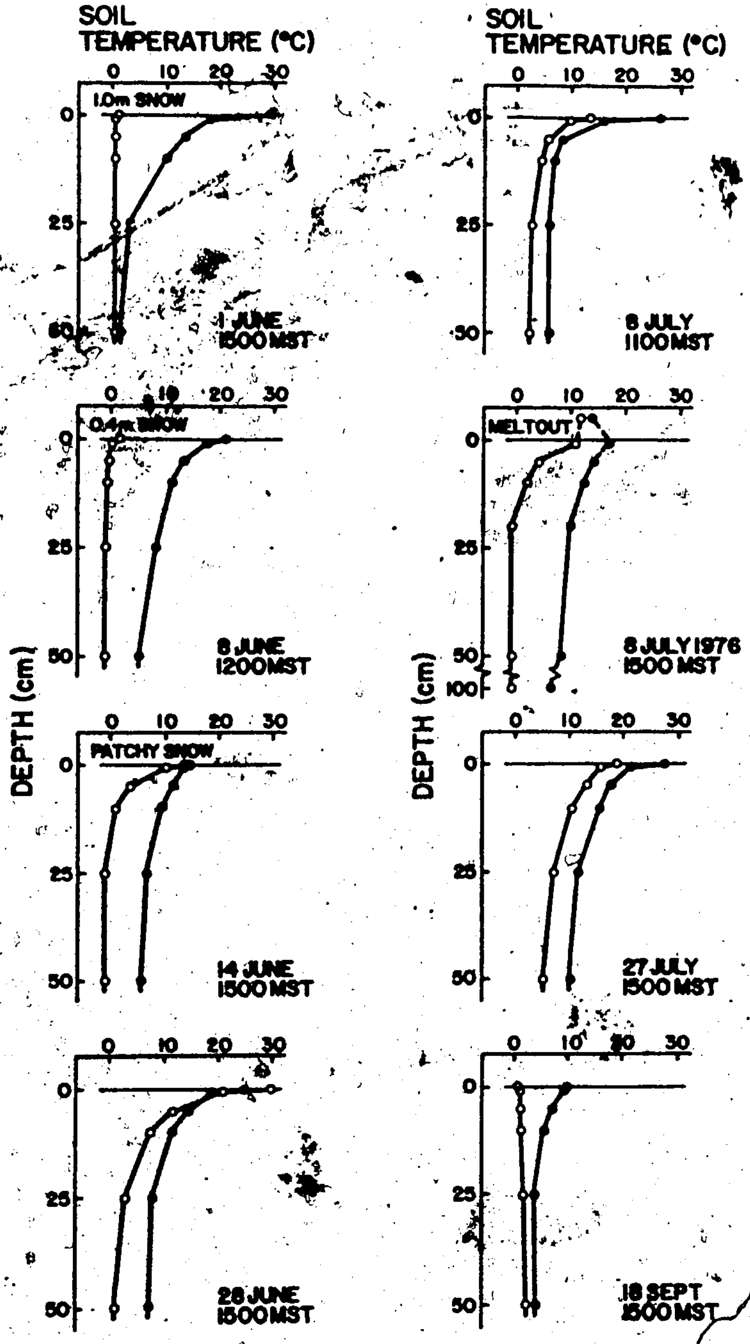


Figure 27. Mid-afternoon soil temperature profiles from the north-facing (O) and south-facing (●) study sites during 1977, with a comparison at meltout to 1976 profiles.

The effect of the L. lyallii sapling canopies on the atmospheric humidity within them was investigated because of the predicted importance of atmospheric drought stress to these t[illegible]. No significant increase was found within the canopies on either site (Fig. 28). These data suggest that the humidity of the free air at 1-2 m is a good indicator of the ambient humidity around the leaves of larch saplings. Small trees on the north-facing site experience slightly higher humidities.

Comparison of 1976-1978 data with 10 yr means (Table 15) shows that June 1977 was an exceptionally sunny, warm and dry month, while August of that year was cloudy, cool and wet. Although July 1976 had much more precipitation than average, it was near normal in radiation, temperature, and humidity. The summer of 1978 most closely matched average conditions in the meteorological parameters considered.

Photosynthetic Capacity of Larix Lyallii

Maximum net assimilation rate (NAR) of detached branches of L. lyallii increased from 15 mg $CO_2 \cdot g^{-1} \cdot hr^{-1}$ (5.9 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, see p. 154) in June to 20 mg $CO_2 \cdot g^{-1} \cdot hr^{-1}$ (6.9 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$) in July (Fig. 29). Wintergreen needles showed much lower maximum rates, 8 mg $CO_2 \cdot g^{-1} \cdot hr^{-1}$ in June. The temperature optimum for deciduous needles in both June and July was 17-18° C. This figure must be taken with some caution, however, because the branches were held in a growth cahmber for 1-2 d before the measurements were taken, and some acclimation may have occurred during this time.

In June net assimilation was still positive at -3° C and at temperatures above 20° C it showed a more rapid decline, than in July. The latter effect results from the great reduction in the rate of dark respiration at temperatures above 15-20° C.

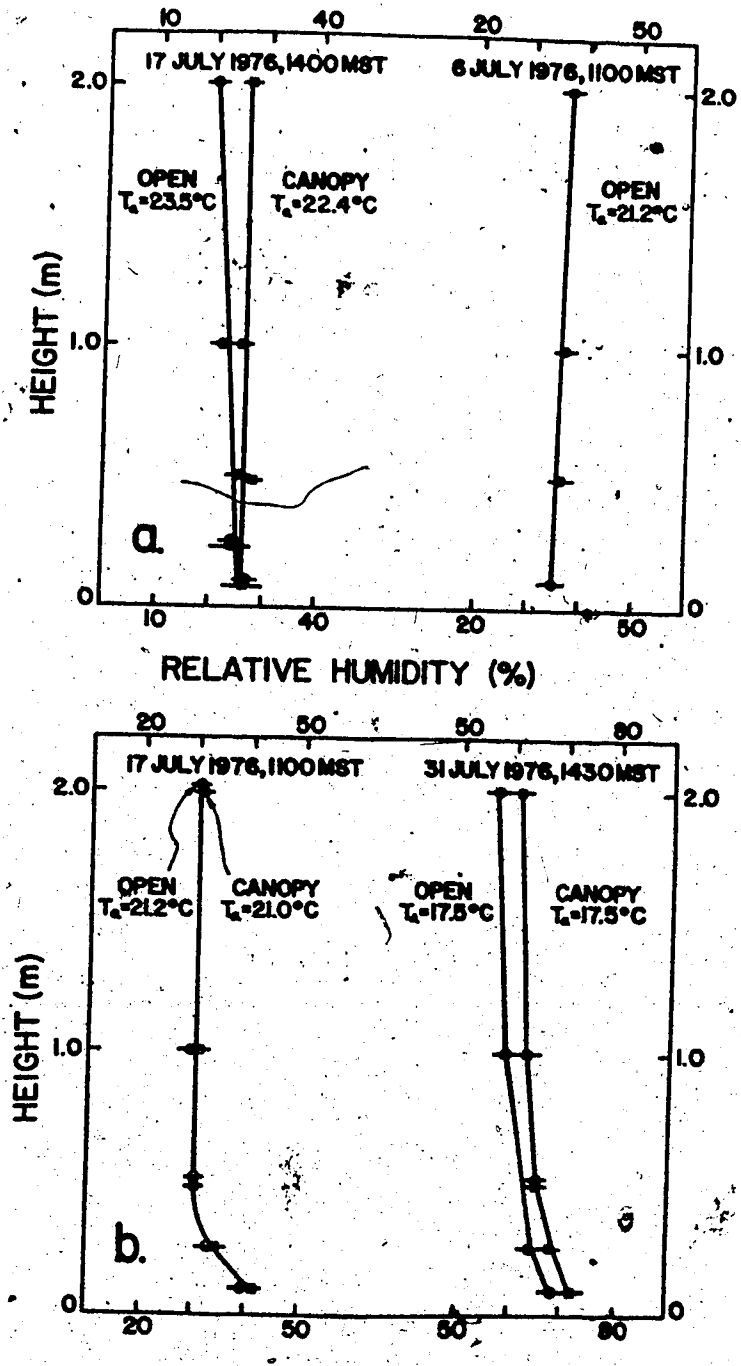


Figure 28. Profiles of relative humidity in the canopy of *Larix lyallii* saplings (squares) and in the free air (circles) on the south-facing (a.) and north-facing (b.) study sites. Means ± SE are shown, n = 3(4). Air temperatures did not vary more than 0.2° C from the top to the bottom of the profiles.

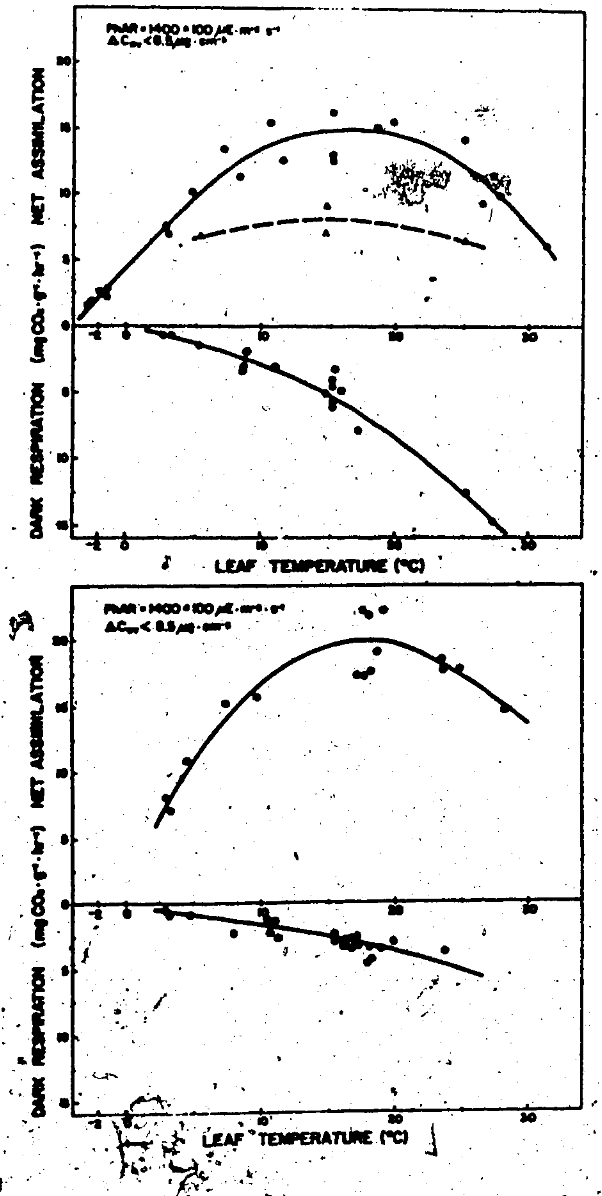


Figure 29. Net assimilation and dark respiration of Larix lyallii deciduous (●) and wintergreen (▲) needles as a function of temperature in June (above) and in July (below). Light and humidity conditions were as indicated. Each point represents a single determination. Data are mainly from 1976, but some from 1977 and 1978 are included.

Light response curves for deciduous needles show that above 9° C very high light levels are required to approach saturation (Fig. 30). The light compensation point also appears to rise rapidly with increasing temperature. Data compiled from all of the photosynthetic studies show that the light compensation point of deciduous needles is 40 $\mu E \cdot m^{-2} \cdot s^{-1}$ at 15° C, but increases rapidly, and is 175 $\mu E \cdot m^{-2} \cdot s^{-1}$ at 25° C (Fig. 31). Wintergreen needles show an even higher light compensation point, ∿160 $\mu E \cdot m^{-2} \cdot s^{-1}$ at 15° C (Fig. 32).

Net assimilation rates have been presented on a dry weight basis because of problems with leaf area determination (see p. 134). Leaf area was estimated geometrically for each branch used for photosynthetic measurement, and for those used in field transpiration measurements. Leaf area to dry weight ratios averaged 2.75 $dm^2 \cdot g^{-1}$, for all branches. There was a slight increase from June to July, and needles from the north-facing site had higher ratios (Table 16).

Using the mean monthly area: weight ratio, maximum NAR are reduced numerically, to 5.9 and 6.9 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ for June and July, respectively, values that are in the lower half of the range for evergreen conifers.

Some of the variability in the photosynthetic data is explained by results of measurements made on detached branches during 1978 (Fig. 33). Regression (Eq. 9) of % of "maximum" NAR on the leaf to air water vapor concentration gradient (Δc_{wv}) shows the highly significant negative correlation of these two variables.

$$\% \ NAR_{max} = -8.4 \Delta c_{wv} + 167.1 \qquad (9)$$

$$r = -.91$$

$$p < .01$$

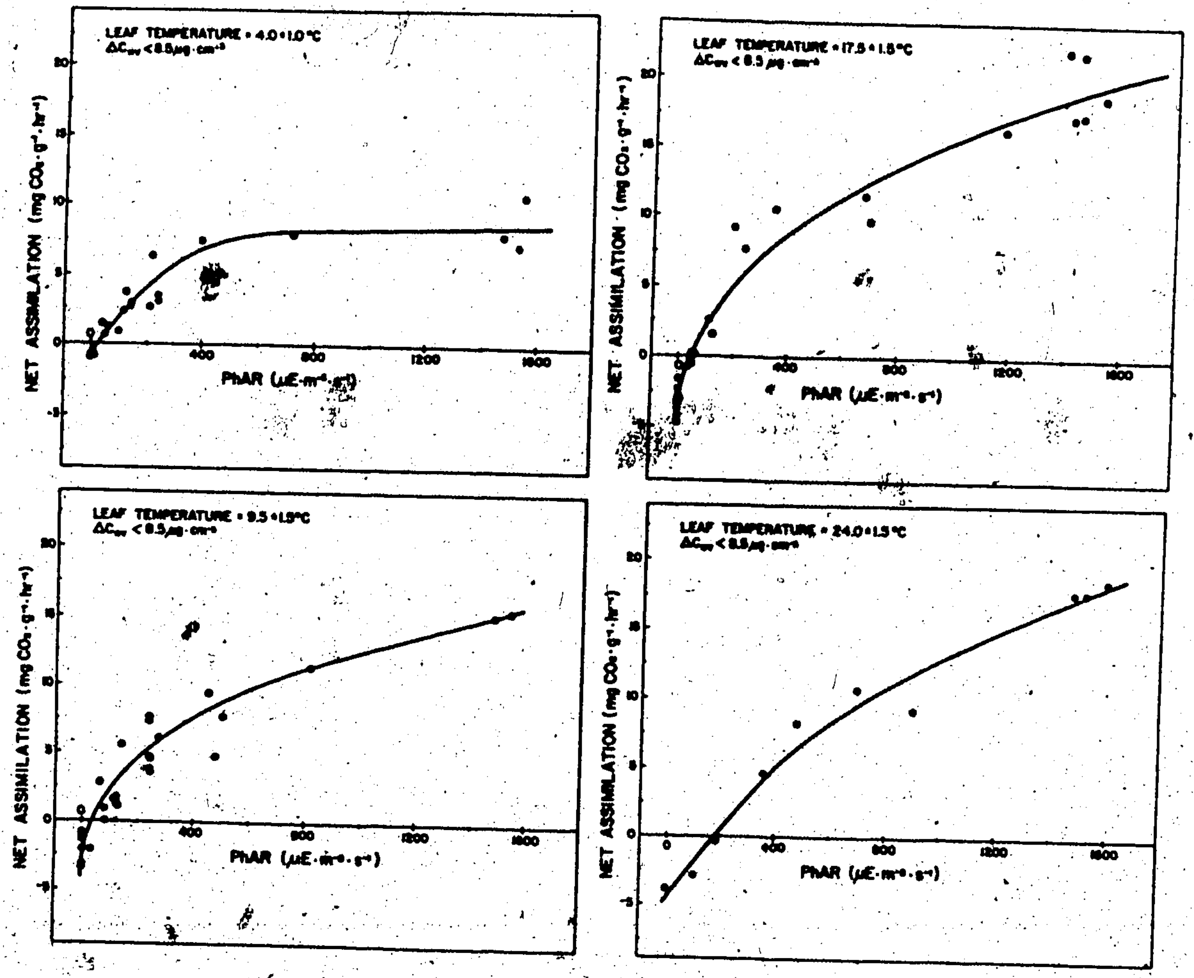


Figure 30. Net assimilation light response curves for deciduous *Larix lyallii* needles in July at 4.0, 9.5, 17.5, and 24.0° C. Each point represents a single determination on a cut branch in the laboratory. Data are mainly from 1976, but some from 1977 and 1978 are included.

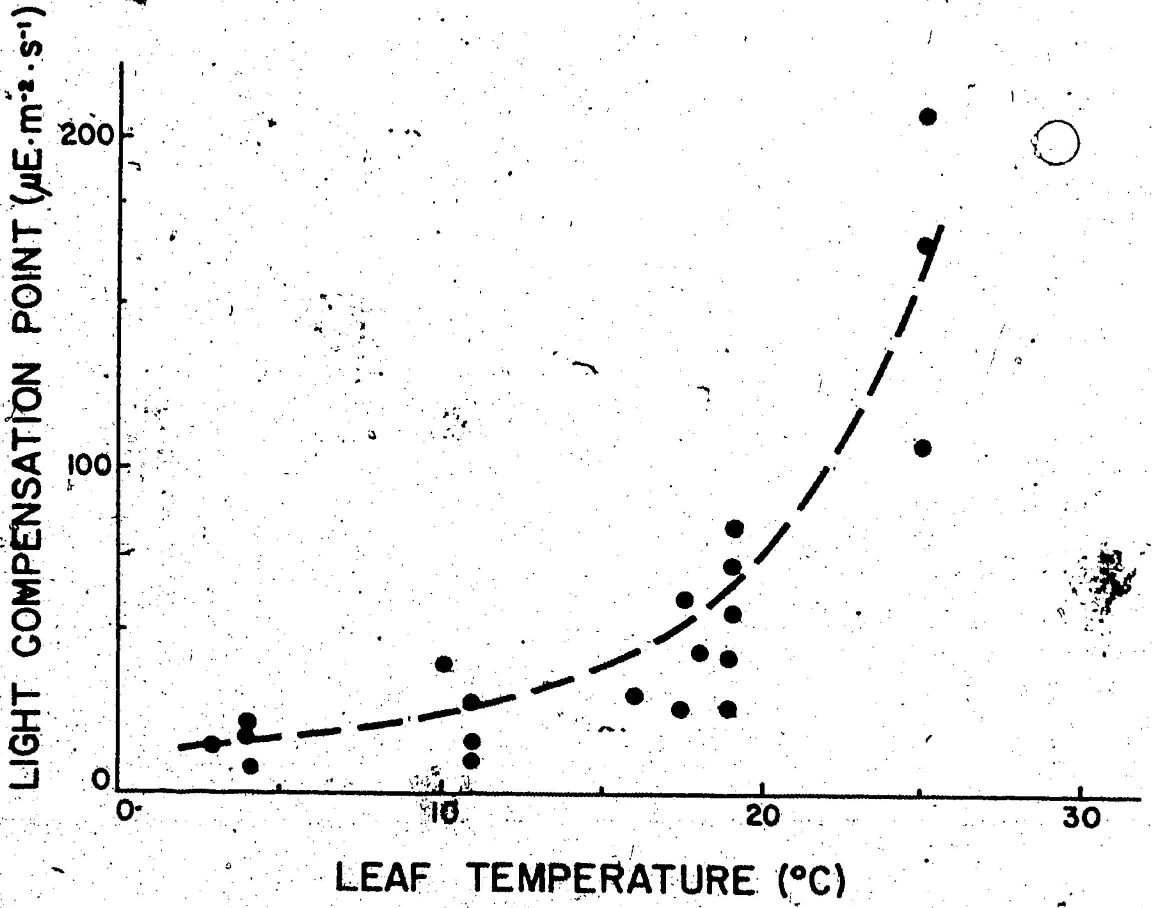


Figure 31. The light compensation point of mature deciduous needles of <u>Larix lyallii</u> as a function of leaf temperature. Each point represents one branch.

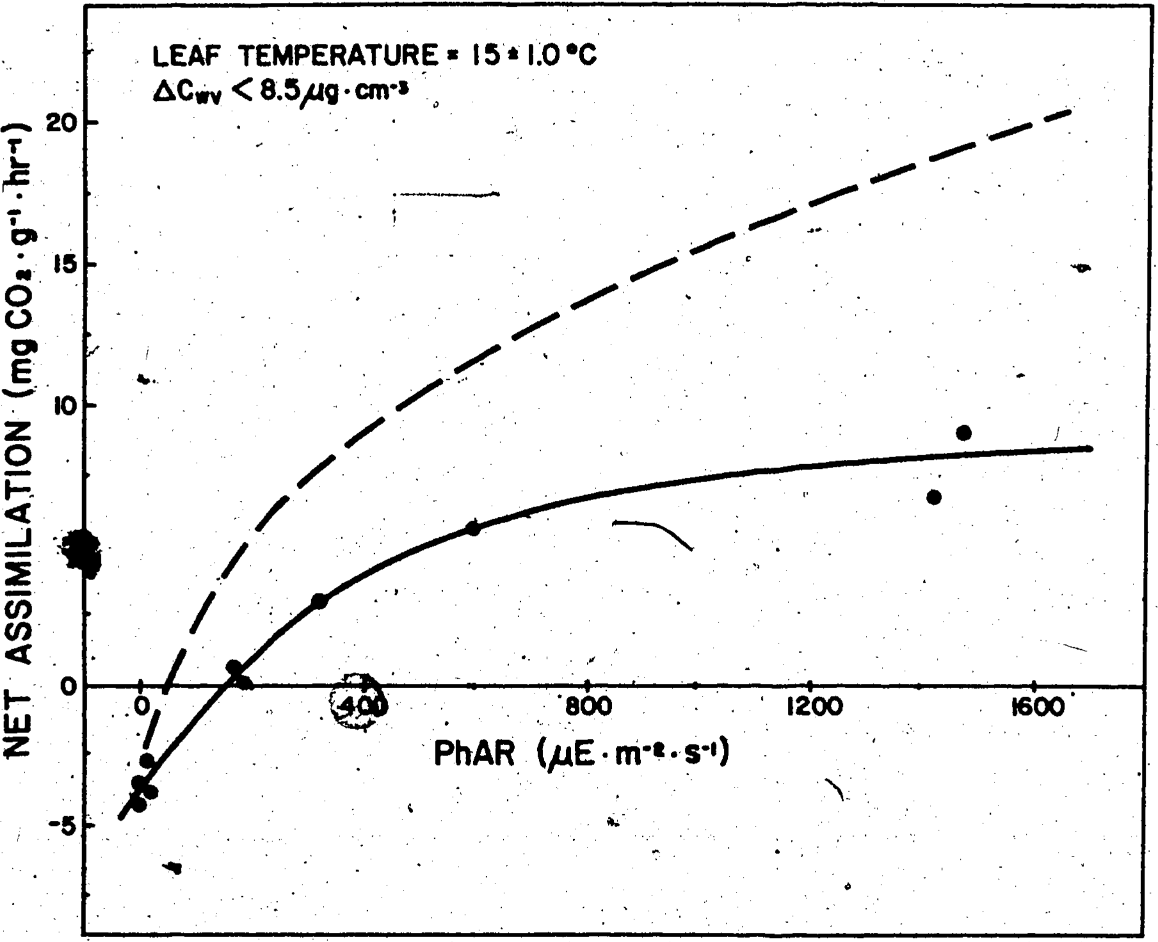


Figure 32. Net assimilation light response curve for wintergreen needles of small *Larix lyallii* trees in June, 1976. The dashed line shows net assimilation of deciduous needles in July at 17.5° C (from Fig. 30).

Table 16. Ratios of estimated leaf area to dry weight for deciduous needles from the north- and south-facing study sites. Monthly data from 1976, 1977, and 1978 were combined.

	Leaf Area/Dry Weight ($dm^2 \cdot g^{-1}$)	
Month	North-Facing	South-Facing
June	2.56	2.51
July	3.05	2.75
August	2.92	2.66

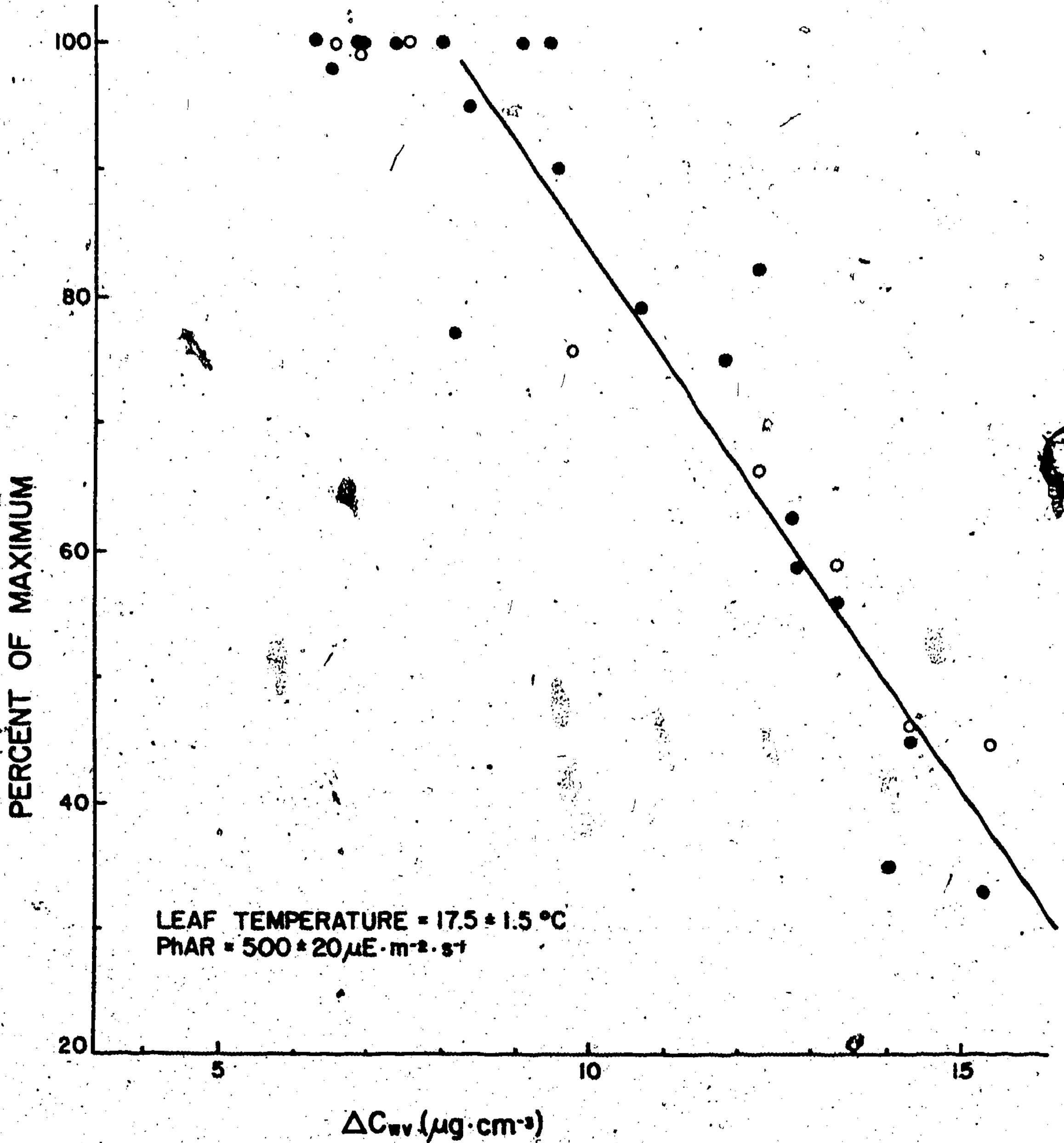


Figure 33. Net assimilation (●) and diffusive conductance (○) of excised *Larix lyallii* branches in response to increasing water vapor concentration differential. Three deciduous needled branches were measured in June and four in July 1978. An approximate correlation of Δc_{wv} to vapor pressure deficit at 17.5°C is: $10\ \mu g \cdot cm^{-3} = 1.3$ kPa.

During the early photosynthetic measurements adequate control of Δc_{wv} was not possible, so some measurements were undoubtedly made on branches which had lower than maximum rates of CO_2 intake. Equation 9 suggests that maximum NAR might be 60% higher than the measured maxima, if measurements could be made at very low Δc_{wv}.

The negative correlation of NAR and Δc_{wv} is due to a similar correlation between diffusive conductance and Δc_{wv} (Fig. 33). During this series of measurements a study of the time required for complete response to humidity changes was conducted. Response to stepwise drops in humidity (increases in Δc_{wv}) was complete within 25-40 minutes. Response to increasing humidity was initially rapid, but required up to three hours for return to pretreatment levels.

In addition to reduced NAR at low humidity (high Δc_{wv}), <u>L. lyallii</u> shows reduced rates in response to low leaf water potentials caused by soil drought. Small potted trees, which had suffered root damage during potting, were unable to maintain positive net assimilation when $\psi < -1.5$ MPa (Fig. 34). Much of the variability of these data are explained by the root damage. This may also account for relatively low levels of water stress causing complete cessation of CO_2 uptake.

An Höfler diagram of leaf water potential and water content data from this experiment shows the remarkable turgor stability of deciduous alpine larch needles (Fig. 35). Although turgor was unchanged throughout the drying experiment, the large reduction in NAR suggests that the stomata were nevertheless closed. Stress hormones (ABA), or sensitivity of the guard cells to them, as a result of the damaged roots, may be responsible for the poor performance of these trees.

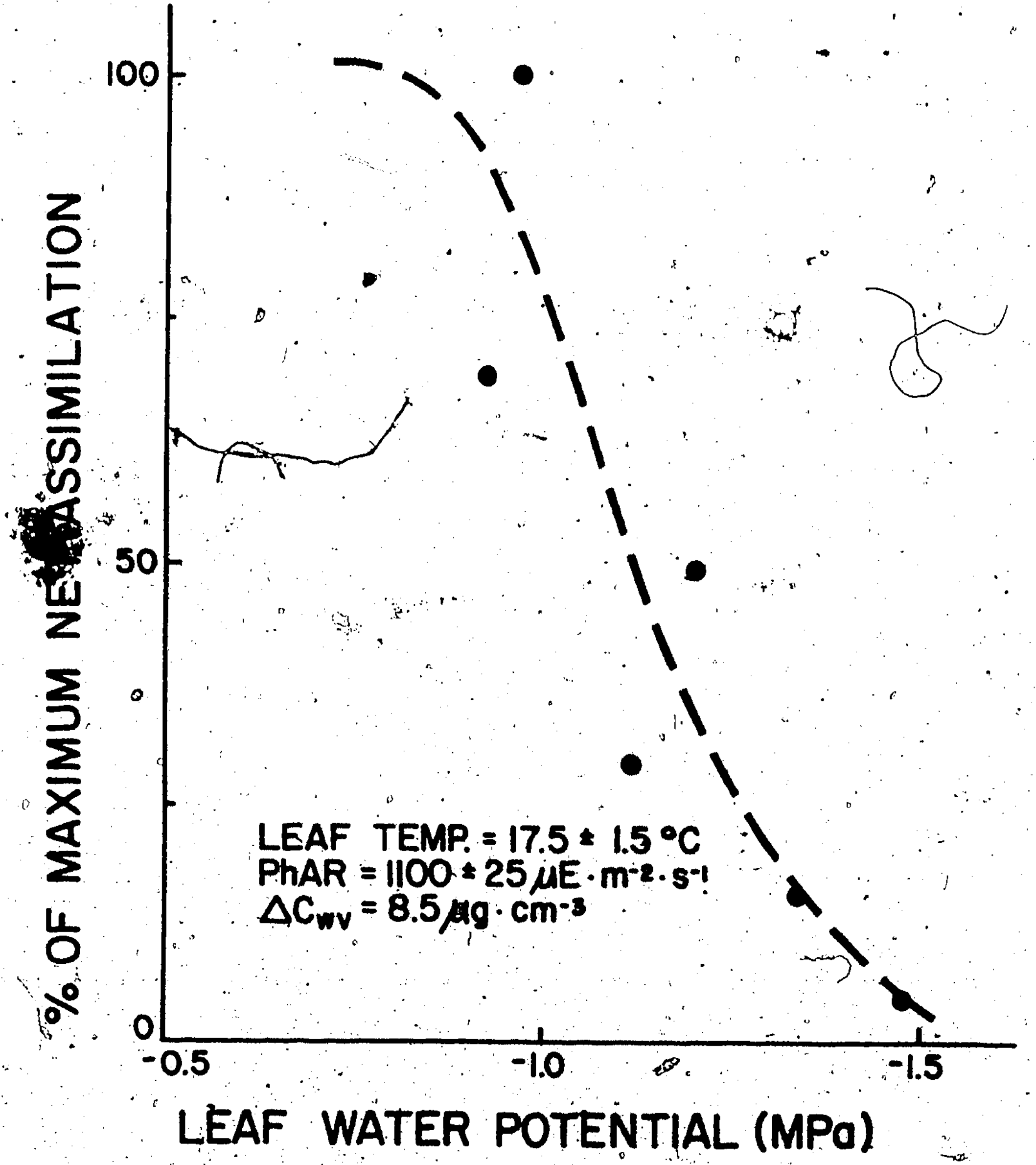


Figure 34. Response of net assimilation of attached branches of potted small *Larix lyallii* trees to decreasing leaf water potential. Each point represents the mean of 3-4 determinations on each of 4 trees. Measurements were made under the temperature, light, and humdidity conditions indicated.

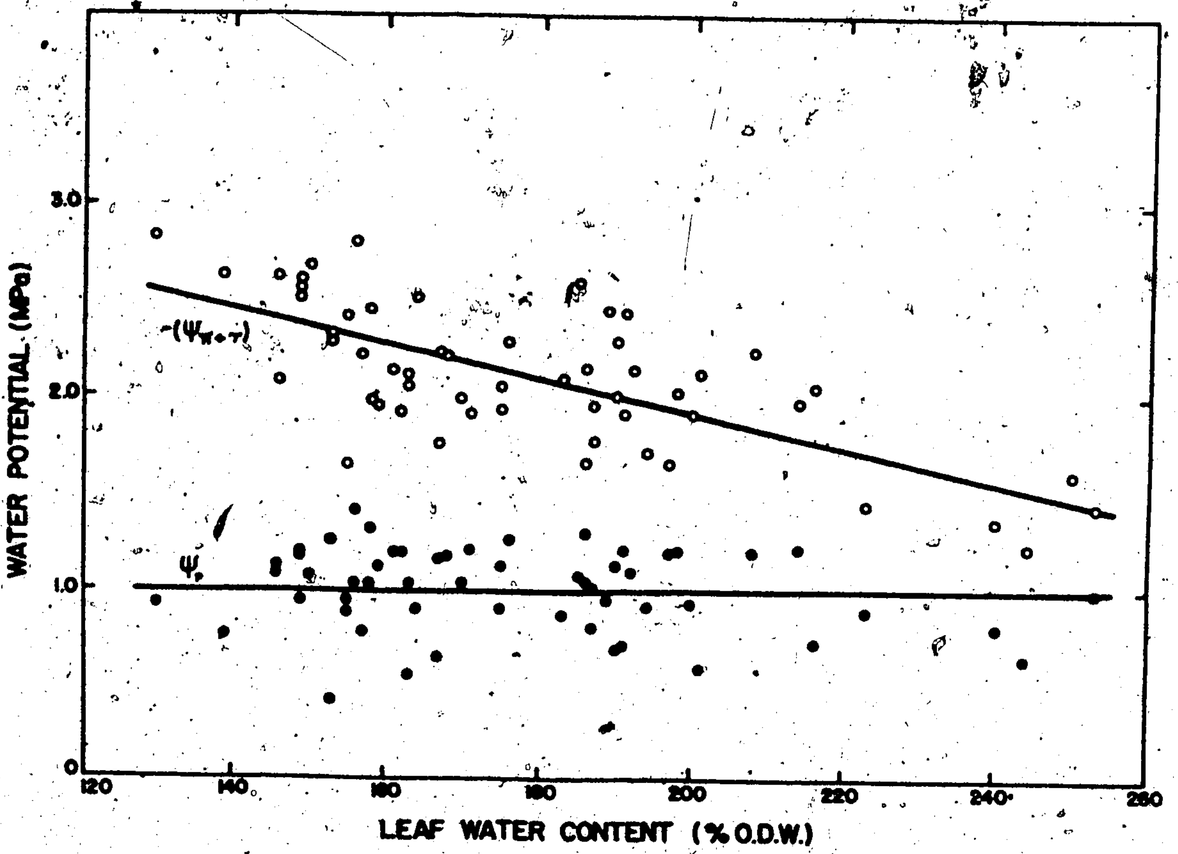


Figure 35. Höfler diagram for deciduous needles of small potted <u>Larix lyallii</u> trees determined during drying experiment. Turgor, ψ_p (●), and negative osmotic plus matric, $-\psi_{\pi+\tau}$ (○), are shown. Note that leaf water content is used here, rather than the standard relative water content.

Another result that supports this is that upon rewatering, net assimilation had recovered to only 25% of NAR_{max} after 1.5 d. The NAR remained at that level, or lower, despite adequate water, for ten more days, at which time the experiment was terminated. During the first few days following rewatering, leaf water potential and content recovered to pre-stress levels.

The drying experiment suggests that small larch trees are subject to large reductions in photosynthetic capacity in response to soil moisture stress, and that these reductions might be long-lasting. To thoroughly examine these possibilities without the complications of root damage would require field gas exchange studies. In this study it was not possible to make field gas exchange measurements. However, photosynthetic measurements of excised branches of field stressed trees were made.

These measurements were made on branches which had had their cut ends in distilled water for 1-2 days. Thus the branches were not under water stress at the time of measurement. The results indicate that soil moisture stress causes a long-term reduction in the photosynthetic capacity of drought-stressed small L. lyallii trees (Fig. 36). The reduction is less in small trees which were also shaded. Shade alone caused no reduction in NAR.

In contrast to the small trees, saplings of L. lyallii showed no reduction in NAR due to the applied drought treatment. This is because the treatment was ineffective (see Response to drought stress).

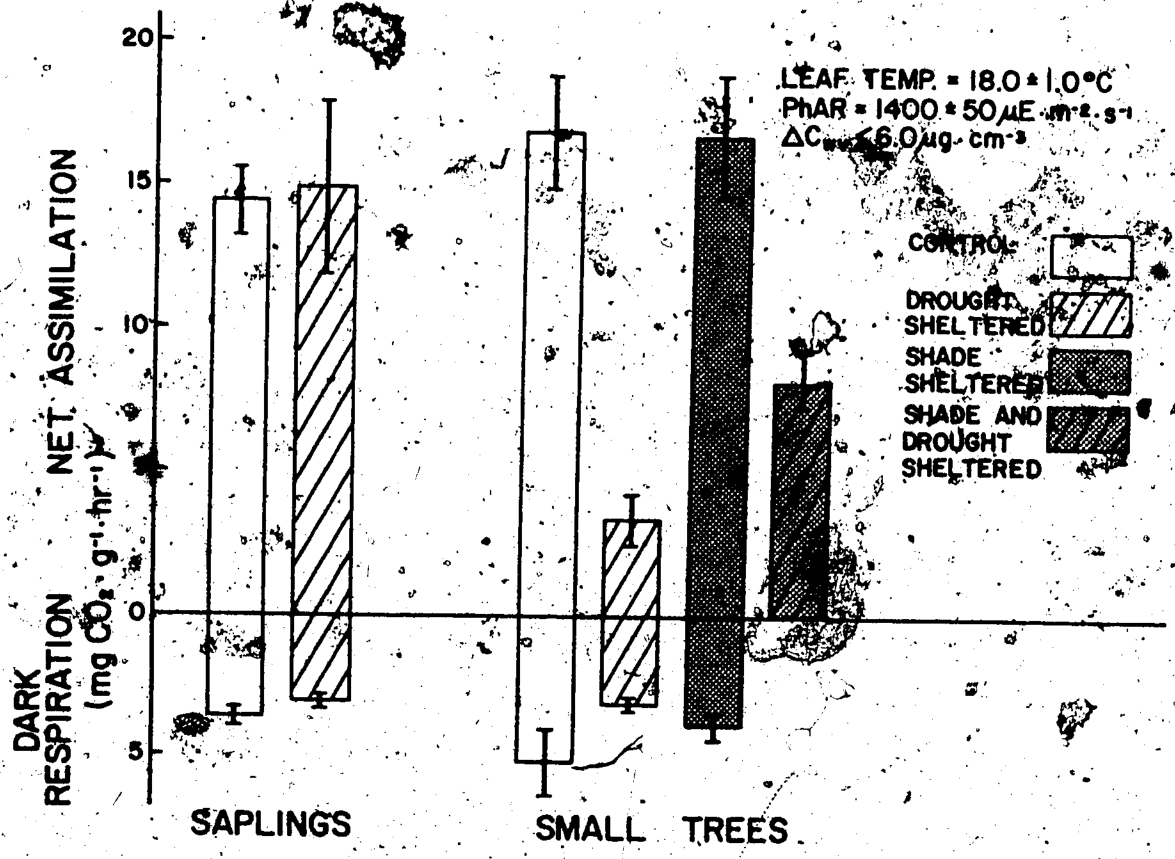


Figure 36. Net assimilation and dark respiration rates of branches excised from the small trees and saplings in the field stress experiment. Mean ± SE, n=5.

Summer Water Relations

The seasonal patterns

Predawn ψ_{Pxylem} of *L. lyallii* rises sharply in the spring, reaching maximum yearly values of -0.2 to -0.5 MPa around May 15 (Figs. 37a and 38a). In 1976, when meltout was late, the late spring and early summer cool, and leaf expansion late (Figs. 15 and 16), predawn ψ_{Pxylem} remained high for several weeks before declining to ∿ -1.0 MPa by 20 June. In contrast, during 1977, ψ_{Pxylem} declined quickly, reaching -1.0 MPa by 31 May, as a result of early snow melt, a warm spring, and early flushing. For the duration of the summer, in 1977, predawn ψ_{Pxylem} was between -1.0 and -1.5 MPa, while in 1976 it rarely fell to -1.0 MPa and rose to -0.4 MPa by the time of abscission. The seasonal pattern of predawn ψ_{Pxylem} is similar in both years even though the values were generally lower during 1977.

The diurnal range of ψ_{Pxylem} is greatest in the spring (Figs. 37a and 38a). Midday values generally do not fall below -1.7 to -1.8 MPa, except on unusually warm, sunny days (i.e. July 26, 1976; Fig 37a). As with predawn ψ_{Pxylem} values, midday values were generally lower in 1977 than in 1976.

Predawn leaf water content of deciduous *L. lyallii* needles increases from midwinter levels (100-140 %) to pre-flushing levels (200-250 %) in April (see Fig. 20). Leaf water content shows another large increase, to a maximum of 380 % by 20-25 June (Figs. 37b and 38b). This increase seems to be loosely correlated with leaf expansion. However, the 1976 water content data are not frequent enough to ascertain this. Leaf water content declined during July to ∿275 %. It was slightly lower during the late

Figure 37. Patterns of water relations parameters of *Larix lyallii* and sympatric evergreen conifers during the 1976 growing season. a.) Larch ψ_{Pxylem} on the north-facing (open symbols) and south-facing (closed symbols) sites. Predawn (mean ±SE, n=7) values are shown by circles and mean (n=7) midday values by triangles. b.) Predawn leaf water contents (mean ±SE, n=7) deciduous larch needles on both sites c.) Predawn water potential (mean ±SE, n=4(3)) and components of deciduous needles on both sites. d.) Predawn (mean ±SE, n=7) ψ_{Pxylem} of the evergreen conifers, compared to the larch predawn pattern (from a.).

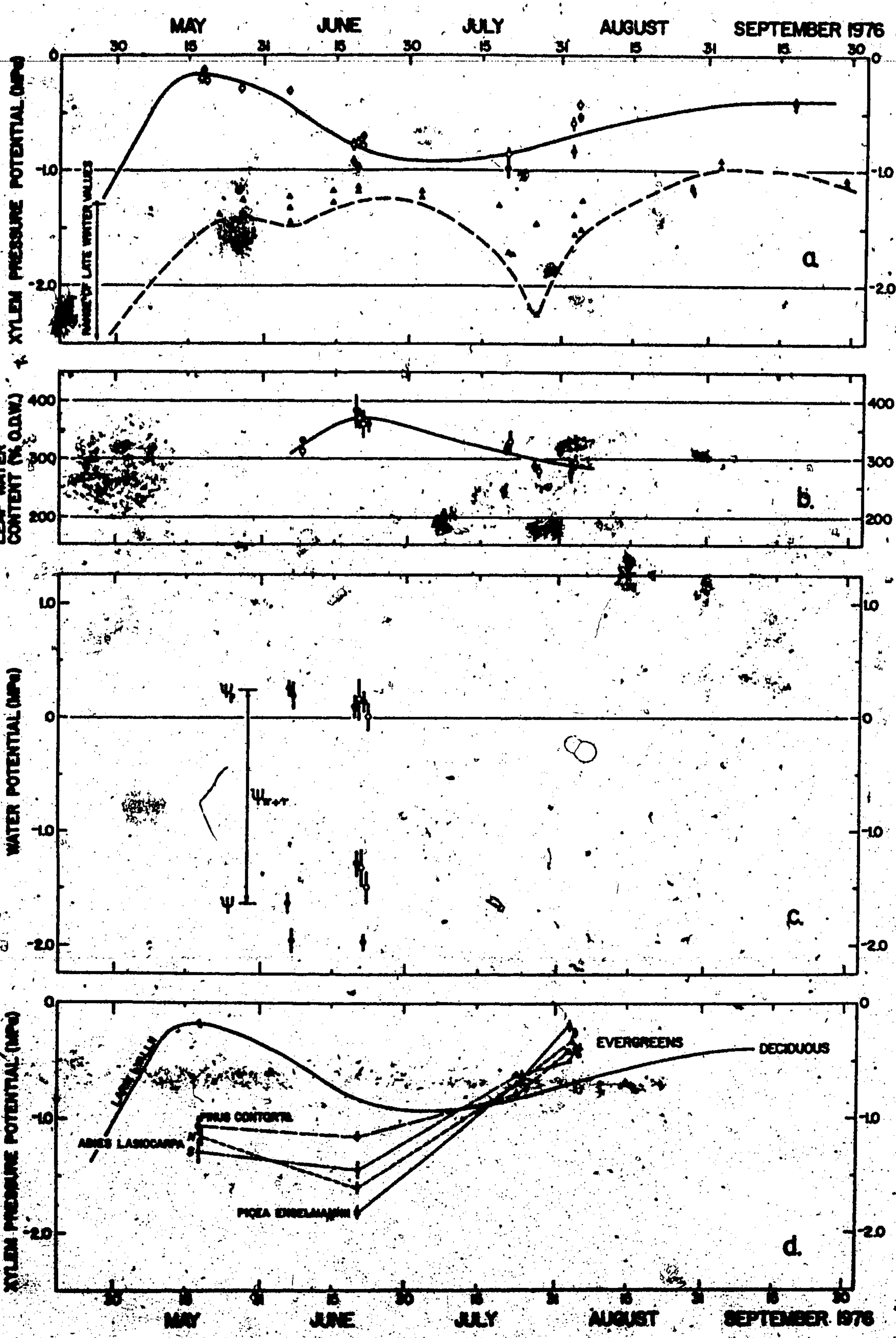
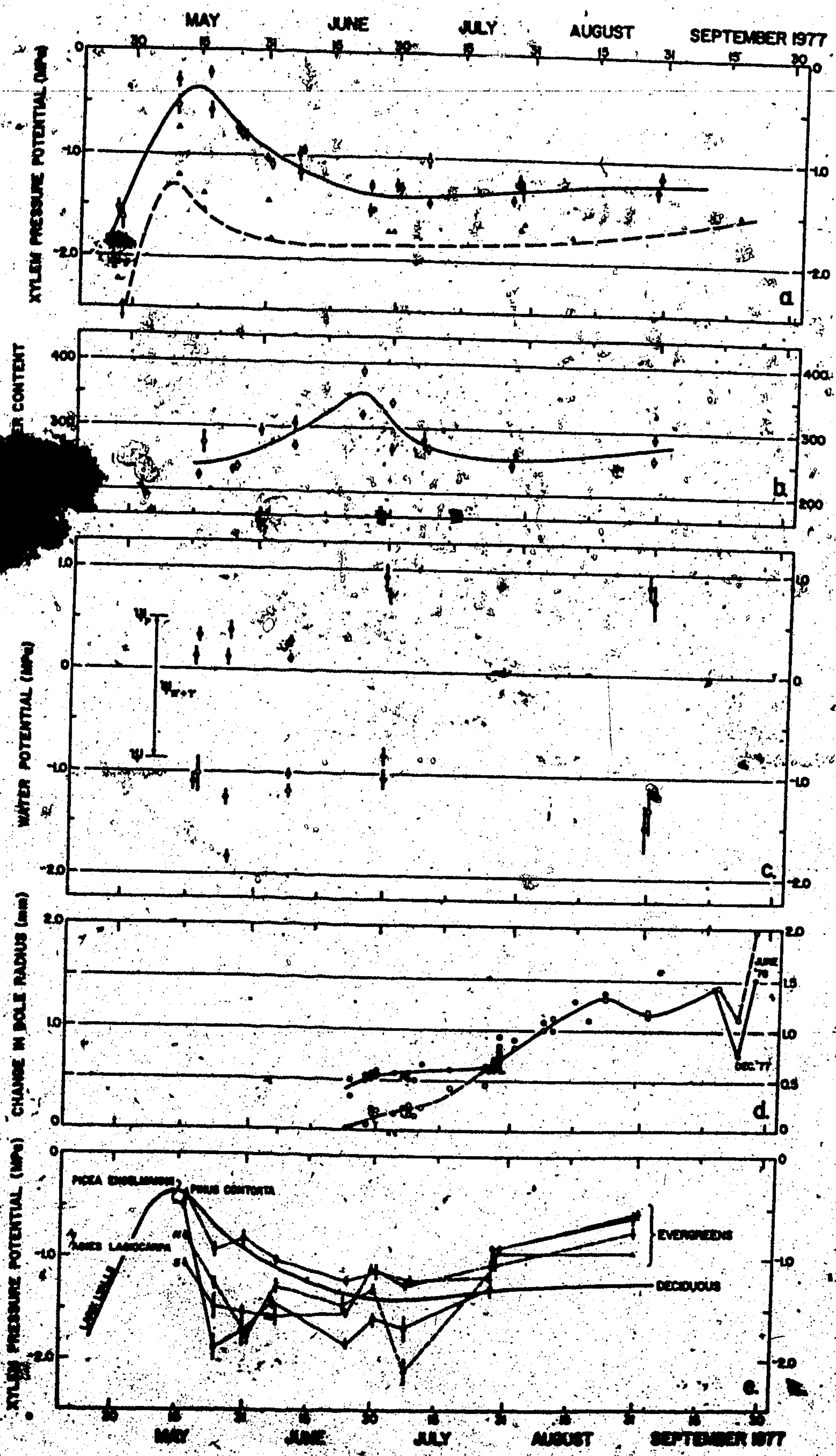

MAY
JUNE
JULY
AUGUST
SEPTEMBER 1976
30
15
31
15
30
15
31
15
31
15
30
XYLEM PRESSURE POTENTIAL (MPa)
0
-1.0
-2.0
RANGE OF LATE WINTER VALUES
a.
LEAF WATER CONTENT (% O.D.W.)
400
300
200
b.
WATER POTENTIAL (MPa)
1.0
0
-1.0
-2.0
ψ_p
$\psi_{\pi+\tau}$
ψ
c.
XYLEM PRESSURE POTENTIAL (MPa)
LARIX LYALLII
PINUS CONTORTA
ABIES LASIOCARPA
N
S
PICEA ENGELMANNII
EVERGREENS
DECIDUOUS
d.

Figure 38. Patterns of water relations parameters of *Larix lyallii* and sympatric evergreen conifers during the 1977 growing season. All parameters are as described in Fig. 37, except that change in bole radius was measured on both sites in 1977 (d.).


MAY
JUNE
JULY
AUGUST
SEPTEMBER 1977
30
15
31
15
30
15
31
15
31
15
30
XYLEM PRESSURE POTENTIAL (MPa)
0
-1.0
-2.0
a
ER CONTENT
400
300
200
b.
WATER POTENTIAL (MPa)
1.0
0
-1.0
-2.0
Ψ_P
$\Psi_{\pi+T}$
Ψ
c.
CHANGE IN BOLE RADIUS (mm)
2.0
1.5
1.0
0.5
0
JUNE '78
DEC '77
d.
XYLEM PRESSURE POTENTIAL (MPa)
PICEA ENGELMANNII
PINUS CONTORTA
ABIES LASIOCARPA
LARIX LYALLII
EVERGREENS
DECIDUOUS
e.

summer in 1977 than in 1976.

Consistent with the low May turgor (ψ_p) shown [illegible] the winter water relations study (see Fig. 20), determinations of predawn ψ_p in the spring of 1976 and 1977 gave low values (Figs. 37c and 38c). High values were obtained for this parameter after water content reached its maximum. Osmotic plus matric potentials ($\psi_{\pi+\tau}$) and total leaf potentials (ψ) appear lower in June 1976 than in 1977. This is the opposite of the relationship shown by ψ_{pxylem} for June of the two years.

A direct correlation was not found between ψ and $\psi_{p_{xylem}}$. Rates of ψ: $\psi_{p_{xylem}}$ determined on the [illegible] sample did, however, remain close to 1:1 (see Fig. 21). The discrepancy between these two parameters is a puzzling and vexing problem. Difficulty with the techniques does not seem to be adequate explanation. In the winter studies large differences between $\psi_{p_{xylem}}$ and ψ were found and a large resistance in the water conduction system linking bud to the already developed xylem was postulated (see p. 99). The differences in these parameters in summer do not show such a clear pattern, thus further research will be needed to solve the problem.

Site differences in the water relations parameters are rarely significant. The differences that do occur appear to be related to differences in soil temperature or atmospheric demand, or to developmental differences.

At least one period of wood growth appears to occur simultaneously from $\sim$20 July to 25 August, on both sites (Fig. 38d). Less overall change to bole radius is shown for the south-facing site, which is the opposite of the growth statistics given in Ch. III. The change in bole radius was measured on only two trees on each site. The reversal may thus be explained by the sampling bias.

Predawn xylem pressure potentials of the evergreen trees which occur with alpine larch on the study sites show a seasonal pattern that is distinctly different than that of the deciduous species (Figs. 37d and 38e). The everygreens are much drier in the spring and early summer and have higher ψ_{Pxylem} during the later part of the summer. The first difference is explained by the small leaf area of L. lyallii in the spring and early summer, and the second suggests that the deciduous needles, when developed, have higher minimum diffusive conductances than the needles of the evergreens.

Based on soil water content data and rooting patterns it was suggested that L. lyallii did not experience soil moisture stress at any time during the summer (see p. 47). Support for this comes from Fig. 39. In July and August and for the 1976 summer as a whole, ψ_{Pxylem} of saplings (when irradiance was ≥ 70 $W \cdot m^{-2}$) was significantly ($p > .01$) negatively correlated ($r = -0.92$, -0.67, and -0.72, respectively) with Δc_{wv}. 1977 data show similar correlations. These correlations and the lack of much variation in the soil water content show that atmospheric demand was the factor most important in determining the water status of L. lyallii saplings in July and August. This is not true in June when low soil temperatures on the north-facing site and amount of leaf area developed, are probably more important.

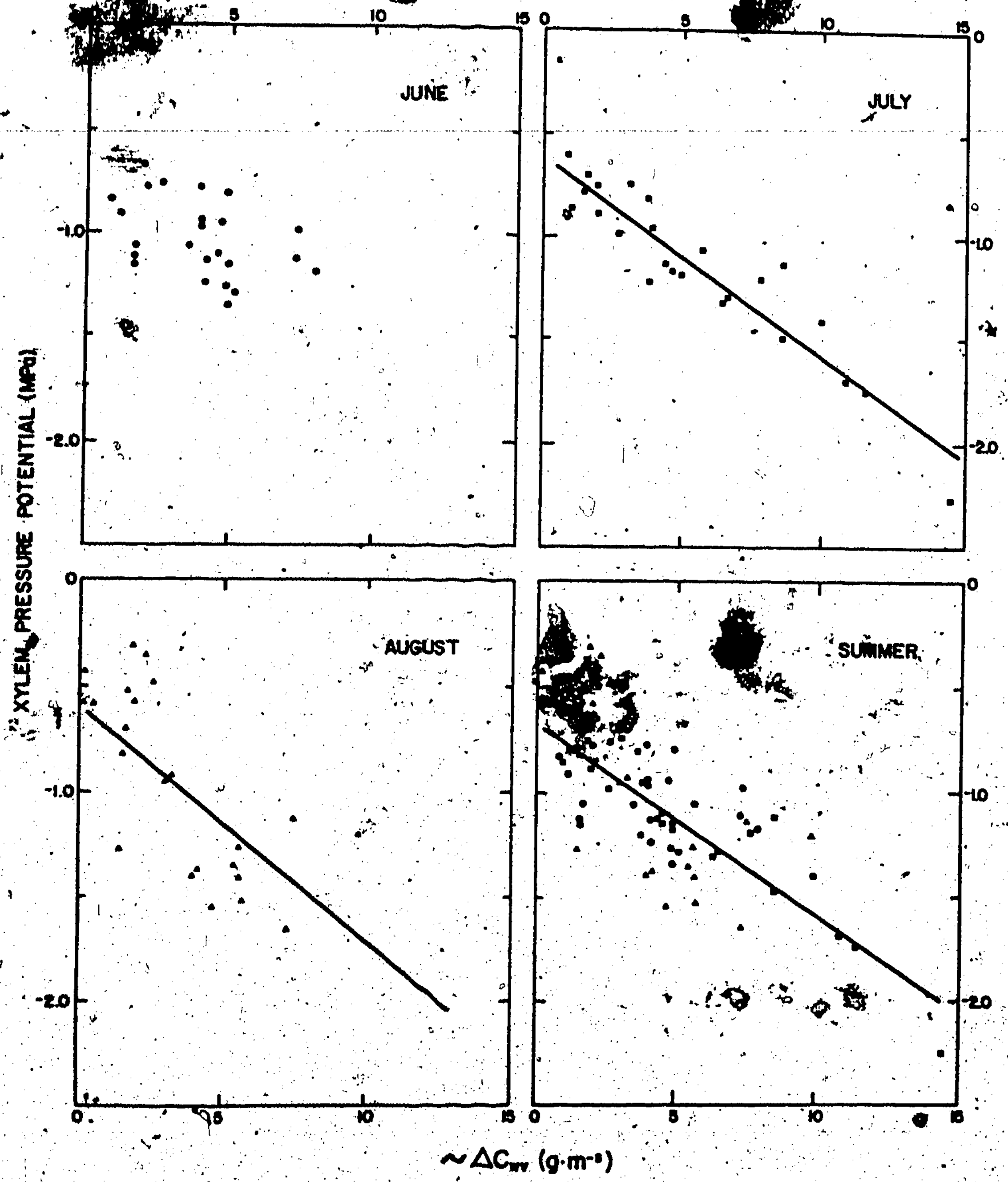


Figure 39. The relationship of ψ_{Pxylem} to the water vapor concentration gradient from leaf to air in June, July, and August, and for the whole summer, 1976.

Diurnal patterns

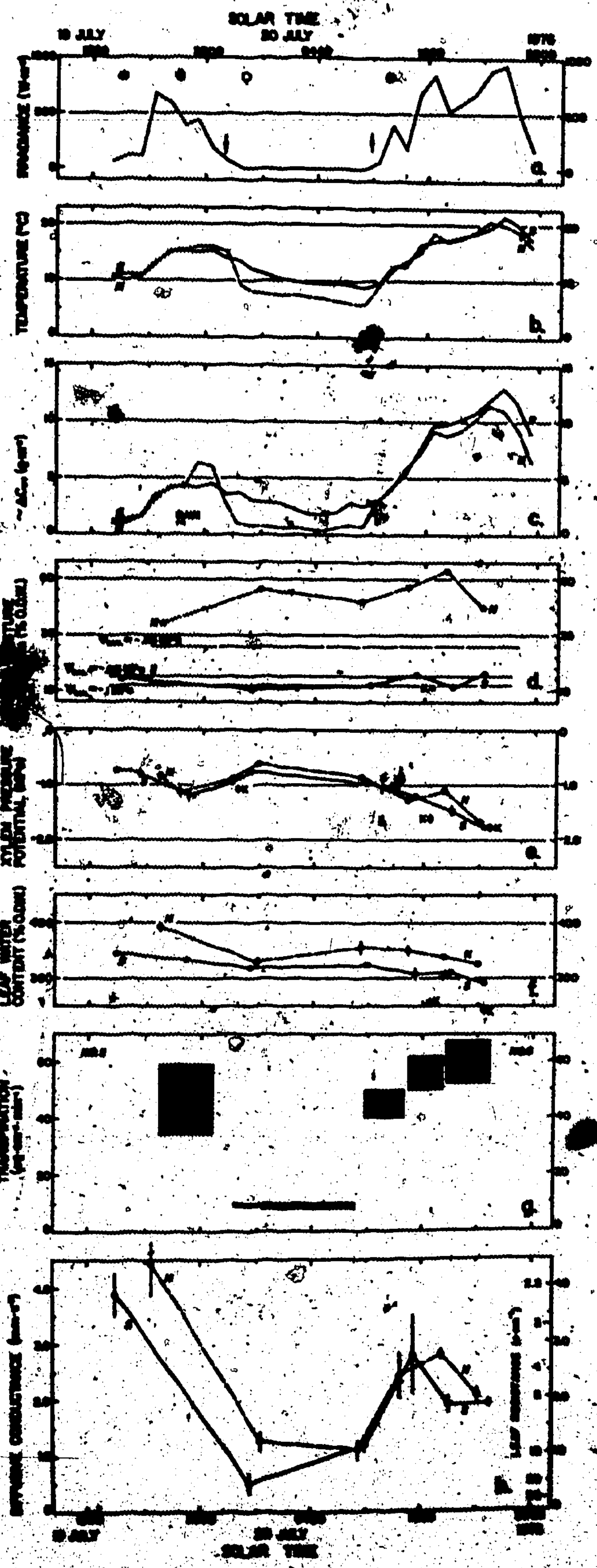
The correlation of ψ_{Pxylem} to Δc_{wv}, shown above, was apparent in the data from each intensive sampling period (Fig. 40c and e). Data from two other intensive samplings are given in Appendix E.

The small changes, when considered in the light of Fig. 35, in leaf water content during a diurnal cycle are also shown in Fig. 40f. Transpiration rates of L. lyallii needled branches reach a maximum of 40–60 $\mu g \cdot cm^{-2} \cdot min^{-1}$ (Fig. 40 and see Appendix E). The increase in transpiration from dawn to 1600 h on 20 July 1976 did not parallel the increase in the water vapor concentration gradient (Fig. 40c and e). This is explained by the decreasing diffusive conductance during the [illegible] period (Fig. 40h). Maximum diffusive conductance recorded for deciduous alpine larch needles was 4.45 $mm \cdot s^{-1}$ ($\equiv 2.25$ $s \cdot cm^{-1}$)(Fig. 40h). Minimum conductances ranged from 0.5 $mm \cdot s^{-1}$ ($\equiv 20$ $s \cdot cm^{-1}$) to 0.17 $mm \cdot s^{-1}$ ($\equiv 59$ $s \cdot cm^{-1}$).

Stomatal opening in response to light is slower in June when the deciduous leaves are still immature. During this period also, maximum conductances are not achieved (Fig. 41). In July and August stomatal opening is rapid with increasing light, and maximum conductivities are obtained.

The midday stomatal closure shown in Fig. 40h suggests that stomata are responding to: decreased leaf water potential, or to increased atmospheric demand. Compilation of diffusive conductance data from L. lyallii saplings showed highly significant negative correlations to atmospheric demand (Fig. 42). These correlations do not exclude the

Figure 40. Environmental and Larix lyallii sapling water relations data from an intensive sampling period, 19-20 July 1976. Environmental parameters: a.) irradiance on the south-facing site (arrows indicate sunset and sunrise, and cloud cover is shown by standard meteorological symbols); b.) air temperatures at 15 cm; c.) approximate (because good leaf temperature data were not available) Δc_{wv} and an indication of precipitation periods; d.) mean soil moisture at -10 cm ($n=4$). Mean ±SE is shown for all water relations parameters: e.) $\psi_{p\,xylem}$ ($n=7$); f.) leaf water content ($n=7$); g.) transpiration of excised branches ($n=7$); h.) leaf diffusive conductance (a resistance scale is also shown) ($n=5$). Note data from the krummholz site (K).


SOLAR TIME
19 JULY
20 JULY
1976
TEMPERATURE (°C)
a.
b.
c.
d.
e.
f.
g.
h.
XYLEM PRESSURE POTENTIAL
LEAF WATER CONTENT
TRANSPIRATION
DIFFUSIVE CONDUCTANCE
LEAF RESISTANCE
19 JULY
20 JULY
SOLAR TIME

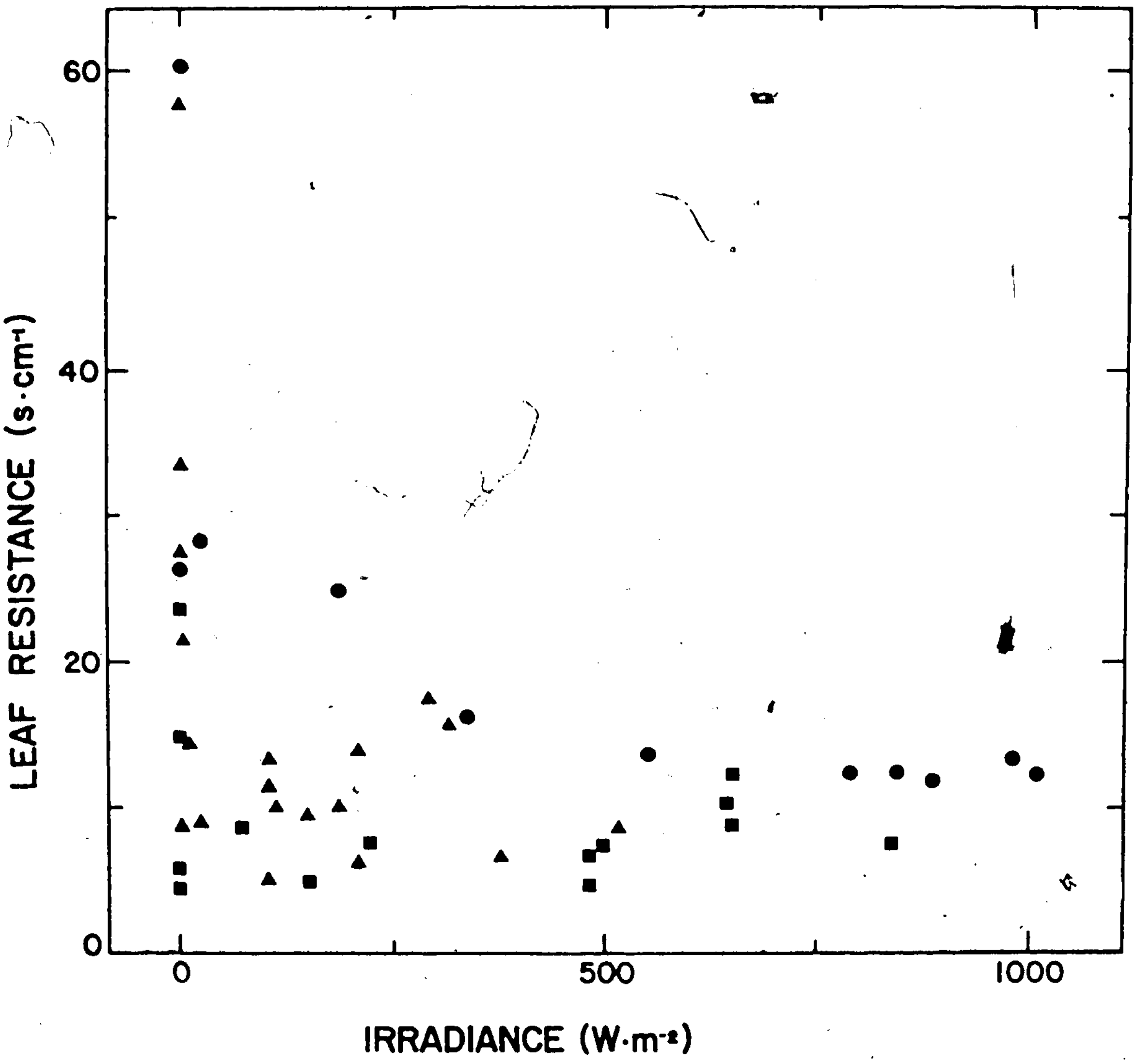


Figure 41. Leaf resistance of deciduous Larix lyallii needles in June (●), July (■), and August (▲) are shown as a function of irradiance at the time of sampling.

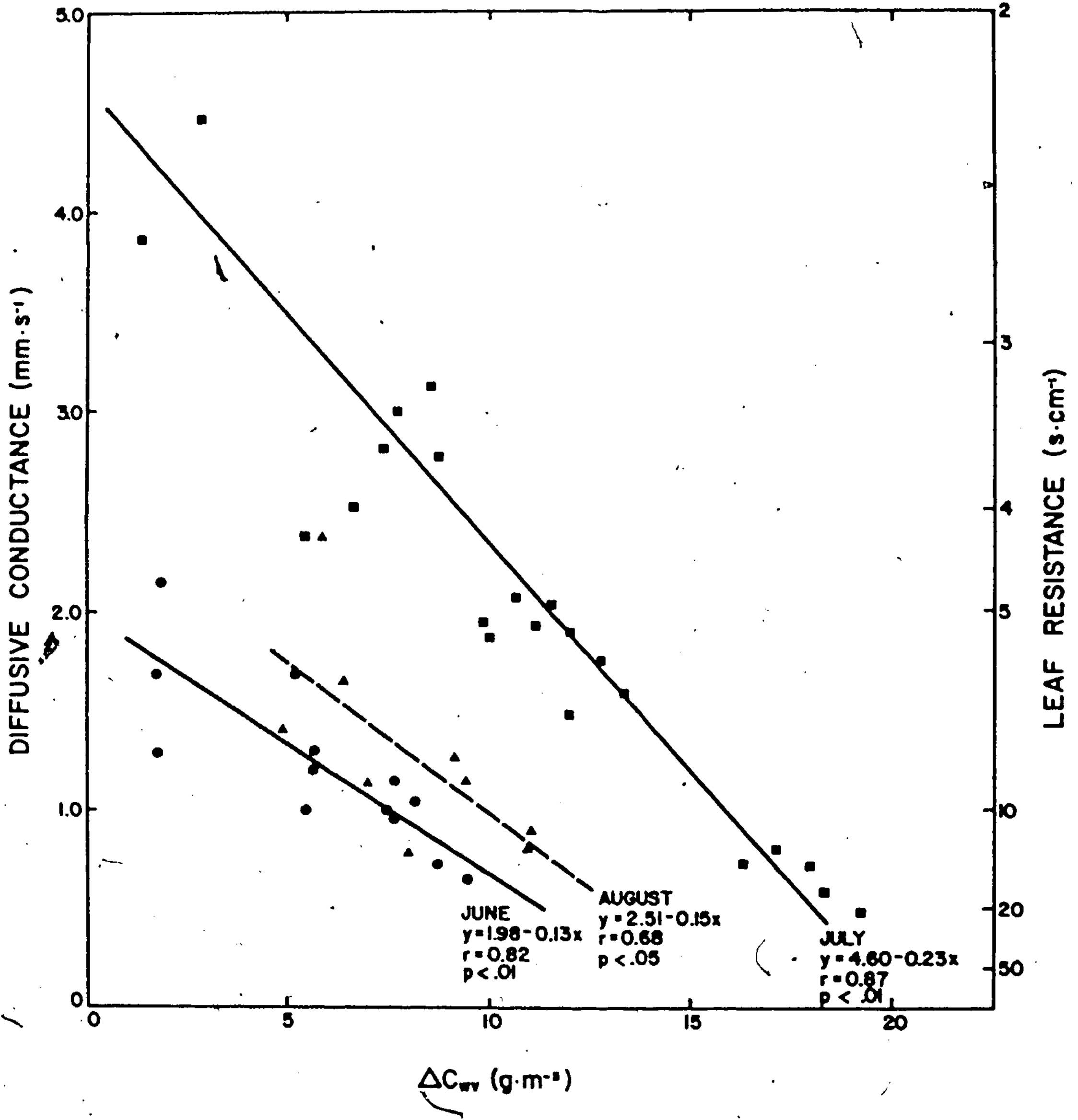


Figure 42. Composite of all diffusive conductance (resistance) data, for deciduous Larix lyallii needles, showing the highly significant negative correlation to the water vapor concentration difference throughout the summer. High water vapor concentration differences in July are due to leaf over temperatures.

possibility that the stomata are also responding to leaf water status, however. This possibility was investigated in the stress experiments.

Responses to drought stress

Saplings

Data from intensive sampling of stressed and control saplings in July and August 1978 (Figs. 43 and 44) were examined for patterns in the response of stomata to environmental factors and to leaf water status. In July deciduous leaves on the stressed trees sampled above and below the polyethylene shelters, had similar ψ_{pxylem} and leaf water content. Also contrary to expectation, needles from control trees had lower water contents than those of stressed trees (Fig. 43e and f). The upper canopy needles of stressed trees had diffusive conductances nearly identical with those of control trees (Fig. 43d). At the same time the needles under the stress shelter had much lower diffusive conductance.

These patterns are similar to those found in August (Fig. 44). The importance of automatic data logging (and good weather) are clearly demonstrated by these data. Because of the clear sky on 8 August 1978, radiation loads on leaves under the stress shelters caused leaf temperatures to rise up to 11° C above air temperatures (Fig. 44b). This caused a much increased Δc_{wv}. During this period diffusive conductances were much reduced in both control and stress trees. Although water potentials and contents of the needles on these trees were not significantly different, diffusive conductances were quite different. The diurnal pattern of response is shown in Fig. 45.

Figure 43. Environmental and water relations data from intensive sampling of deciduous needles on control and stressed sapling Larix lyallii on 13 July 1978. Environmental parameters: a.) irradiance and cloud cover and type; b.) air temperature in the open (●), and leaf temperature in the open (○) and under the drought stress shelters (□); c.) calculated Δc_{wv} in the open (○) and under the shelters (□). Mean ±SE are shown for all water relations parameters: d.) diffusive conductance (n=4); e.) leaf water content (n=5); and xylem pressure potential (n=5). Symbols are labeled in d.

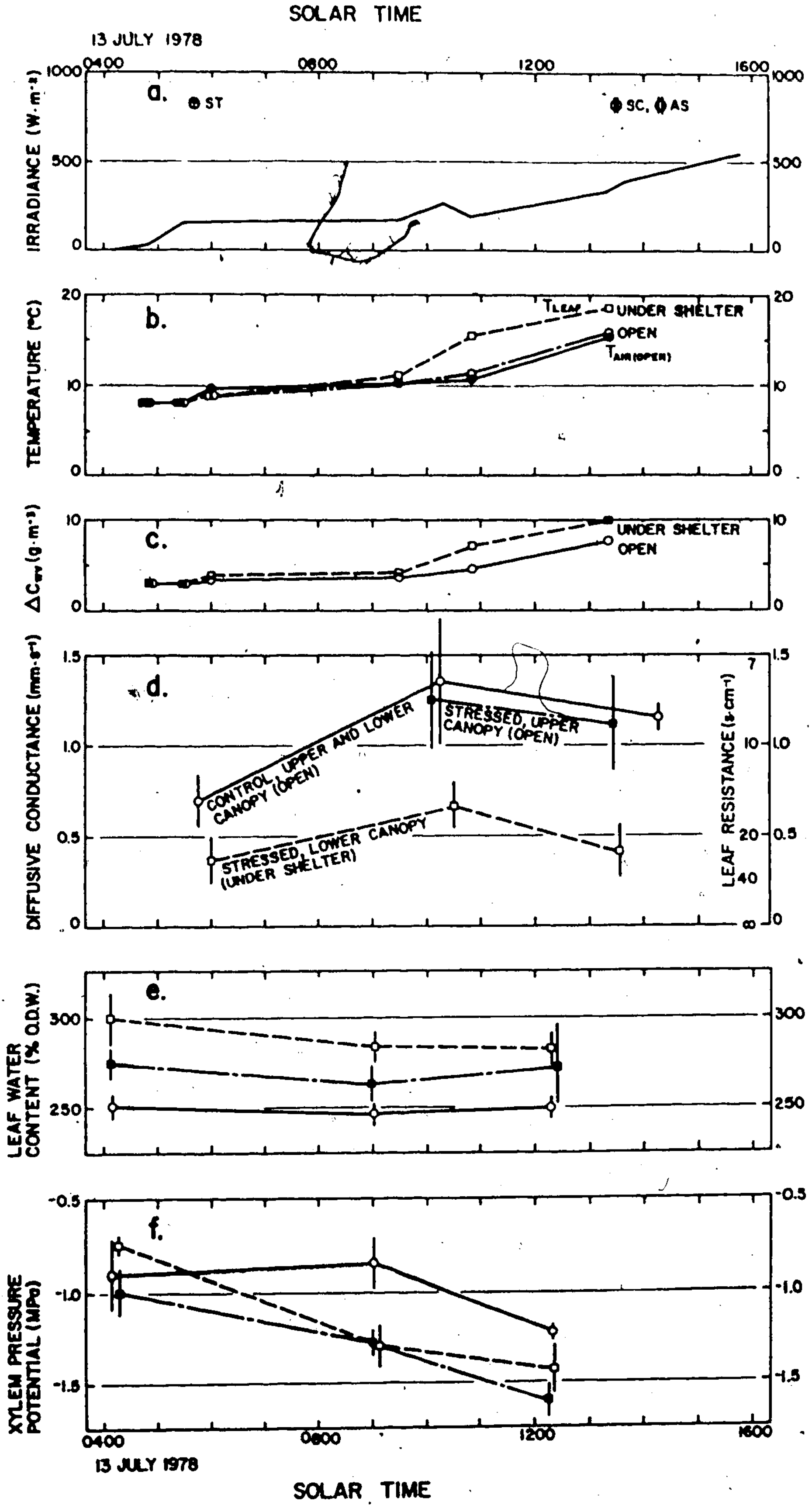
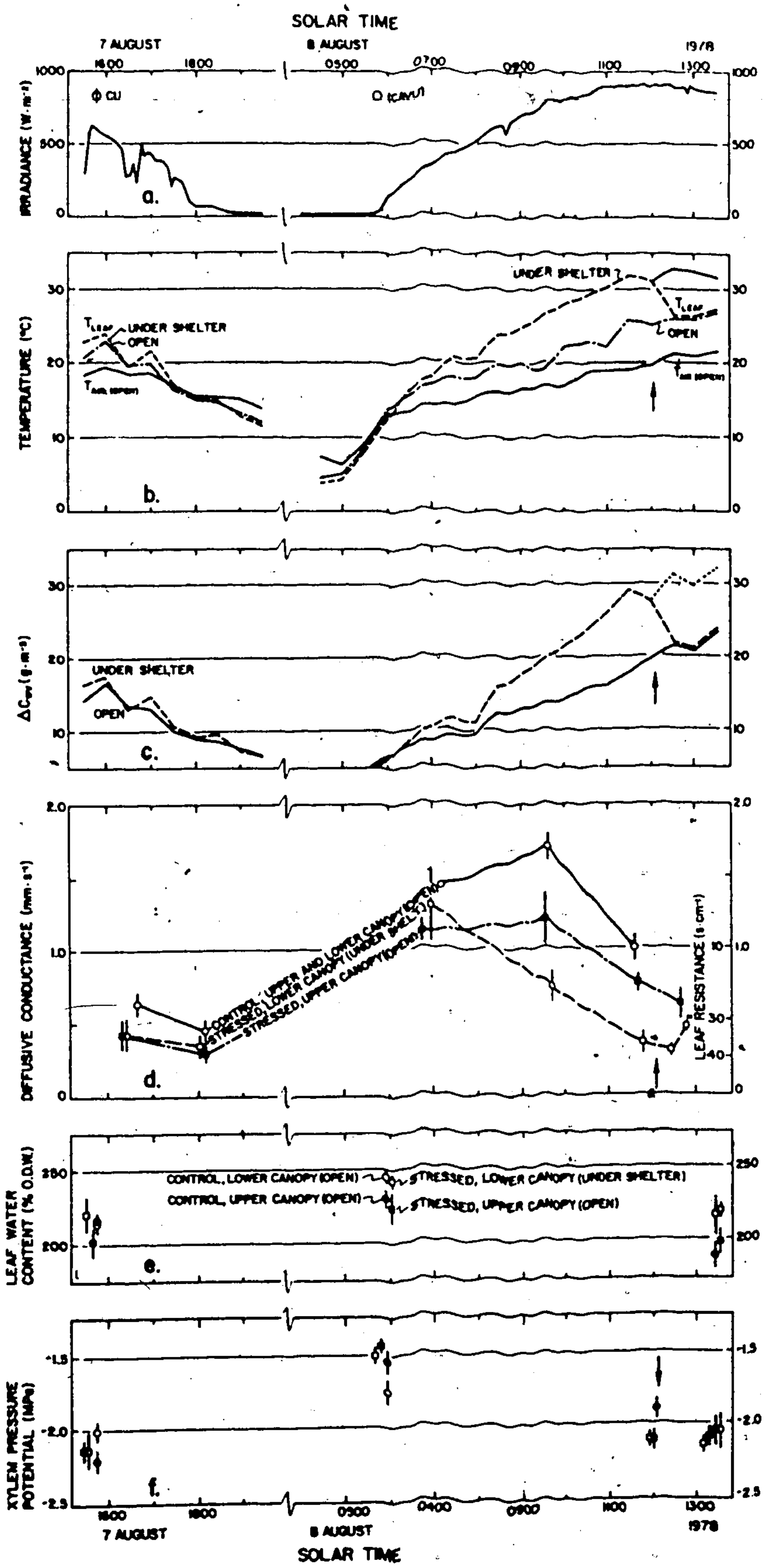

SOLAR TIME
13 JULY 1978
0400
0800
1200
1600
a.
ST
SC, AS
IRRADIANCE (W·m⁻²)
1000
500
0
b.
TEMPERATURE (°C)
T LEAF
UNDER SHELTER
OPEN
T AIR (OPEN)
20
10
0
c.
ΔCwv (g·m⁻³)
UNDER SHELTER
OPEN
10
0
d.
DIFFUSIVE CONDUCTANCE (mm·s⁻¹)
CONTROL, UPPER AND LOWER CANOPY (OPEN)
STRESSED, UPPER CANOPY (OPEN)
STRESSED, LOWER CANOPY (UNDER SHELTER)
LEAF RESISTANCE (s·cm⁻¹)
1.5
1.0
0.5
0
7
10
20
40
∞
e.
LEAF WATER CONTENT (% O.D.W.)
300
250
f.
XYLEM PRESSURE POTENTIAL (MPa)
-0.5
-1.0
-1.5
0400
0800
1200
1600
13 JULY 1978
SOLAR TIME

Figure 44. Environmental and water relations data from intensive sampling of deciduous needles on control and stressed sapling Larix lyallii on 7-8 August 1978. Environmental parameters are as in Fig. 43, but because data was recorded every 5 min no points are shown. The arrow indicates the time of removal of the drought stress shelter. Water relations parameters are as in Fig. 43 with diffusive conductance sample size increased to n=5. In addition, needles from the lower canopy of control trees were sampled. Symbols are labeled in d. and e.


SOLAR TIME
7 AUGUST
8 AUGUST
1978
1600
1800
0500
0700
0900
1100
1300
IRRADIANCE (W·m⁻²)
1000
500
0
ϕ CU
O (CAVU)
a.
TEMPERATURE (°C)
30
20
10
0
UNDER SHELTER
T LEAF
UNDER SHELTER
OPEN
T AIR (OPEN)
b.
ΔC vw (g·m⁻³)
UNDER SHELTER
OPEN
c.
DIFFUSIVE CONDUCTANCE (mm·s⁻¹)
2.0
1.0
0
CONTROL, UPPER AND LOWER CANOPY (OPEN)
STRESSED, LOWER CANOPY (UNDER SHELTER)
STRESSED, UPPER CANOPY (OPEN)
LEAF RESISTANCE (s·cm⁻¹)
10
30
40
d.
LEAF WATER CONTENT (% O.D.W.)
250
200
CONTROL, LOWER CANOPY (OPEN)
STRESSED, LOWER CANOPY (UNDER SHELTER)
CONTROL, UPPER CANOPY (OPEN)
STRESSED, UPPER CANOPY (OPEN)
e.
XYLEM PRESSURE POTENTIAL (MPa)
-1.5
-2.0
-2.5
f.

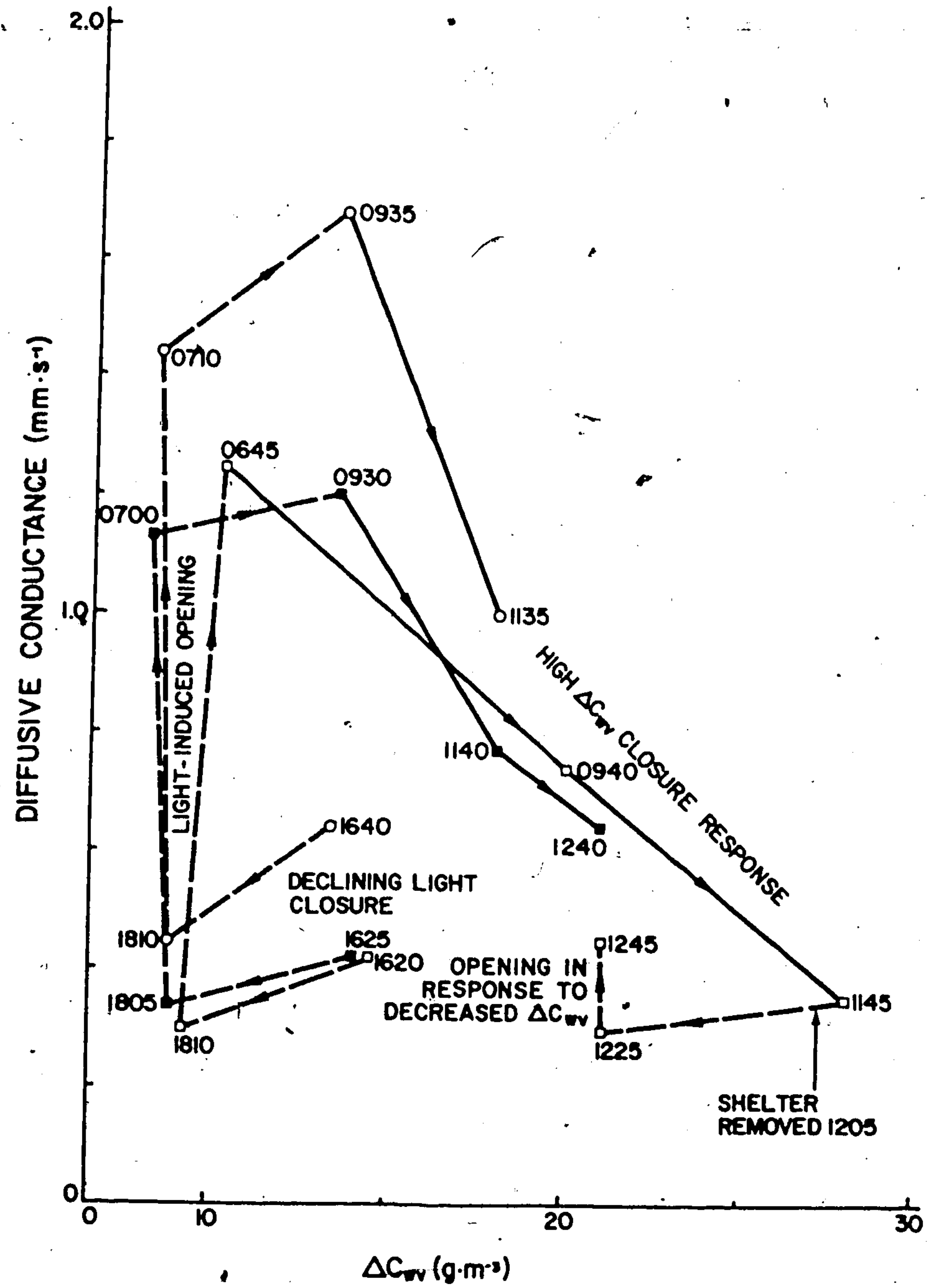


Figure 45. Diurnal patterns of diffusive conductance illustrating similarities and differences between responses of deciduous needles on control (○) and stressed (above shelter, □; below shelter, ■) trees to light and Δc_{wv}. Data were extracted from Fig. 44 .

Deciduous leaves of stressed trees, both above and below the shelters responded to increasing Δc_{wv} in a similar manner, by rapidly reducing stomatal conductance when $\Delta c_{wv} > 14$ $g \cdot m^{-3}$. This response occurred several hours later in the upper canopy leaves than it did in those from the lower canopy, in concert with the different rate of increase in Δc_{wv}. Control deciduous leaves also began to have reduced conductance when $\Delta c_{wv} > 14$ $g \cdot m^{-3}$. At any level of atomspheric demand, however, they had higher conductance than did stressed leaves. The response patterns to increasing or decreasing light are smaller in the three leaf types (Fig. 43).

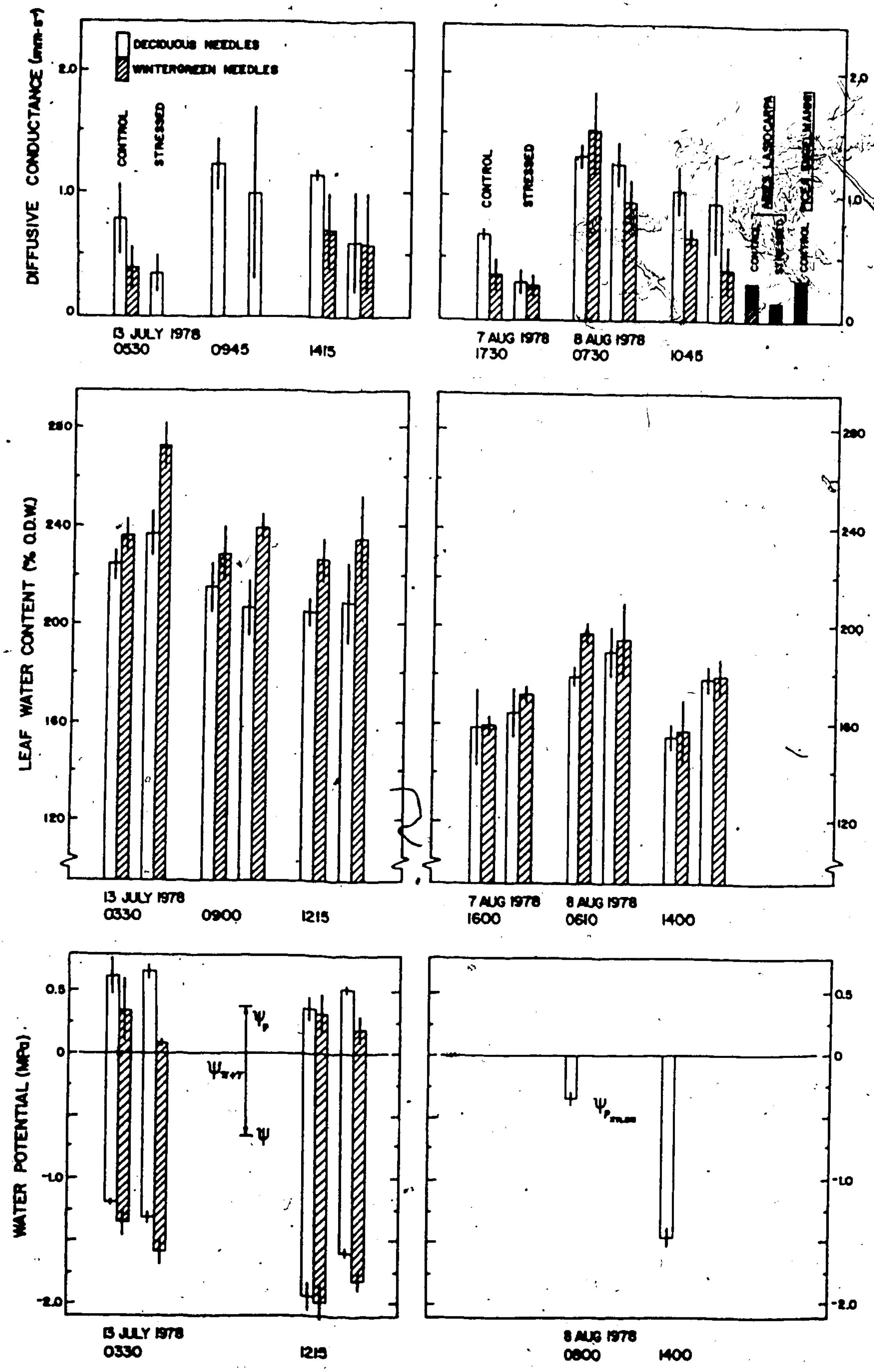
Removal of the experimentally induced high Δc_{wv} caused a rapid opening response of the stomata of lower canopy stressed leaves. The time course of this response is similar to that found in the gas-exchange studies (p. 160).

To summarize, these data show that the stress history of deciduous leaves appears to control the potential maximum diffusive conductance. Stomata of both stressed and control leaves then respond similarly to high atmospheric demand, which causes decreased diffusive conductance. The response to light also appears to be similar.

Small trees

Leaf water contents of stressed deciduous and wintergreen needles of small L. lyallii trees were always the same or higher than similar control needles (Fig. 46). The wintergreen leaves also had higher water contents and usually lower diffusive conductances than deciduous leaves. On 8 August the diffusive conductance of the winter-

Figure 46. Water relations parameters of deciduous and wintergreen needles from control and drought stressed small Larix lyallii. Data are from the two sampling periods illustrated in Figs. 44 and 45. Environmental data and sample sizes are given there. Within each group of four bars, the arrangement of treatment and leaf type remains as it is labeled in the upper boxes. Times and dates are indicated for each group.


DECIDUOUS NEEDLES
WINTERGREEN NEEDLES
DIFFUSIVE CONDUCTANCE (mm·s⁻¹)
0
1.0
2.0
CONTROL
STRESSED
13 JULY 1978
0530
0945
1415
7 AUG 1978
1730
8 AUG 1978
0730
1045
CONTROL
STRESSED
ABIES LASIOCARPA
CONTROL
PICEA ENGELMANNII
LEAF WATER CONTENT (% O.D.W.)
120
160
200
240
280
13 JULY 1978
0330
0900
1215
7 AUG 1978
1600
8 AUG 1978
0610
1400
WATER POTENTIAL (MPa)
0.5
0
-1.0
-2.0
Ψp
Ψπ+τ
Ψ
Ψp
13 JULY 1978
0330
1215
8 AUG 1978
0800
1400

green needles decreased more rapidly than that of deciduous needles as Δc_{wv} increased (Fig. 46). This type of response may have contributed to the higher water contents of the wintergreen needles.

Although the data have high variability, it appears that deciduous needles on small L. lyallii have drought stress responses that are similar to those on saplings. Wintergreen leaves appear to reduce their diffusive conductances more quickly, thus maintaining higher water contents, and perhaps potential maximum conductances (Fig. 46).

It is surprising that such small differences were caused in water status of stressed and control small trees. The differences were even smaller in the saplings. This suggests that the drought stress shelters were not large enough to reduce the soil moisture in the rooting zone of these trees. Soil water contents at 10 cm depth were lower under the drought stress shelters (7.4%) than in the open (9.8%), but the difference is not large. The deeply penetrating roots, especially of the saplings, were probably able to obtain water from lateral flow into the area under the shelters. The drought stress shelters, while not very effective in reducing soil moisture, did effectively increase the atmospheric demand experienced by the stressed trees.

DISSCUSSION

The general objective of this chapter was to investigate the disadvantages of the deciduous habit in summertime timberline environments The results of the photosynthetic and water relations studies have shown two environmental factors, light and atmospheric moisture demand, to be most important in limiting L. lyallii to timberline habitats.

The light compensation point (~160 $\mu E \cdot m^{-2} \cdot s^{-1}$) of wintergreen leaves on small trees (Fig. 32) is extremely high compared with light compensation points of other timberline trees: 10-35 $\mu E \cdot m^{-2} \cdot s^{-1}$ for black spruce (Vowinckel et al. 1975, Black 1977), 130 lux ≈ 30 $\mu E \cdot m^{-2} \cdot s^{-1}$ for cembran pine (Tranquillini 1979), and 0.03-0.08 $cal \cdot cm^{-2} \cdot min^{-1} \approx 80-150\ \mu E \cdot m^{-2} \cdot s^{-1}$ for tamarack (Auger 1974).

Light levels measured within the subalpine forest at Marmot Creek Basin were 155-175 $\mu E \cdot m^{-2} \cdot s^{-1}$ under clear skies. At the same time PhAR in dense stands of larch saplings was 280-450 $\mu E \cdot m^{-2} \cdot s^{-1}$. Thus, the high light compensation point of wintergreen leaves, which constitute the majority of leaf biomass for the first five years of an alpine larch seedling's life (see Fig. 14), explains the lack of young larch trees on the floor of the subalpine forest. The open woodland stands which L. lyallii forms are probably also related to its poor shade tolerance when young.

Light compensation points of mature deciduous needles of L. lyallii (see Fig. 31) include the range given by Auger (1974) for L. laricina (see above). Maximum photosynthetic rates for these two species are also similar, 20-22 mg $CO_2 \cdot g^{-1} \cdot hr^{-1}$, and again demonstrate the similarity of the ecology of these two North American species, despite their widely differing habitats (Auger 1974, Arno 1970).

Maximum diffusive conductances of deciduous alpine larch needles are high (4.45 $mm \cdot s^{-1}$). They agree with maximum conductances of deciduous broad-leaved trees (Davies and Kozlowski 1974, Federer and Gee 1976), but are much higher than those of timberline evergreen trees (Kaufman 1976, Slatyer 1976). Even relatively low atmospheric evaporative demands cause sharp reductions in this high maximum conductance. Both field and laboratory studies have demonstrated this response (Figs. 33, 42, and 45).

Many others have shown similar linear decreases in stomatal conductance in response to increasing atmospheric demand (Lange et al. 1971, Schulze et al 1972, Federer and Gee 1976, Kaufmann 1976, and Lösch 1977, among others) or analyzed the importance of this response in controlling plant water status (Hall et al. 1976, Cowan 1977, and Farquhar 1978). For L. lyallii the importance of the reduced stomatal conductances caused by increased atmospheric demands is, as with all land plants, a reduced carbon gain (Raschke 1975). Reduction in carbon gain caused by high atmospheric demands is the second main reason that alpine larch is limited to the timberline region, where atmospheric demands are usually low (Tranquillini 1979).

Temperature and humidity data from Environment Canada (1968-1978) show that in Marmot Creek Basin the vapor pressure deficit averages 66% higher at 1700 m than at 2300 m at the timberline. Using this information and Fig. 42 it is possible to estimate that total carbon uptake by alpine larch in July would be reduced ~40% from timberline to 1700 m in the subalpine forest, by humidity responses alone. The slightly higher temperatures at the lower elevation would not make any significant increase in photosynthetic uptake to compensate for this decrease.

The high light compensation point of needles on young trees, together with the sensitivity of the species to low atmospheric moisture, makes L. lyallii a poor competitor with the subalpine forest evergreens. These factors explain to a large extent the restriction of alpine larch to the timberline zone where open habitats are common and atmospheric demands low. They also explain the extremely patchy occurrence of alpine larch in the southern portion of its range, where it is found on cool, north-facing slopes at very high elevations, and only on talus or avalanche slopes or boulder piles at lower elevations (Arno 1970). These are sites where competing evergreen trees grow poorly, if at all, and atmospheric moisture demands are low, while soil moisture availability would be reliably high.

In ecological studies, such as the present one, it is nearly impossible to eliminate all other possible explanations for an observed phenomenon or pattern (Caldwell pers. comm.). Rather reasonable explanations must be tenatively accepted until data which better supports alternate explanations, or clearly refutes the proposed hypothesis(es), is put forward. Thus, the use of the two simple responses of L. lyallii to environmental conditions as explanation for its altitudinal zonation seems justified.

L. lyallii is also very sensitive to soil moisture deficits, and more importantly shows long-term photosynthetic reductions in response to drought stress. These reductions persist after leaf water status improves, suggesting that internal control, perhaps by ABA (Raschke 1975), prevents stomatal opening following stress events. The ecological significance of these responses is that alpine larch is restriced to regions or sites where regular summer rains or edaphic conditions keep soil moisture high. Regular precipitation also helps maintain high humidity, which is important for the maintenance of high diffusive conductances and rapid CO_2 uptake rates.

The distribution of L. lyallii in the region affected by Pacific summer storms in northwestern USA and southwestern Canada (Arno and Habeck

1972) supports the idea that regular summer rainfall is important for L. lyallii. If this is the case, the absence of alpine larch from timberlines in the drier southern Rocky Mountains and the Sierra Nevada is understandable. Where this species is found in regions with only 2-3 $cm \cdot month^{-1}$ summer rainfall, it is restricted to sites where edaphic conditions maintain high levels of soil moisture.

The features of L. lyallii physiology discussed above put this species at a disadvantage to timberline evergreens, by restricting larch to regions and sites where the requirements for reliable summer moisture are met. High moisture requirements are understandable when one considers the correlation of high photosynthetic rates and low diffusive resistances in this C-3 species.

L. lyallii has a much higher photosynthetic capacity, based on dry weight, than most other conifers, which are evergreen. Other species of Larix have similar high photosynthetic capacities (Auger 1974, Tranquillini 1979). On a leaf area basis, however, alpine larch and the other Larix species have net assimilation rates similar to the rates of evergreen conifers (Sestak et al 1974). This suggests that mesophyll resistances in Larix species are similar to other conifers. The high dry weight basis net assimilation rates are due to low specific mass leaves. Low specific mass leaves were found in L. lyallii (see Table 16) and have been reported for other Larix species (Tranquillini 1979). Leaves with low specific mass, and high (weight basis) photosynthetic capacity provide the largest possible carbon gain per invested carbon of any short-lived leaf. Apparently alpine larch makes up for its yearly carbon losses (by leaf fall, etc.) and short growing season by this adaptive strategy. The deep rooting habit and early, rapid leaf and shoot expansion are also important adaptations that allow L. lyallii to exist in the severe timberline habitats to which it is restricted.

CHAPTER VI

INTEGRATION

All of the factors shown to be important to the growth and dominance of Larix lyallii at timberline are interrelated, and result from its deciduous habit. Great resistance to, and tolerance of, winter desiccation results from alpine larch's lack of leaves in winter. This morphological characteristic makes the area of cuticle which must be thickened far less than the area that would have to be thickened were leaves present as with evergreens. Thus, a deciduous tree should have to expend less energy to, and be able to more quickly develop, high desiccation resistance. The lack of leaves also means that the area susceptible to radiational heating and evaporative water loss, especially in spring, is less than for evergreens. Therefore, deciduous species are subjected to lower potential water losses in winter. Tolerance of the immature tissues of overwintering L. lyallii buds to winter desciccation is great. Due to their isolation from the xylem during winter, they also strongly resist desiccation. Because of its resistance and tolerance to winter desiccation, L. lyallii suffers 30-64% less winter desiccation damage than sympatric evergreen trees.

A number of other features resulting from the deciduous habit contribute to less winter damage. These include lower wind and snow loads, and less susceptibility to avalanche breakage or fungal attack.

Since all of these winter advantages derive from the deciduous habit, it is hypothesized that other typical timberline deciduous trees (see Ch I) should show similar advantages to those of L. lyallii. For these advantages to be realized, especially the difference in desiccation damage, a desiccating winter environment is required.

Another result of the deciduous habit is the need to make rapid carbon gains for the duration of the short growing season. Alpine larch is able to accomplish this by the combination of a number of characteristics. Alpine larch produces leaves with high leaf area to weight ratios that are advantageous because low carbon investment is necessary for high subsequent carbon gain. This is reflected in the high day weight basis net assimilation rates. Low carbon investment requirements mean that a large photosynthetic surface can be produced very quickly in the spring. Alpine larch expands shoots and leaves simultaneously and early in the season. Leaf expansion is accompanied by large increases in water content, suggesting that during expansion as little carbon as possible is being invested in the leaves.

Early initiation of shoot expansion and its completion before the end of July means that at least one full month is available for thickening the cuticle on the current year's twigs. This is extremely important for the development of winter desiccation resistance discussed above (see also Tranquillini 1979).

The high diffusive conductances associated with the requirement of C-3 deciduous species for high photosynthetic capacity mean that water use is high throughout the summer. Restrictions on water availability or high evaporative demands cause these conductances to decline, significantly reducing carbon gain. These interactions appear to restrict <u>L. lyallii</u> to areas where summer precipitation is high and regular, or to sites where edaphic factors contribute to reliable soil moisture and cool air. In its habitat, <u>L. lyallii</u>

is not subjected to great soil or atmospheric drought. Thus conductances and potential photosynthetic carbon gains remain high.

Photosynthetic rates of deciduous alpine larch needles continue to increase at very high light intensities. Light compensation of these needles is high, and that of wintergreen needles is extremely high. In the open habitats where alpine larch occurs it is seldom shaded by other trees. Thus the limitations imposed by shade are not felt, These limitations, however, are important in preventing the growth of young trees within the spruce-fir subalpine forest. Furthermore, the reductions in carbon uptake due to high atmospheric demands impose an additional limitation to the growth of L. lyallii at lower elevations, in the subalpine forest, where atmospheric moisture levels are lower.

Young alpine larch have wintergreen needles, which are very susceptible to winter and spring desiccation damage. Since these trees are so small, however, they are usually covered by snow in winter and the probability of having the damage-susceptible wintergreen needles exposed is minimal. The advantage, on the other hand, is that the wintergreen leaves appear to be less susceptible than deciduous needles due to drought stress in the summer. This is because their more rapid stomatal closure response to low atmospheric humidity allows them to maintain higher leaf water contents. This response reduces photosynthetic capacity during periods of stress, however, as having wintergreen needles also effectively lengthens the period during which photosynthetic CO_2 uptake can occur.

Wintergreen leaves have higher light compensation points than deciduous needles, but are held in fewer numbers by small trees on shady sites than by those on open sites. On open sites approximately 28% of the total needle biomass is held in wintergreen needles until the trees are 20-25 yr. It is at this age that rapid height growth of L. lyallii begins. Concomitant with the rapid height growth is increased production of deciduous needles. It appears that the change to deciduous needles may be initiated when the root system becomes sufficiently developed to assure an adequate supply of water all summer. At that point the need for the drought stress resistance of the wintergreen needles is less important and more deciduous needles, of higher photosynthetic capacity, will allow more rapid height growth. The changing importance of the two types of needles is an extremely interesting problem, and it emphasizes again the relative advantages of deciduous versus evergreen habits for timberline trees. Since the wintergreen leaves are usually protected from desiccation by snow, no advantage would be gained by the young tree being deciduous. Also the summer advantages of evergreen type needles are needed for establishment, when drought stresses are greatest.

That small alpine larch maintain a substantial commit~~t~~ment to wintergreen needles until rapid height growth begins and the tree is exposed to damaging winter conditions, supports the hypothesis for a desiccating winter environment as a precondition for the occurrence of the deciduous habit. Because of similar vegetational zonation, and the apparent need for wintergreen needles during establishment, it is hypothesized that constraints similar to those operating of L. lyallii in summer are also important for other deciduous trees at timberline. Specifically it is hypothesized that typical deciduous timberline trees will show large decreases in otherwise high leaf diffusion conductances in response to high atmospheric demands or soil moisture deficits.

These two hypotheses, for summer and winter, must be taken together as a single hypothesis explaining the correlation of deciduous trees at timberlines to areas where climates show the following features. Deciduous timberline trees should be restricted to areas where regular summer rains or edaphic conditions maintain soil moisture and reduce atmospheric demands, and where severely desiccating winter conditions occur allowing the deciduous trees an advantage over evergreens, which are always either sympatric or occur in the subalpine forests just below.

Verification of such general hypotheses as these will require many years and study by many people. A number of approaches need to be pursued. The distribution of timberline species needs to be carefully documented and climatic data compiled from timberline areas (both deciduous and evergreen dominated) of the world. Ecophysiological studies, concentrating on diffusive conductance and its response to environmental conditions, and winter water relations, need to be done on a number of typical deciduous timberline species. Finally, careful field photosynthetic studies and carbon budget modelling need to be undertaken. The results of these studies will greatly increase our understanding of the variety of causes of evergreen and deciduous timberlines.

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APPENDIX A

Typical time course of equilibration of dissected buds and wintergreen needles sampled in winter and typical chamber psychrometer calibration curves.

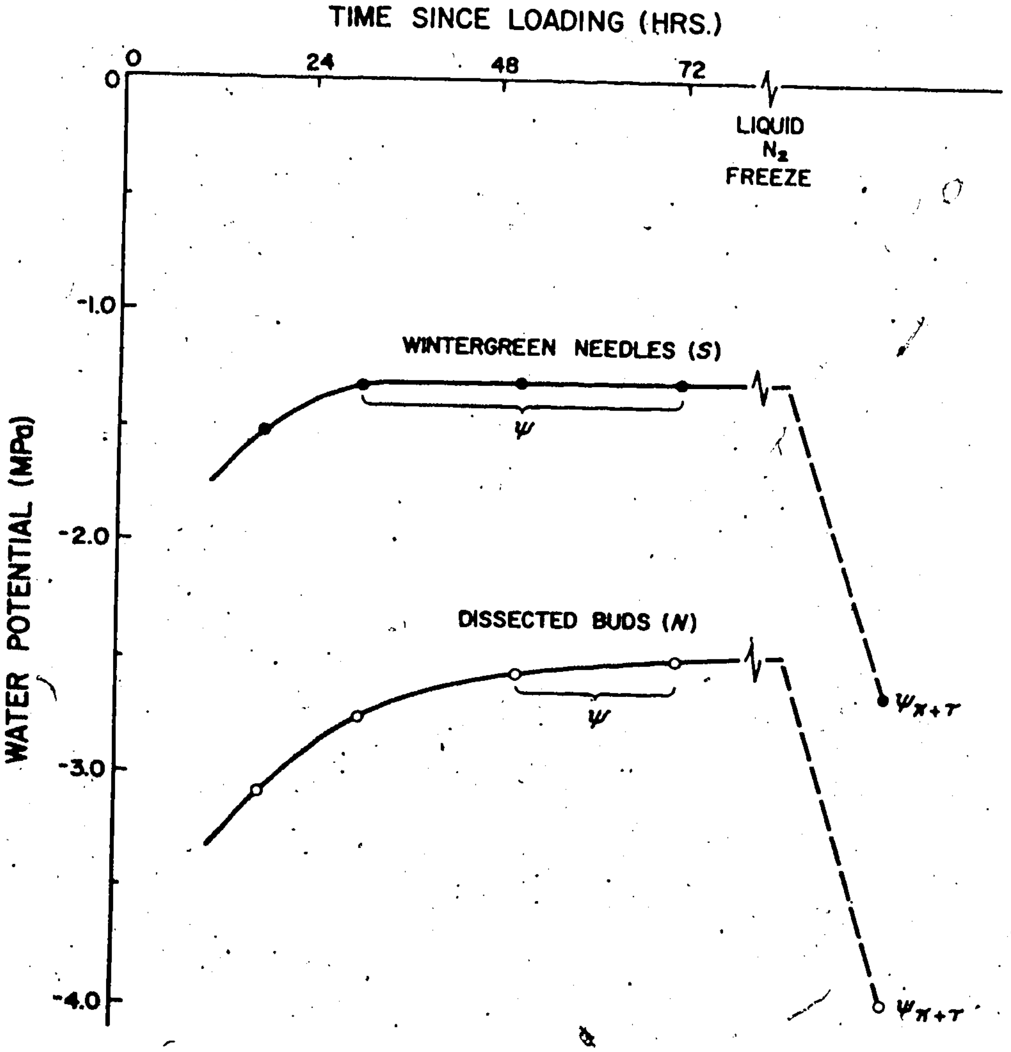


Figure 47. Time course of equilibration of dissected buds, north-facing site, and wintergreen needles, south-facing site, sampled in October.

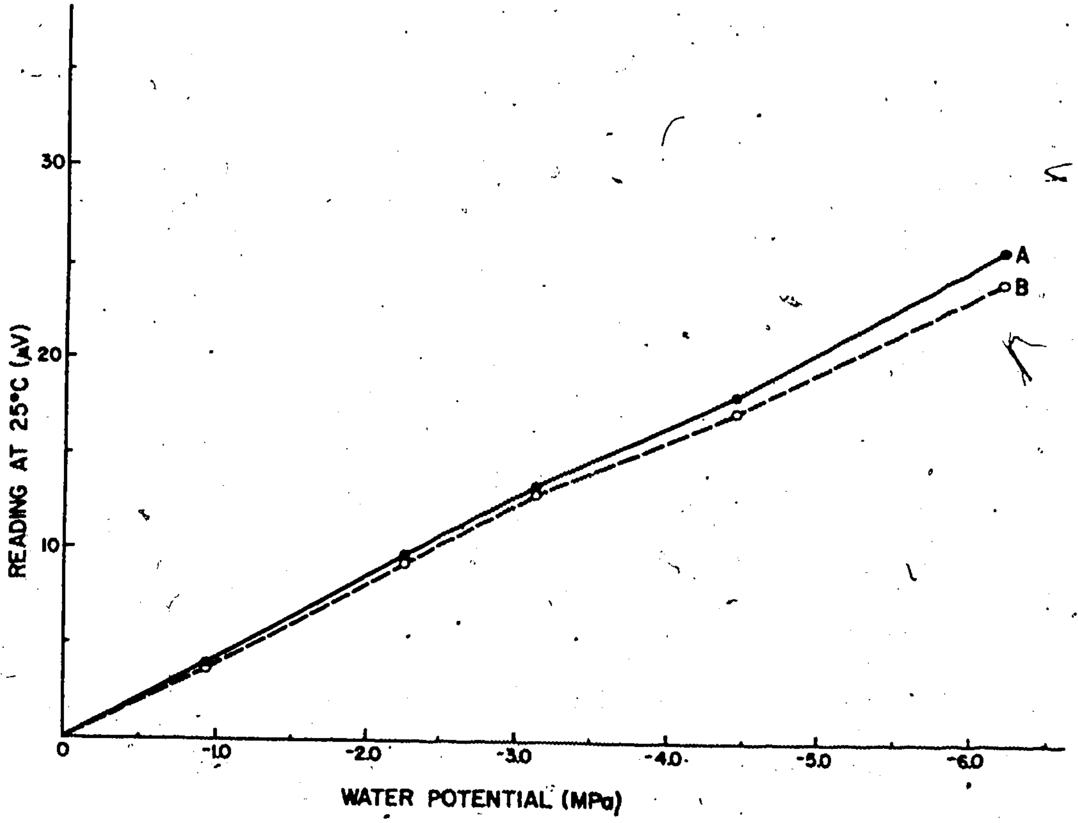
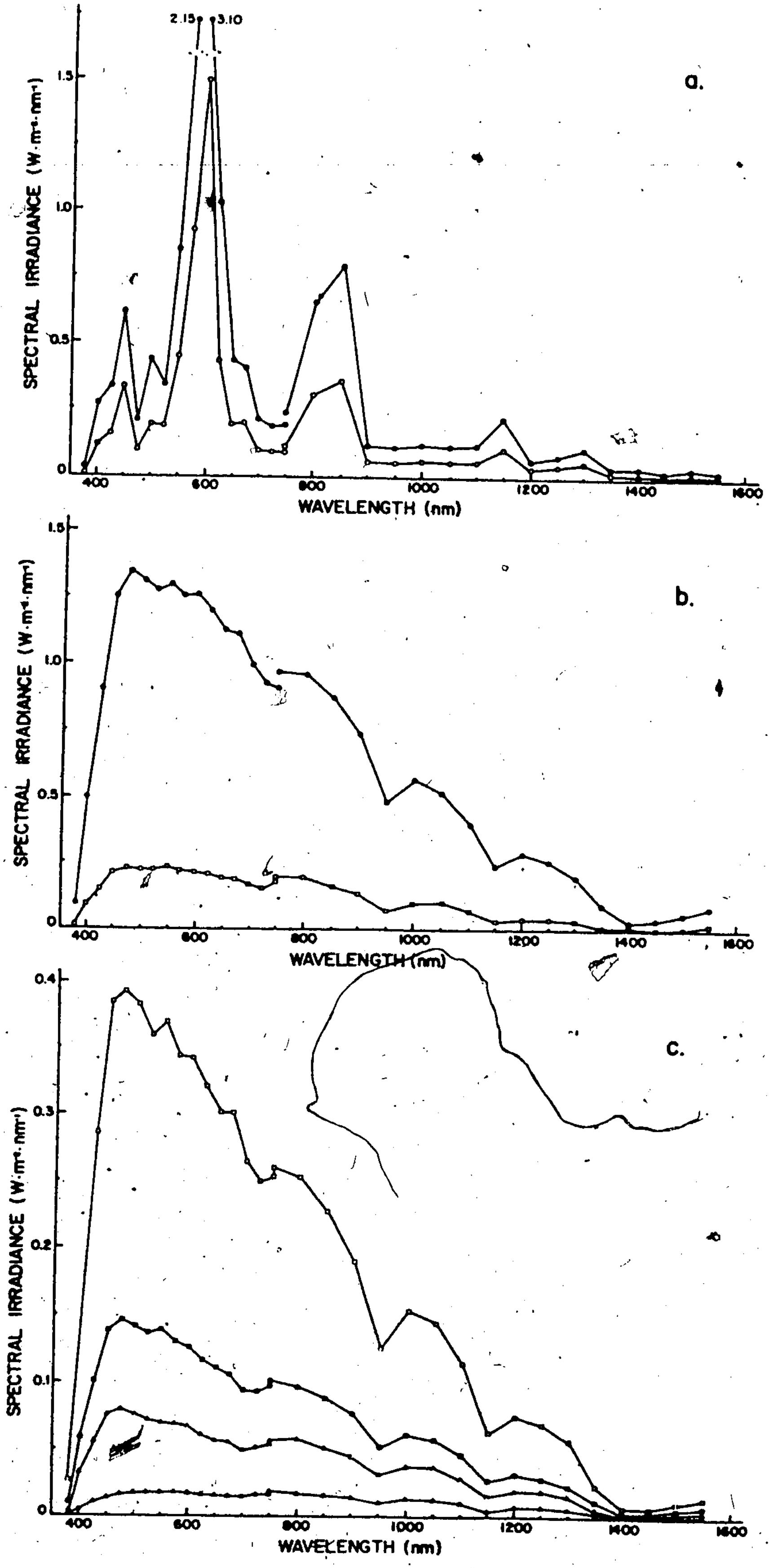


Figure 48. Calibration curves for two psychrometers, A and B.

APPENDIX B

Spectra from the field sites, under experimental shelters and within the large gas-exchange cuvette. Data were taken with an ISCO SR spectroradiometer with direct or remote heads. Calibration was done with an ISCO SRC spectroradiometer calibrator.

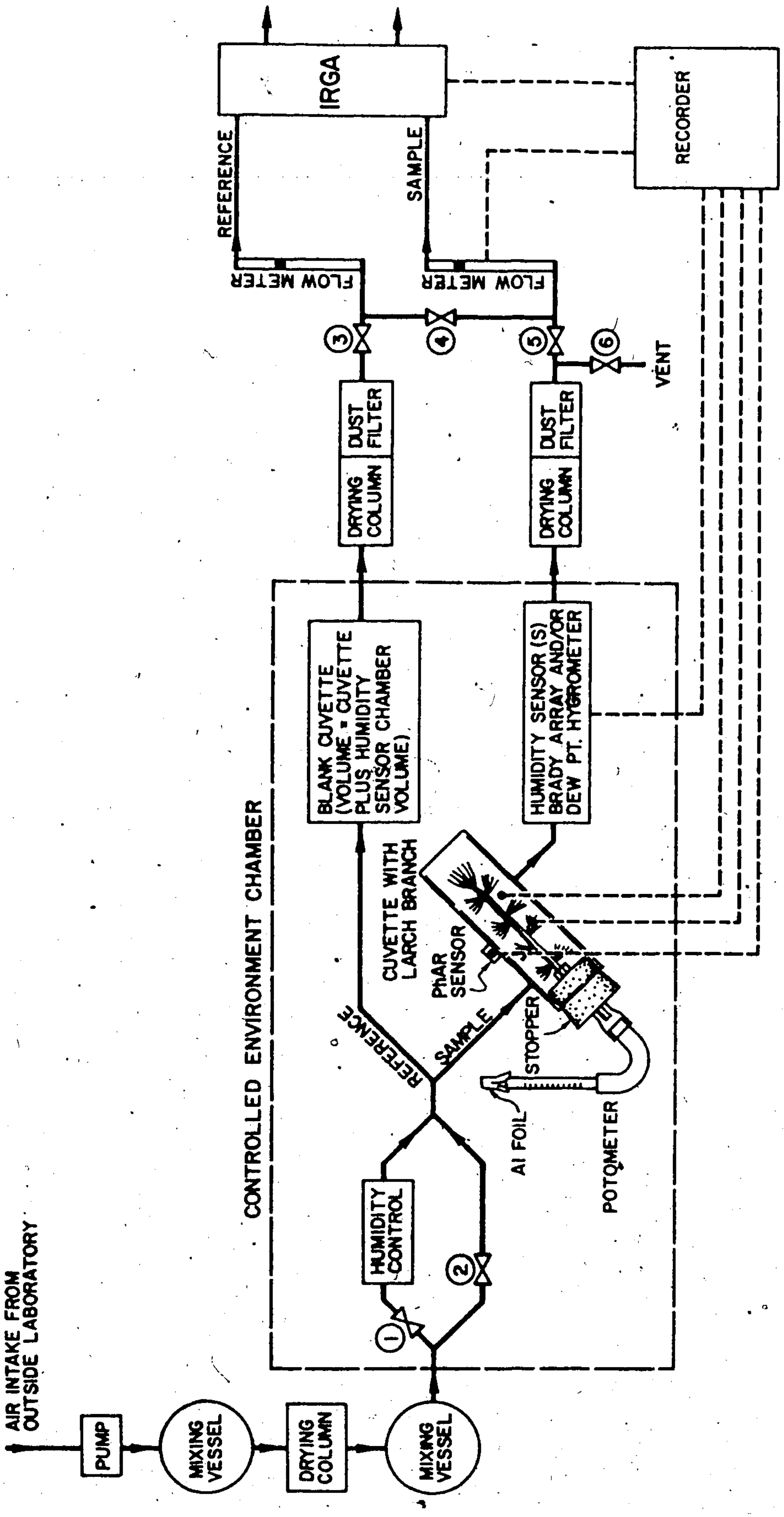
Figure 49. Comparison of light quality under various laboratory and field conditions. Note scale differences. a.) Within Siemens cuvette inside high light intensity growth chamber, when PhAR = 1500 $\mu E \cdot m^{-2} \cdot s^{-1}$ (●) and when PhAR = 700 $\mu E \cdot m^{-2} \cdot s^{-1}$ (○). b.) At the field site at 1230 MST under clear sky on 17 July 1976 (●), and under an overcast sky on 19 July 1976 (□). c.) On 27 August 1977 with stratocumulus overcast: in the open, PhAR = 630 $\mu E \cdot m^{-2} \cdot s^{-1}$, 1420 MST (□); in the spruce-fir-larch subalpine forest, PhAR = 195 $\mu E \cdot m^{-2} \cdot s^{-1}$, 1300 MST (■), and 110 $\mu E \cdot m^{-2} \cdot s^{-1}$, 1330 MST (△); under experimental shade stress shelter, PhAR = 25 $\mu E \cdot m^{-2} \cdot s^{-1}$ (open PhAR = 630 $\mu E \cdot m^{-2} \cdot s^{-1}$), 1530 MST (▲).


2.15
3.10
a.
SPECTRAL IRRADIANCE (W·m⁻²·nm⁻¹)
1.5
1.0
0.5
0
400
600
800
1000
1200
1400
1600
WAVELENGTH (nm)
b.
SPECTRAL IRRADIANCE (W·m⁻²·nm⁻¹)
1.5
1.0
0.5
0
400
600
800
1000
1200
1400
1600
WAVELENGTH (nm)
c.
SPECTRAL IRRADIANCE (W·m⁻²·nm⁻¹)
0.4
0.3
0.2
0.1
0
400
600
800
1000
1200
1400
1600
WAVELENGTH (nm)

APPENDIX C

Flow diagram of mini-cuvette gas-exchange system.

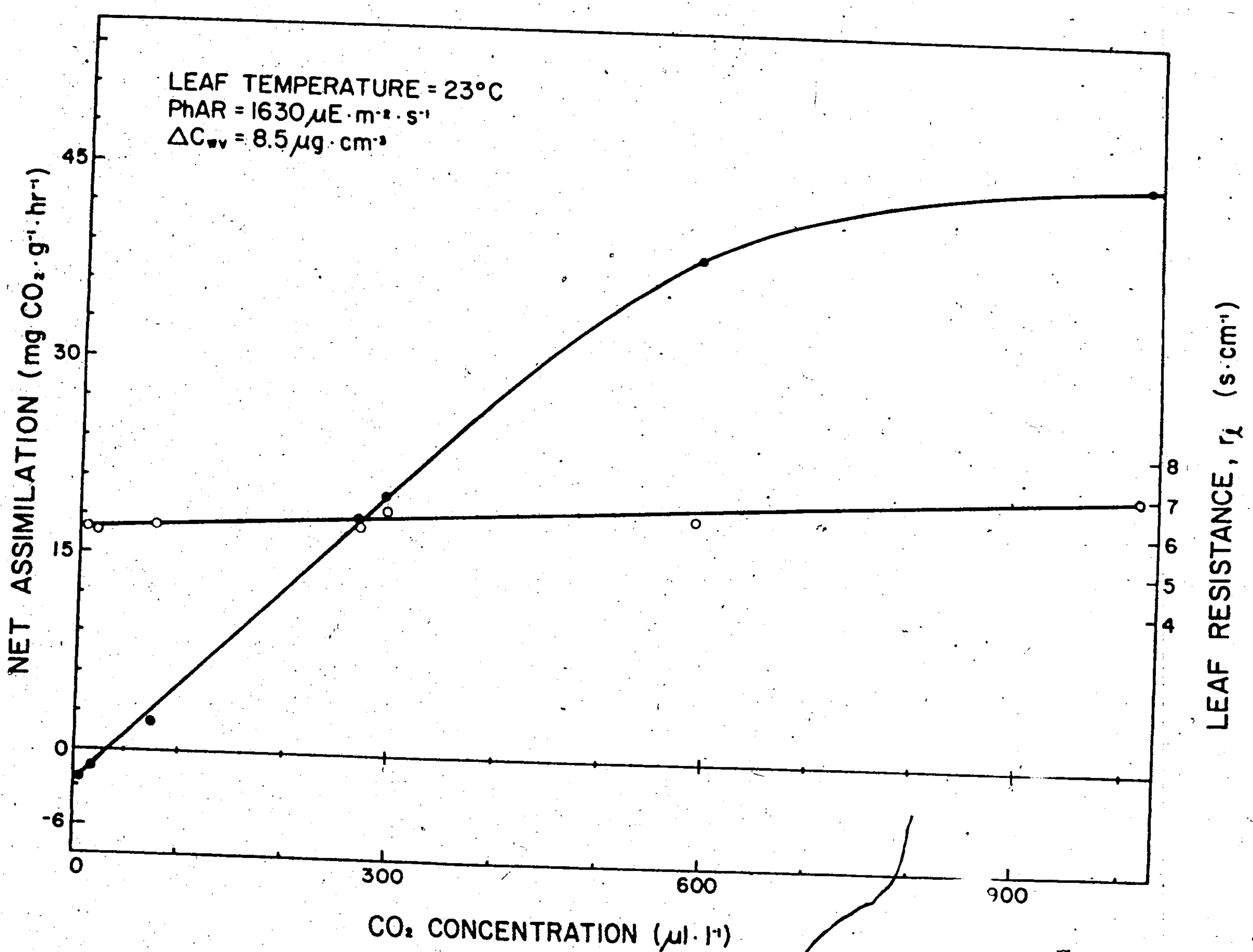
Figure 50. Flow diagram of mini-cuvette gas-exchange system. Tubing is shown by solid lines, and electrical connections by dashed lines. Valves 1 and 2 were used to adjust the humidity of the inlet air, and valves 3 and 5 were used to balance flow rates of the sample and reference airstreams. Valves 4 and 6 were closed when making measurements. While zeroing the IRGA, however, they were opened and valve 5 was closed.


AIR INTAKE FROM OUTSIDE LABORATORY
PUMP
MIXING VESSEL
DRYING COLUMN
MIXING VESSEL
CONTROLLED ENVIRONMENT CHAMBER
①
②
HUMIDITY CONTROL
REFERENCE
SAMPLE
Al FOIL
POTOMETER
STOPPER
PhAR SENSOR
CUVETTE WITH LARCH BRANCH
BLANK CUVETTE (VOLUME = CUVETTE PLUS HUMIDITY SENSOR CHAMBER VOLUME)
HUMIDITY SENSOR (S) BRADY ARRAY AND/OR DEW PT. HYGROMETER
DRYING COLUMN
DUST FILTER
DRYING COLUMN
DUST FILTER
③
④
⑤
⑥
VENT
FLOW METER
FLOW METER
REFERENCE
SAMPLE
IRGA
RECORDER

APPENDIX D

Net assimilation of <u>L. lyallii</u> deciduous needles in response to changing CO_2 concentration, determined on an automated gas-exchange system designed and built by D.W.A. Whitfield, Botany Department, University of Alberta, Edmonton, Alberta.

Figure 51. Net assimilation of alpine larch deciduous needles as a function of CO_2 concentration under the conditions indicated. CO_2 compensation point is ~35 $\mu l \cdot l^{-1}$. Simultaneous determinations of leaf resistance are also shown (○).


LEAF TEMPERATURE = 23°C
PhAR = 1630 µE · m⁻² · s⁻¹
ΔCwv = 8.5 µg · cm⁻³
NET ASSIMILATION (mg CO₂ · g⁻¹ · hr⁻¹)
45
30
15
0
-6
0
300
600
900
CO₂ CONCENTRATION (µl · l⁻¹)
LEAF RESISTANCE, rℓ (s · cm⁻¹)
8
7
6
5
4

APPENDIX E

Environmental and water relations data from diurnal sampling periods in June and August 1976.

Figure 52. Environmental and *Larix lyallii* sapling water relations data from an intensive diurnal sampling period, 19-20 June 1976. Environmental parameters are as described for Fig. 40, with the addition of soil temperatures at the indicated depths (d.), and excluding soil moisture on the north-facing site, which could not be sampled because of snow. Water relations data are also shown as in Fig. 40, except that $\psi_{\pi+\tau}$ (Mean ±SE, n=3) of deciduous needles on both sites is shown with $\psi_{P_{xylem}}$ in f.

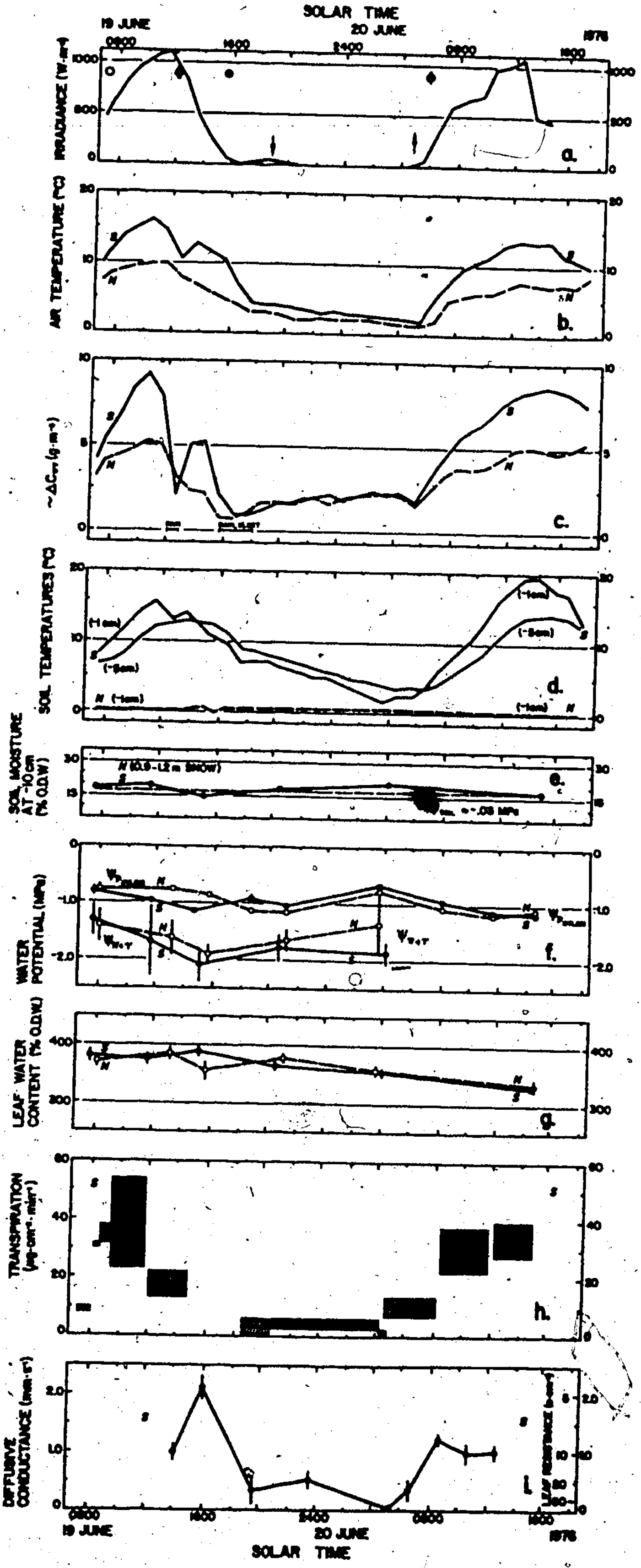
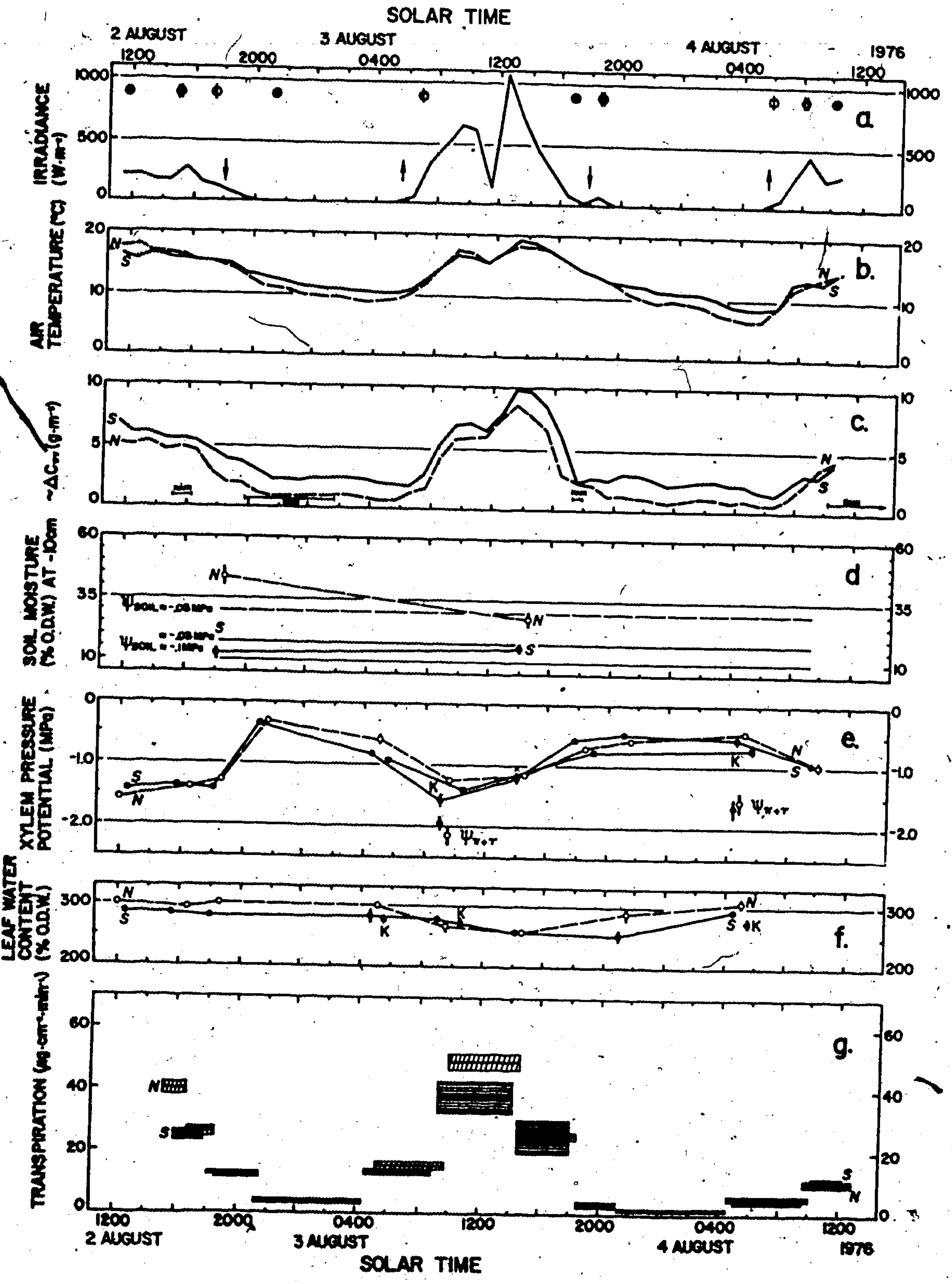

SOLAR TIME
19 JUNE
20 JUNE
1976
0800
1600
2400
0800
1600
IRRADIANCE (W·m⁻²)
0
500
1000
a.
AIR TEMPERATURE (°C)
0
10
20
S
N
b.
~ΔC (g·m⁻³)
0
5
10
S
N
c.
SOIL TEMPERATURES (°C)
0
10
20
(-1 cm)
(-5cm)
N (-1cm)
S
d.
SOIL MOISTURE AT -10 cm (% O.D.W.)
15
30
N (0.5-1.2 m SNOW)
S
e.
WATER POTENTIAL (MPa)
0
-1.0
-2.0
Ψ
S+T
N
S
f.
LEAF WATER CONTENT (% O.D.W.)
300
400
N
S
g.
TRANSPIRATION (µg·cm⁻²·min⁻¹)
0
20
40
60
S
h.
DIFFUSIVE CONDUCTANCE (mm·s⁻¹)
0
1.0
2.0
LEAF RESISTANCE (s·cm⁻¹)
S
i.
0800
1600
2400
0800
1600
19 JUNE
20 JUNE
1976
SOLAR TIME

Figure 53. Environmental and *Larix lyallii* sapling water relations data from an intensive diurnal sampling period, 2-4 August 1976. Environmental parameters are as in Figs. 40 and 52. Water relations data are as in Figs. 40 and 52, excluding diffusive conductances which were unavailable due to instrument failure.


SOLAR TIME
2 AUGUST
3 AUGUST
4 AUGUST
1976
1200
2000
0400
IRRADIANCE (W·m⁻²)
0
500
1000
a.
AIR TEMPERATURE (°C)
N
S
0
10
20
b.
~ΔCw (g·m⁻³)
S
N
0
5
10
c.
SOIL MOISTURE (% O.D.W.) AT -10cm
N
S
Ψsoil = -.05 MPa
Ψsoil = -.1 MPa
10
35
60
d
XYLEM PRESSURE POTENTIAL (MPa)
S
N
K
Ψπ+τ
0
-1.0
-2.0
e.
LEAF WATER CONTENT (% O.D.W.)
N
S
K
200
300
f.
TRANSPIRATION (μg·cm⁻²·min⁻¹)
N
S
0
20
40
60
g.