GROWTH AND ECOPHYSIOLOGY OF WESTERN REDCEDAR (*THUJA PLICATA* DONN EX. D. DON) SEEDLINGS GROWN UNDER THREE DIFFERENT SHADE CONDITIONS

by

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Growth and ecophysiology of western redcedar (Thuja plicata Donn. ex D. Don) seedlings grown under three different shade conditions

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ABSTRACT

Western redcedar was greenhouse grown from seed under three shade conditions: 100% (Full Sun, FS), 49% (Moderate Shade, MS), and 27% (Deep Shade, DS) of ambient light. Samples were taken periodically over their first, second and third growing season for growth analysis, chlorophyll-*a* fluorescence, CO_2 exchange rates and pigment content.

Different light growing environments showed a significant effect ($\alpha<0.05$) on most growth components: root weight ratio (RWR), leaf weight ratio (LWR), specific leaf area (SLA), and leaf area ratio (LAR) of western redcedar, with the best growth occurring under moderate shade. All treatments exhibited a similar pattern in RGR for shoot and total plant biomass. RGR root was significantly higher ($\alpha<0.05$) in FS seedlings in the first year growth.

Seedlings allocated more dry matter to shoot than to root as growth light intensity decreased. Consistently higher root to shoot (R/S) ratios in FS seedlings were found with mean R/S ratios for 1990, 1991 and 1992 of 0.46, 0.62, 0.54 compared to 0.31, 0.32 and 0.28 for MS, and 0.25, 0.26, 0.28 for DS seedlings respectively.

In general, FS seedlings had lower chlorophyll-*a,b* and total chlorophyll (*a+b*), but higher carotenoid to chlorophyll (*car/chl*) ratio than MS and DS seedlings.

Photosynthetic rates (P_N) declined toward winter, reached a minimum in February 1991 and a maximum in July. Overall, P_N (mg $CO_2.h^{-1}.g\ odw^{-1}$) was in order of DS>MS>FS. P_N (mg $CO_2.h^{-1}.dm^{-2}$) was higher in FS than in MS and DS seedlings in 1991 and 1992. The F_{var} fluorescence transients, especially maximum fluorescence (sF_p) and steady state fluorescence (sF_t), regardless of the shade treatments, had almost identical patterns to P_N rates in response to the seasonal growing condition. The decline in P_N to an over-wintering state from October to March 1991 in FS seedlings was accompanied by the development of a bronzed leaf color under high light-low temperature stress in winter. This color was also observed in seedlings exposed to drought stress in summer. A strong relationship (R^2 = 0.83) between P_N (sF_o basis) and sF_t was found regardless of the shade treatments. Strong relationships were also found between initial fluorescence, sF_o, (R^2 = 0.98), sF_p (R^2 = 0.91), sF_t, (R^2 = 0.91), the ratio of variable to maximum fluorescence, sF_v/F_m, (R^2 = 0.96) and excitation photon flux density.

FS seedlings reached drought stress (near 0 APS rate) sooner (34 days) than MS (37 days) and DS (43 days) seedlings.

Results suggest that moderate shading provides the best growing environment for western redcedar.

ACKNOWLEDGMENTS

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Western redcedar seeds were kindly provided by the Seed Center, B.C. Ministry of Forests, Surrey, B.C., through Dr. R.C. Brooke. Financial support was generously provided by Canadian International Development Agency (CIDA) through Eastern Indonesia University Development Project (EIUDP).

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INTRODUCTION

Western redcedar (*Thuja plicata* Donn ex. D. Don) is an important softwood species in Western North America. It grows from southern Alaska, south into northern California and eastward to Idaho, Montana and eastern British Columbia (Minore, 1990). In Canada, western redcedar is commonly associated with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.).

In 1988 - 1989, western redcedar was the second most planted tree in coastal British Columbia, involving some 5.5 million trees of nursery-grown seedlings (British Columbia, Ministry of Forests Report, 1989). Since the success of a forest plantation is in part dependent on the quality of the seedlings, the production of high quality seedlings is essential. Of the many environmental factors affecting the production of high quality seedlings, light is one of the most important in relation to photosynthesis, and hence growth and development.

Both artificially and naturally regenerated seedlings may be exposed to a wide range of light environments from deep shade to full sunlight, that affect their growth and survival in the field. For example, clear-cuts offer

conditions of full sunlight and potential drought in summer which maximize environmental stress for seedlings. In contrast, a full canopy might be so dense that filtered light below the canopy has both a reduced photon flux density (PFD) and ratio of red to far-red (R:FR) radiation (Vazquez-Yanes & Smith, 1982; Morgan *et al.* 1985; Messier & Bellefleur, 1988). Low light intensity may limit dry matter production (Stoutjesdijk, 1972; Goodfellow & Barkham, 1974). Therefore, assessing seedling ability to adapt morphologically and physiologically to different light environments during growth is crucial.

Depending on the amount of light available during growth, plants have the ability to respond in two distinctive ways: (1) the high-light growth response, which is found in sun leaves of trees and high-light plants; (2) the low-light growth response as found in shade leaves and low-light plants (Lichtenthaler, 1981). These two growth responses have been observed not only for leaves of the same species, but also for leaves of the same plant (Cormack & Gorham, 1953; Jackson, 1967; Nobel, 1976; Loach, 1967, 1970; Smith & Nobel, 1977; Lichtenthaler, 1981). For plant physiologists, this light-plant growth relationship is categorized into sun or shade leaves at the leaf level, and sun or shade plants at the plant level. Thus, for a single growing tree it is possible to have both extreme sun leaves

on the tree top and the extreme shade leaves in the inner tree canopy. For foresters and horticulturists, however, the concept of a light-plant growth relationship is mainly concerned with the tolerance of a species to shade, *i.e.*, the ability to establish, survive and grow under low light conditions and high root competition (Baker, 1949; Daniels *et al.* 1979; Kimmins, 1987). Shade tolerance is a useful concept in successional dynamics of forest development. However, a tree growing in a forest understory is affected by many environmental components within the understory (Daniels *et al.* 1979; Kozlowski *et al.* 1991). Because shade tolerance lacks an absolute scale and objectively defined classes, the concept is often contradictory. For example, Baker (1949) and Krajina (1969) listed western redcedar as a very shade tolerant species. Krajina (1969) even added that the shade tolerance of western redcedar is one of the highest, because this species is edaphically very demanding. On the contrary, Schmidt (1955) found that this species did not have all the characteristics usually associated with a shade tolerant species, and the degree of shade tolerance might change depending on the environmental conditions in which they grew. Along the Pacific Northwest coast, this species may be less shade tolerant in cool environments than it is in warmer environments (Schmidt, 1955). Minore (1972, 1983, 1990), Klinka *et al.* (1990) and Kozlowski *et al.*

(1991) considered this species to be an intermediate shade-tolerant tree species, as it has been found to grow to maturity in both full sunlight and full shade environments (Bolsinger, 1979). However, in many cases drought and high soil surface temperature damaged seedlings in full sunlight, whereas in full shade poor root penetration caused drought damage to the seedling (Sharpe, 1974). The germination and survival of seedlings were found to be the best in moderate shade and poorest in heavy shade (Minore, 1972). In terms of day length, Krasowski & Owens (1991) observed that a combination of day length and moisture stress affect shoot elongation, regardless of the time and duration of applied treatments. More recently Carter and Klinka (1992) who investigated the variation of shade tolerance of western redcedar concluded that this species is a shade tolerant species on slightly dry and fresh sites.

A moderate shade tolerant plant has the ability to acclimate to different light environments (Smith, 1981). Such a plant may grow well in full sun light, but is also able to grow in shade by acclimating morphologically and physiologically so that it can better utilize the low light in shaded conditions. In low light environments, morphological development is typified by an increase in leaf area, a decrease in both leaf thickness, and in stomatal density (Boardman, 1977; Smith, 1981; Lichtenthaler, 1981;

Givnish, 1988). Physiological responses, on the other hand, are characterized by an increase in total amount of chlorophyll per unit fresh weight, a decrease in maximum net photosynthetic rates, light compensation point, dark respiration rate, chlorophyll *a/b* ratio, and maximal stomatal conductance due to less stomata (Boardman, 1977; Björkman, 1981; Friend, 1975; Lichtenthaler, 1981; Smith, 1981). Changes in light compensation point, dark respiration rate, total chlorophyll content, and chlorophyll *a/b* ratio allow the plant to better utilize the low photon flux density (PFD) present in shade conditions (Boardman, 1977; Lichtenthaler, 1981).

Very few ecophysiological investigations have been done with western redcedar. Many questions related to different light growing environments still need to be addressed: are there differences in growth rates and survival, are there differences in photosynthetic and chlorophyll fluorescence (F_{var}) patterns during the year, and do the western redcedar seedlings develop the same features as found in typical sun and shade plants? These are several unanswered questions that need to be examined if success of a western redcedar plantation is to be achieved.

This study combines the analysis of growth of western redcedar seedlings grown in different light environments, with the assessment of seasonal changes in photosynthetic

activity by using CO_2 exchange and chlorophyll fluorescence. CO_2 exchange is important because it is basic to primary production, and chlorophyll fluorescence because it is useful in examining ways in which the photosynthesis process may be influenced by environmental stresses (Bolhàr-Nordenkampf *et al.*, 1989; Krause & Somersalo, 1989). Since changes in the photosynthetic rate and/or in dissipative heat emission will also cause changes in fluorescence emission, the assessment of chlorophyll fluorescence can be used as an indicator of a plant's photochemical and photosynthetic processes (for reviews see Krause & Weis, 1991; Vidaver *et al.* 1991; Walker, 1992; Bolhàr-Nordenkampf & Öquist, 1993).

The assessment of chlorophyll fluorescence has been applied in studies of chilling injury (Havaux & Lannoye, 1984; Hetherington & Öquist, 1988), cold tolerance (Sunblad *et al.* 1990), freezing, drought and excessive radiation (Powles, 1984), plant stress detection (Lichtenthaler & Rinderle, 1988; Lichtenthaler, 1988, 1990), ecophysiological research (Lichtenthaler *et al.* 1986), forest decline and effects of air pollution on plants (Bolhàr-Nordenkampf *et al.* 1989).

Chlorophyll fluorescence assessment has also been widely used in physiological research on conifers including study on the seasonal activity of photosynthesis (Hawkins &

Lister, 1985; Lichtenthaler *et al.* 1989; Vidaver *et al.* 1988, 1989, 1991; Brooke *et al.* 1989, 1990), stress evaluation (Toivonen & Vidaver, 1988; Bolhàr-Nordenkampf & Lechner, 1988), forest decline (Lichtenthaler & Rinderle, 1988; Bolhàr-Nordenkampf *et al.* 1989), frost hardening and dehardening (Strand & Öquist, 1988; Öquist & Malmberg, 1989; Gillies, 1993), water stress (Toivonen & Vidaver, 1988), light stress (Öquist & Malmberg, 1989), provenance differences (Vidaver *et al.* 1989, 1991), and seedling stock quality test (Hawkins & Binder, 1990).

The objectives of this research were to :

i) determine the growth and developmental pattern of western redcedar seedlings grown under different light environments;

ii) compare seasonal patterns of photosynthesis, and chlorophyll fluorescence resulting from growth in different shade conditions;

iii) compare the physiological response of seedlings from the three light environments to water stress.

MATERIALS AND METHODS

Plant Material and Establishment

Western redcedar seedlings were grown from seed, supplied by B.C. Ministry of Forests, Seed Centre, Surrey[1]. These seeds had been stored in a dry condition in a refrigerator for about one year before being germinated without stratification since this pretreatment is not needed for seeds from coastal low elevations (Minore, 1983, 1990). Seeds were sown on 14 May 1990, on moist filter paper in covered petridishes, which helped to maintain a high humidity. Each dish containing approximately 150 seeds was placed in a growth room under a 16 *h* photoperiod and average temperatures of 23±2 ^{o}C day and 20±2 ^{o}C night.

After ten days, all seedlings with two or more cotyledons were transplanted into a 4:1 loam : peatmoss potting mixture in supercells®[2] (diameter 4.1 cm, volume 164 ml). The inside of these tubes has four vertical rib structures, which help prevent circular oriented root growth. Loss of soil mix through bottom drainage holes was reduced by placing a pumice stone covered with 0.5 cm of

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[1] Seedlot 9151, origin: 50^{o} 07' N, 127^{o} 24'W, altitude 520 m, Artlish-Kaouk R, Vancouver Island, British Columbia.
[2] Stuewe and Sons, Corvallis, Ore. USA

peat moss in each tube before addition of the soil. Each tube was tamped uniformly in an attempt to provide seedlings with a similar soil density. The soil surface in each container was covered with white sand to a depth of approximately 0.5 cm to help protect the seedlings from fungal diseases such as damping-off. Tubes were placed in a special tray (RL98 Tray,Stuewe and Sons, density of 5 cells per dm^2) (Fig. 1) that was designed to hold the tubes suspended above the bench. Trays were placed in the greenhouse under moderate shade (one layer of gray fiberglass screen, which reduced incoming radiation by about 49%). After one month (18 June, 1990), seedlings were placed under each shade treatment (see *Experimental Design*).

Of 882 trees planted, 336 trees were used as reserve trees including the border trees (around the edges of the trays which were not considered as experimental trees).

It is important that plant materials used in growth analysis have approximately the same size at the start of the treatments. Seedlings were pre-selected to meet a relatively uniform size, as suggested by Evans (1972), at the beginning before any sample was randomly selected.

The greenhouse temperature and humidity were recorded daily with a hygrothermograph located at the full sun treatment site (Fig. 2). The seedlings were watered as evenly as possible using a mist sprayer. The watering

Fig. 1. Supercell® tubes and RL98 ray used to grow western redcedar in this research. The arrangement of the fiberglass screen used to reduce light in the shaded treatments is also shown.

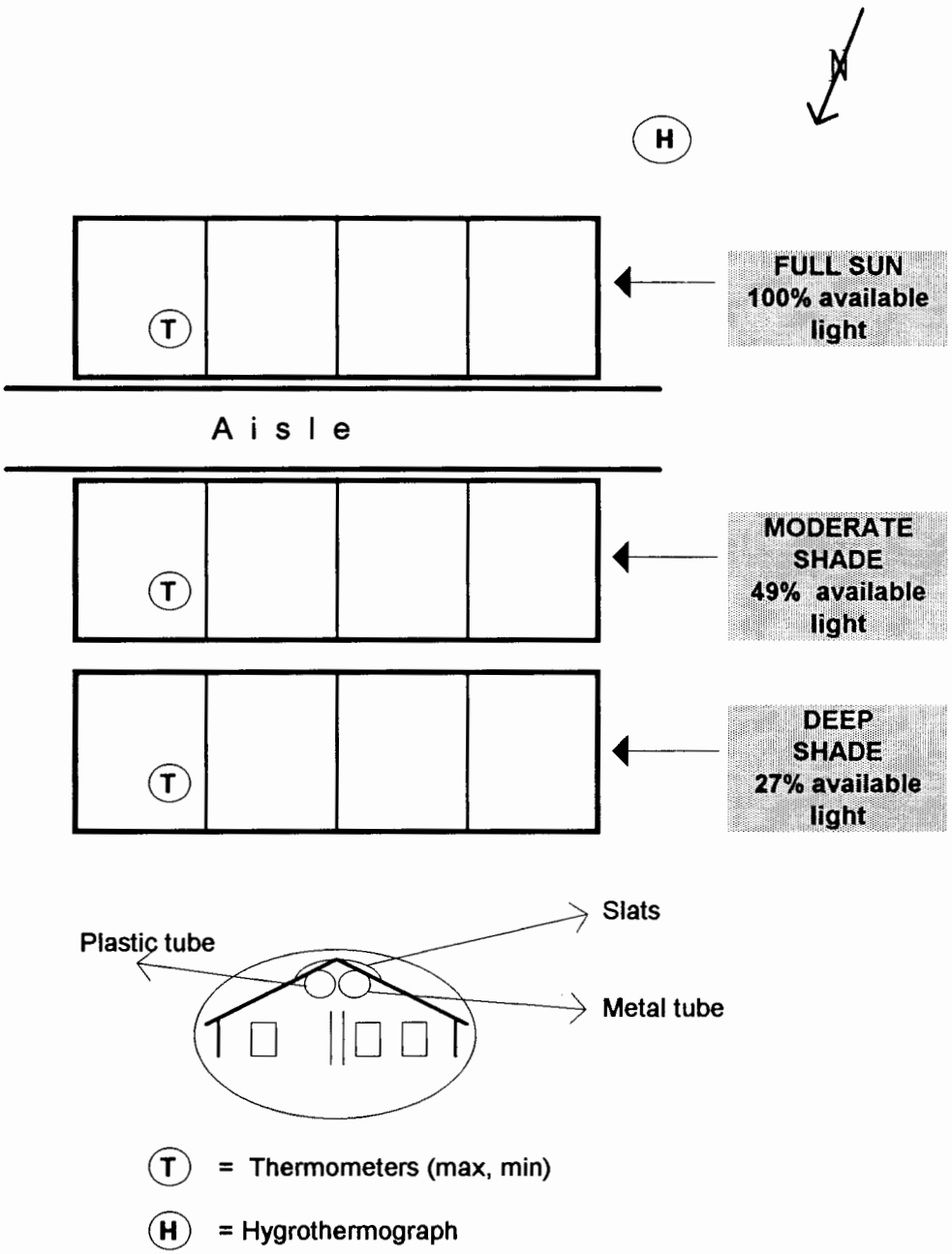
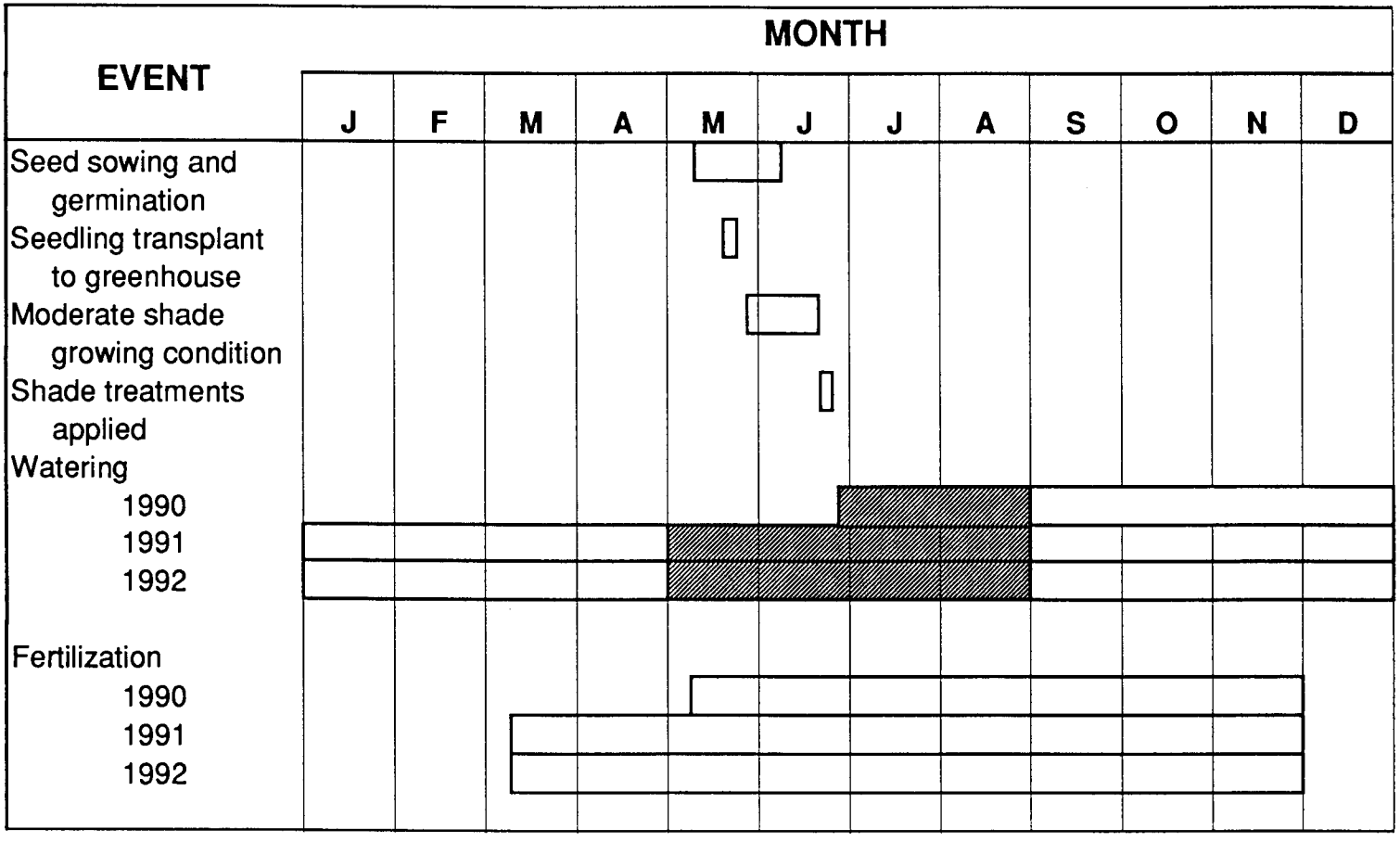


Fig. 2. Arrangement of the four RL98 trays used for each shade treatment in the greenhouse, including the placement of hygrothermograph and thermometers. Figure in the ellipse shows the greenhouse roof construction that influences the light conditions in the greenhouse.

frequency varied from one to three times per day, dependent on the weather, until seedlings were well established. During early growth, up to age of 3-4 months (between June to August 1990), full sun seedlings were watered 2-3 times a day on very hot days, as they are reported to be very sensitive to high soil surface temperatures (Minore, 1983, 1990), but only watered once in the morning on cool overcast days (Fig. 3). Occasionally, to prevent high temperatures and drought in summer, shade slats on the greenhouse roof were lowered to reduce light. On a clear sunny day (13 June 1994), the slats lowered PFD to about 58% (FS), 62% (MS) and 73% (DS) of incoming radiation.

At 5 months of age (October 1990), all seedlings were watered at the same frequency with about the same amount of water. This was done to minimize the effect of different soil moisture contents between the shade treatments. As a consequence, full sun seedlings would likely experience more drought stress conditions than the moderate shade and deep shade seedlings. This confounding effect was further studied in a separate experiment during summer 1991 (see methods for *Drought experiment*).

Fertilization was given beginning June 28,1990 (at about 1.5 months of age) using Stern's Miracle-Gro containing 15% N, 30% P, 15% K and micronutrients (0.2% Bo,



Note : FS seedlings were watered more frequently than MS and DS seedlings

Fig. 3. Germination, shade treatment application, watering and fertilization schedule for the experimental western redcedar seedlings

0.7% Co, 0.15% Fe, 0.15% Mn, 0.0005% Mb, 0.06% Zn, and 12.5% Cl). About 10 ml of fertilizer solution (concentration: 3.75 $ml.l^{-1}$ of tap water) was given using a hand sprayer every two weeks from late June to late November of 1990, and early March to late November in both 1991 and 1992 (Fig. 3).

Experimental Design

The experiment was designed to be completely randomized within three treatments: 100 percent (control, full sun, FS), 49 percent (moderate shade, MS) and 27 percent (deep shade, DS) ambient light. The different shade conditions were obtained by placing gray fiberglass screen on wooden frames above and around the trays containing the seedlings. A single layer of screen provided 49% ambient light and a double layer of screen reduced light to 27% of ambient light. Seedlings in the full sun treatment (100% ambient light) were grown without any screen. The spectrophotometric measurement of fiberglass screen absorbance showed little effect on the red to far red (R:Fr) ratio.

Photon flux density (PFD) (photosynthetic active radiation (PAR) 400-700 nm) for each shade treatment was measured at five different points horizontally (right above

and below the screen at the canopy level) using a LICOR® Model 185, Lincoln, NE, USA quantum sensor. For 1- and 2-year-old seedlings, PFD was also measured under the canopy right above the soil. Light measurements were conducted at different times of the year under both sunny and cloudy conditions to measure the effect of shade treatment at different solar altitudes. Diurnal differences in light intensity above the screen and in combination with the light obstruction by the greenhouse construction were measured monthly from June to December 1993, every two hours starting before mid-day to late afternoon under clear sunny sky conditions. The effect of greenhouse roof support and ventilation structures and the roll-up roof slats on light conditions within the greenhouse were evident in some of the light measurements taken.

To monitor the effect of shading on the seedlings' ambient temperature, weekly minimum and maximum temperatures were taken at seedling height in each treatment from July 1991 to June 1992.

During the summer, it was noted that seedlings on the edges of the shade treatments were more susceptible to potential drought due to the greenhouse ventilation system. Transparent plastic was placed around the screen sides to protect the seedlings from this effect.

Measurements

(a) Growth characteristics

Changes in plant morphology, seedling height, date of new spring growth following winter dormancy, and leaf characteristics (color changes and scale-like leaf formation) were recorded to define the phenological responses of the seedlings to shade treatments. These features, together with dry weight data, were useful in identifying sun and shade modifications to the seedlings resulting from the shade treatment applied.

Data for the growth analysis were obtained by destructively sampling five randomly selected seedlings from each treatment at every harvest date to provide dry weight and leaf area data (Fig. 4). Seedlings were separated into leaf, stem and root components before oven-drying at 80^{o}C for at least 48 hours or to a constant weight (Fig. 4).

Difficulties in estimating leaf area of conifers with complex scale-like leaf shapes such as western redcedar have been described by Cregg (1992), who concluded that measurement of projected surface area of *Juniperus scopulorum* and *J. virginiana* leaves was a reasonable method to be used. Leaf area in this research was determined by photocopying the leaf on to a transparent plastic overlay on

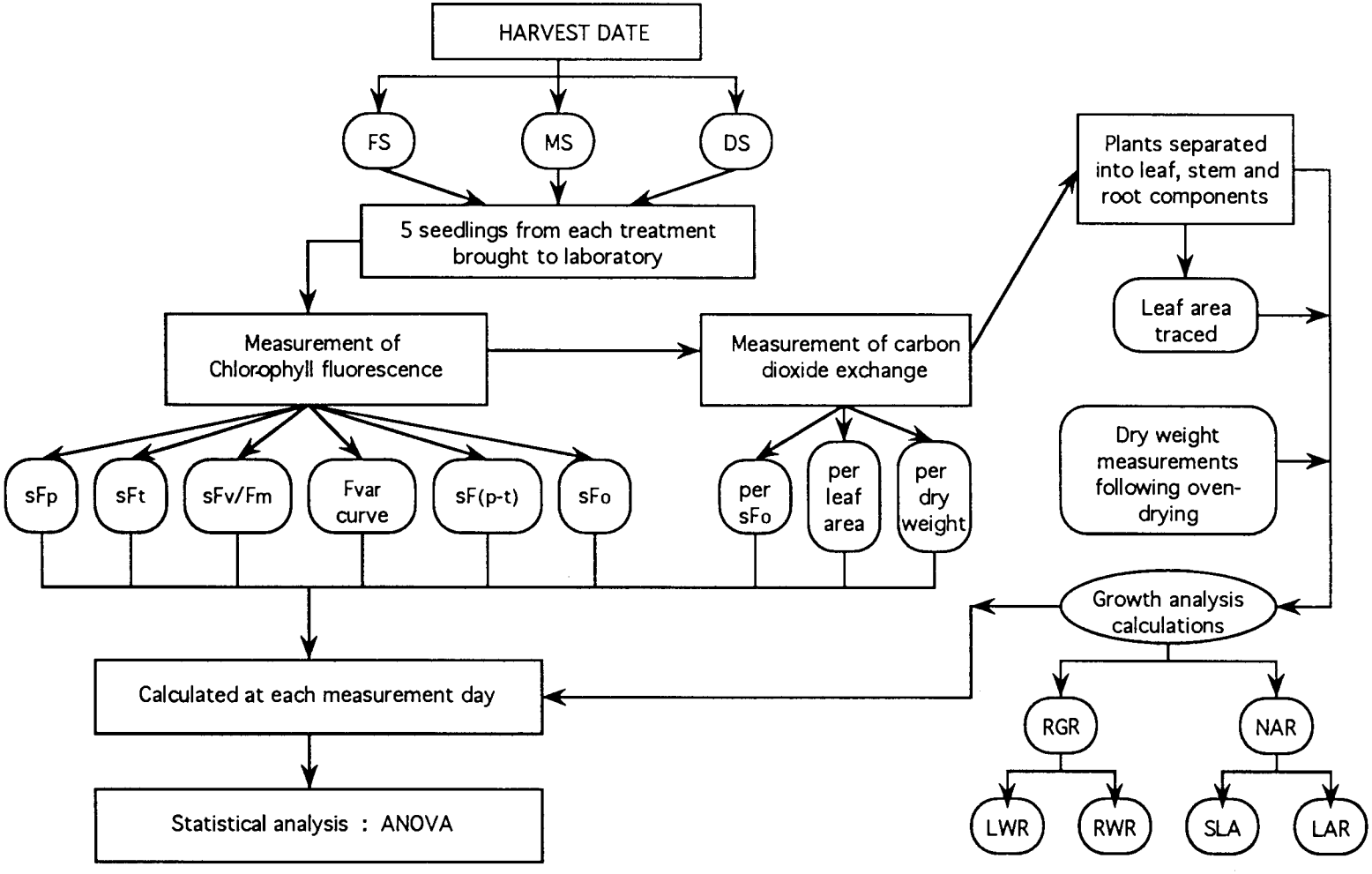


Fig. 4. Flow diagram of harvest measurements (see Text for abbreviation)

mm graph paper, and counting squares covered by the projected leaf surface. Leaf area was expressed in dm^2 for one surface.

After the destructive samples were taken, empty locations in the trays were replaced with new trees from the reserve group to ensure uniform shade conditions for each seedling within each treatment.

The partitioning of dry matter by seedlings from each treatment was calculated at each harvest by determining ratios of individual plant components to total plant weight, resulting in leaf weight ratio (LWR), stem weight ratio (SWR), root weight ratio (RWR), and specific leaf area (SLA).

From the dry weight and leaf area data, relative growth rate (RGR), and the net assimilation rate (NAR) for each time period between successive harvests was calculated following Hunt (1990) :

$$RGR = \frac{Log_e W_2 - Log_e W_1}{t_2 - t_1} \quad (weight.weight^{-1}.time^{-1})$$

$$NAR = \frac{W_2 - W_1}{t_2 - t_1} \cdot \frac{Log_e W_2 - Log_e W_1}{A_2 - A_1} \quad (weight.dm^{-2}.time^{-1})$$

where:

W_1 and W_2 are the mean total plant dry weights, and A_1 and A_2 are the mean total projected single surface area of leaf per plant, respectively, between two harvest times, t_1 and t_2.

There are some difficulties in applying relative growth rate analysis technique to a tree due to the continuous accumulation of non-productive tissue as its age increased, *i.e.*, the annual accumulation of new growth becomes smaller in proportion to its total weight as the tree becomes older (Brand *et al.* 1987). Consequently, over long periods of time, the RGR of older trees becomes very small and may no longer be sensitive to the treatment applied, and RGR becomes inversely related to total biomass accumulated (Brand *et al.* 1987). For this reason, different base harvests (t_1) were used in the calculation of RGR as follows: (1) the first harvest (31 July 1990) was used for all successive harvests as the base harvest for the 3-year period of the research (see Jolliffe *et al.* 1988), and (2) the first harvest in each calendar year was used as the base harvest for determining RGR's of all harvests within that particular year, *i.e.*, 31 July 1990 for 1990 harvests, 02 February 1991 for 1991 harvests, and 14 April 1992 for 1992 harvests. The same approach was applied for the NAR data.

(b) Chlorophyll fluorescence

Not all light captured by green chloroplast pigments is used to drive photosynthesis. Some of the absorbed light is dissipated as heat, and some is re-emitted as fluorescence (Vidaver *et al.* 1991). Since the processes of photosynthesis, heat dissipation and fluorescence emission are competitive (Krause *et al.* 1988; Bolhàr-Nordenkampf *et al.* 1989; Bolhar-Nordenkàmpf & Öquist, 1993), changes in the photosynthetic rate and/or in dissipative heat emission will also cause changes in fluorescence emission. Therefore, the assessment of chlorophyll fluorescence can be used as an indicator of a plant's photochemical and photosynthetic processes (for reviews see Krause & Weis, 1991, Vidaver *et al.* 1991; Walker, 1992; Bolhàr-Nordenkampf & Öquist, 1993).

There are three main types of fluorometer systems, (1) Time-resolving systems which record "Kautsky" curves to measure F_o and F_m for calculation of F_v/F_m and $t_{1/2}$ (*e.g.*, Branker, Richard Branker Research, Ottawa (Hawkins & Binder, 1990), Plant stress meter (PSM), BioMonitor AB, Umea, Sweden (Öquist & Wass, 1988; Bolhàr-Nordenkampf & Öquist, 1993); (2) Modulated systems which allow a continuous measurement of fluorescence signal from a leaf exposed to light of any wavelength (*e.g.*, PAM Fluorometer 101, Walz, Effeltrich, Germany, Modulated Fluorescence Measuring System (MFMS), Hansantech, King's Lynn, UK (Bolhàr-Nordenkampf & Öquist,

1993)); and (3) Integrating Fluorometer systems, which allow the measurement of fluorescence signals from the entire shoot (stem and needles) in an integrating sphere (Toivonen & Vidaver, 1984; Dubè & Vidaver, 1990, Vidaver *et al.* 1991).

The first two types of fluorometer record the "Kautsky" signals from a relatively small (few square millimeter) leaf surface area. The third type of fluorometer system is designed to integrate the fluorescence emission signals from an entire shoot. As a result, difficulties in obtaining data on the physiological status of a seedling through selecting proportional samples from a shoot that has foliage of different physiological age (such as several samples of a few needles from different parts of the shoot) can be avoided. For conifer seedlings, the integrating sphere fluorometer has some decisive advantages compared with the first two fluorometer types (Hawkins & Binder, 1990; Vidaver *et al.* 1991).

Two kinds of integrating fluorometer were used in this research : (1) Model 1.5 Fluoroscan, sphere ϕ of 20 cm, Intec Inoventures, Inc. B.C. Canada, for 1990 and 1991 data, and (2) Pacific Fluorometer Corp., B.C. Canada with sphere ϕ of 10 cm and 22.5 cm for 1992 data. The smallest sphere was used to reach higher excitation PFD's (400 $\mu mol.m^{-2}.s^{-1}$). The chlorophyll fluorescence signals were mostly obtained from the entire shoot unless otherwise indicated, and thus

represent an integrated fluorescence transient for the whole seedling. Data processing was interfaced to a computer (Dubè & Vidaver, 1990).

Prior to chlorophyll fluorescence measurements, seedlings taken from the green house were well watered and light pretreated for a minimum of 30 minutes at 500 $\mu mol.m^{-2}.s^{-1}$ (provided by quartz halide lamps) to allow acclimation to room temperature at moderate light intensities. During light acclimation, each seedling was covered with a ventilated transparent plastic bag to maintain humidity and to protect the seedling from possible drought stress. Light intensity was measured by putting the light probe at seedling height inside the transparent plastic. Seedlings were then dark pretreated for at least 30 minutes to assure an initial zero photochemical activity and CO_2 fixation state (Vidaver *et al.* 1991).

Chlorophyll fluorescence was measured after placing the seedling shoot into the spherical cuvette of the integrating fluorometer in darkness and the fluorescence signals was monitored for 300 s for most of the experiments. The scan rate was fast enough to capture the "Kautsky" signals as indicated in Fig. 5A&B. During chlorophyll fluorescence measurements, the excitation light level in the sphere had a PFD of 100 $\mu mol.m^{-2}.s^{-1}$, provided by a tungsten halogen lamp, Syvania® EJL 150W 12V. The excitation light was

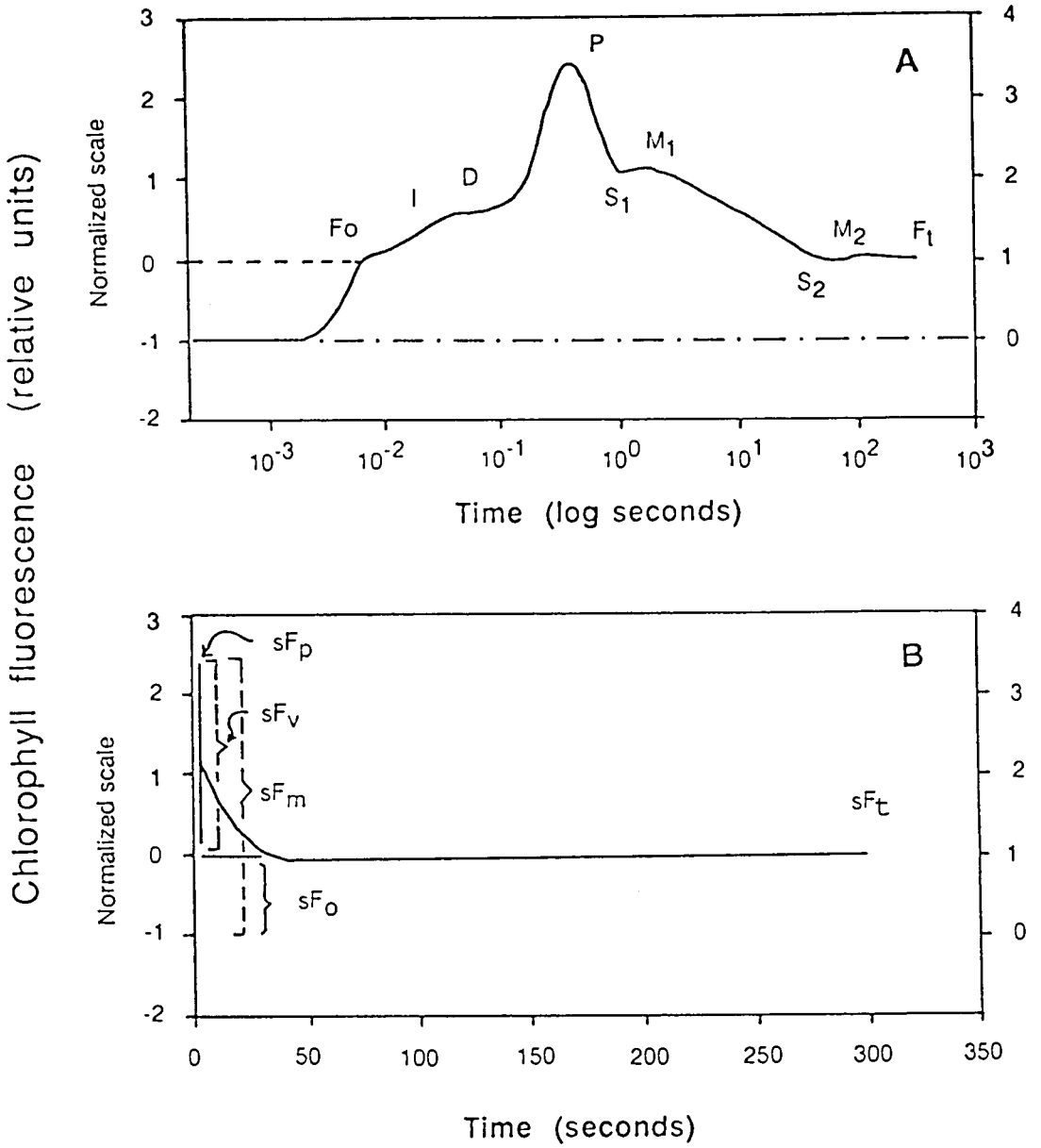


Fig. 5. Typical 300s chlorophyll fluorescence induction transient in logarithmic time scale (**A**) and arithmetic time scale (**B**). Transient features in Fig. 5A represent components of Kautsky curve as defined by Papageorgiou (1975). Fig. 5B represents selected components of F_{var} fluorescence and elements used to calculate the sF_v/F_m ratio as described in Materials and Methods. Scale on the right of Figure 5A and B was used to calculate the sF_v/F_m ratio. The use of lower case "s" in Fig. 5B is explained on p. 28.

measured at the sphere surface but calibrated to the centre of the sphere with a LI-COR® Model LI-185A radiometer with a quantum sensor.

A typical western redcedar time course of chlorophyll fluorescence with constant illumination is characterized by a complex fluorescence induction or Kautsky curve, as depicted in Fig. 5A&B. Unless otherwise indicated, all curves for western redcedar represent the average response of 5 seedlings and data were normalized to compensate for different seedling sizes according to Vidaver *et al.* (1989, 1991).

The normalization procedure assigns 1.0 unit to the F_o signal (mV). F_o is proportional to the total emitting sources of chlorophyll fluorescence from the sample and represents a state where no photochemical event is initiated (Papageorgiou, 1975; Lichtenthaler & Rinderle, 1988).

The relative value of F_{var} is approximated by :

$$F_{var} = \frac{F_v - F_o}{F_o}$$

where:

F_{var} is normalized variable fluorescence at time t

F_v is non-normalized fluorescence at time t

F_o is O-level fluorescence (Fig. 5A) as numerator representing the baseline correction and as denominator representing the amount of plant tissue present.

Characteristics and interpretation of key points of the fluorescence transient are summarized below from the literature (see Krause & Weis, 1991; Vidaver *et al.* 1991; Seaton & Walker, 1992; Bolhàr-Nordenkampf & Öquist, 1993 for additional detail).

Initial fluorescence, F_O, in practice is a rapid or immediate rise in fluorescence emission to an initial (O) level, when the fluorometer shutter is fully opened. Physiologically, F_O is the state where fluorescence emission occurs with all PS II reaction centers open and the photosynthetic membrane is in a non-energized state, *i.e.*, the primary acceptor (Q_A) is fully oxidized (Van Kooten & Snel, 1990; Bolhàr-Nordenkampf *et al.* 1989; Vidaver *et al.* 1991). As an initial fluorescence emission which is relatively constant before the initiation of photochemical events, F_O is a useful level against which the subsequent signals of fluorescence can be normalized or standardized (Vidaver *et al.* 1991). F_O was once regarded as constant or non-variable fluorescence (Lichtenthaler & Rinderle, 1988). However, many results have been reported that F_O changes with time, PFD, *etc.* (Bilger & Schreiber, 1986; Björkman & Demmig, 1987; Demmig & Björkman, 1987; Seaton & Walker, 1992).

The variable fluorescence (F_{var} (or F_V)) rise to P from F_O occurs as the electron acceptor Q_A pool becomes

increasingly reduced under continuous illumination. The light energy will then drive Q_A fully reduced and fluorescence will reach its maximum as all traps close.

Fluorescence decline from P reflects the light activation of electron transport capacity at the photosystem I (PS I) acceptor side as well as the development of a number of overlapping "fluorescence quenching" processes as photosynthesis is allowed to commence in continuous light. For example, non-photochemical quenching (Q_N) develops as the transthylakoid proton gradient (ΔpH) develops. Accordingly, energy is increasingly dissipated as heat rather than fluorescence, and the efficiency of electron transfer falls (Harbinson, *et al.* 1989; Horton *et al.* 1990).

Steady state fluorescence, F_t, was estimated after a five minute scan and the difference from F_p to F_t are related to CO_2 assimilation (Hipkins & Baker, 1986).

The ratio of variable to maximum chlorophyll fluorescence (F_v/F_m) is considered a measure of potential primary photochemical efficiency (see Butler, 1978), since it relates to the probability of a photon absorbed by the chlorophyll matrices being utilized to drive PS II photochemistry (Baker & Horton, 1988). The F_v/F_m ratio at 77K has been found to be remarkably constant (0.832±0.004 for non-stressed C_3 plants) among many species and ecotypes (Björkman & Demmig, 1987). At room temperature, F_v/F_m

ratios very similar to those at 77K can be obtained for non-stressed plants, provided that conditions are chosen to eliminate or minimize effects of carbon metabolism (high light after dark incubation) (Krause & Somersalo, 1989).

Most F_v/F_m ratios reported in the literature are derived from data where F_o is determined at very low PFD so that no components of the photochemical reaction involved in the photosynthetic process will be initiated. F_{max} (P or F_m) is then usually driven to a maximum by a pulse of very high PFD. In this research, however, F_o was measured using the same light intensity (PFD of 100 $\mu mol.m^{-2}.s^{-1}$) as used for measurement of variable fluorescence and is designated sF_o. Because the same excitation light intensity was used for most experiments in this research, changes in the F_v/F_m ratios should follow the same pattern as reported for other work with conifers, *i.e.*, stressed western redcedar seedlings should have lower F_v/F_m ratios than those in non-stressed plants (see Bolhàr-Nordenkampf & Lechner, 1988; Krause & Somersalo, 1989; Bolhàr-Nordenkampf & Öquist, 1992). Ratios calculated for western redcedar, however, are not directly comparable with published ratios using different excitation light intensities for the determination of F_o and F_{max}. Therefore, the F_v/F_m ratio may be considered as an indicator of PS II activity rather than efficiency when measured under possible subsaturating light

levels (Strand & Lundmark, 1987), and called sF_v/F_m, to distinguish it from the usually reported F_v/F_m in the literature. The sF_v/F_m ratio was calculated in relative units from the normalized fluorescence transient (see Fig. 5B) by the formula :

$$sF_v/sF_m = \frac{(sF_p)}{(sF_p + sF_o)}$$

where:
sF_v is measured at the time of peak variable fluorescence (sF_p), measured at 100 $\mu mol.m^{-2}.s^{-1}$,
sF_m is maximal fluorescence ($sF_p + sF_o$), measured at 100 $\mu mol.m^{-2}.s^{-1}$.

Data analysis was done for several components of the Kautsky curve (see Fig. 5B), *i.e.*, sF_o, initial fluorescence; sF_p, maximum chlorophyll fluorescence; sF_t steady state fluorescence; sF_v/F_m, the ratio of the induced to the maximum chlorophyll fluorescence (sF_{max}) at the time of peak fluorescence (P or sometimes M) (Hipkins and Baker, 1986), and $sF_{(p-t)}$, the difference between the maximum fluorescence (P or M) and sF_t (Hawkins & Lister, 1985).

(c) Apparent photosynthesis (P_N) and dark respiration (R_D)

Carbon dioxide exchange of intact seedlings was measured following the F_{var} measurement using a Beckman model 865 Infra-red gas analyzer (IRGA) in a closed system (Fig. 6). Before measuring CO_2 exchange, sampled seedlings were pre-treated with two different light intensities, provided by quartz-halide lamps. The first light pre-treatment was 400 $\mu mol.m^{-2}.s^{-1}$ for 15 minutes to acclimate seedlings to a moderate light level under laboratory conditions. The seedlings were then exposed to 650 $\mu mol.m^{-2}.s^{-1}$ light levels for a minimum of 30 minutes, comparable to the P_N measurement light levels.

Light was filtered through a 11.5 cm deep water heat filter to reduce the infra-red component so that cuvette temperatures could be maintained close to room temperature of about 22±2 °C. The entire shoot, unless otherwise indicated, was used for CO_2 exchange measurement using a method modified from Jarvis & Catsky (1971) and described by Williams (1973).

The measuring air circuit consisted of a Plexiglass cuvette, a "cold-finger" or drier bypass to condense out water resulting from plant transpiration, the IRGA,

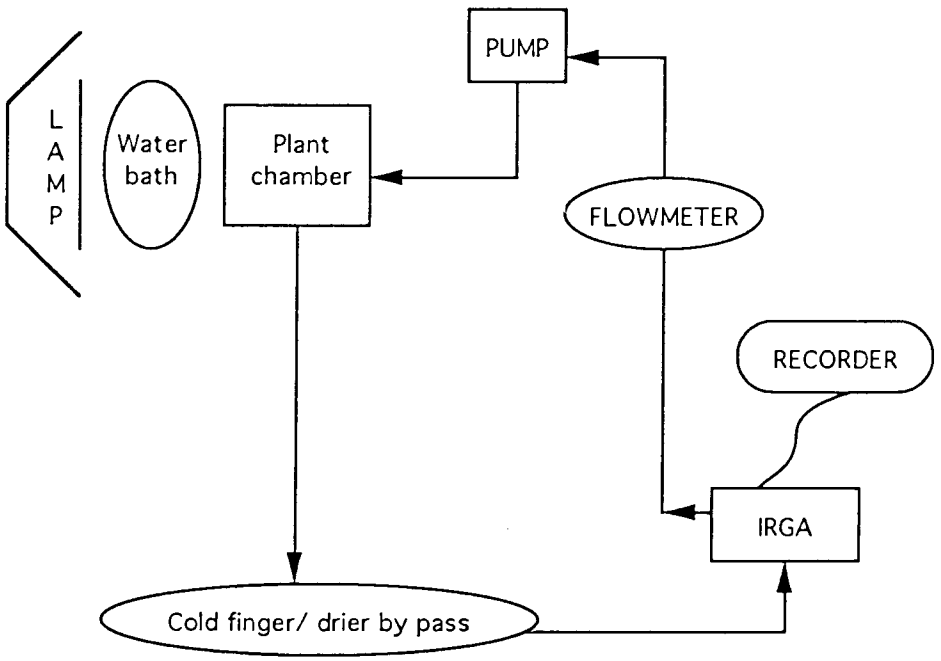


Fig. 6. Flow diagram of the CO_2 exchange measurement system

Matheson® flowmeter model 604, CA, USA, and a diaphragm pump (Hartmann & Braun®, model 2, Germany) interconnected with tygon tubing. Volume of the measuring system was 334 ml excluding the plant cuvettes. Cuvette volume ranged from 415 to 1419 ml depending on size of the seedling being measured. The plant cuvettes were made of a clear 3 mm Plexiglass and were rectangular in shape. The base part of the chamber was a rectangular Plexiglass plate (11 mm thick) which was grooved to hold the chamber and was slotted in the middle to insert the plant stem during measurement. Plants were sealed in the chamber (cuvette) with Apiezon Q during P_N and R_D measurements.

Before and after CO_2 exchange assessment on each measurement day, the IRGA was calibrated by using nitrogen as the zero reference and CO_2 for the upscale calibration. The instrument was zeroed by circulating the N_2 through both the reference and the sample cells of the analyzer at a flow rate of 3.2 $l.min^{-1}$. The upscale calibration was done by circulating CO_2 (340 ppm CO_2 *v/v* in air, Linde, Canada) through the sample cell again at a flow rate of 3.2 $l.min^{-1}$. During CO_2 exchange measurements, nitrogen was 'trickled' at a lower flow rate through the reference cell. Air at normal CO_2 concentration (338 to 390 ppm CO_2), at room temperature (22±2 °C) and about 80-85% RH was pumped through the chamber with a minimum air flow of 5.5 $l.min^{-1}$. The CO_2 content of

the air stream in a closed circuit was monitored and displayed on a Metrohm® chart recorder model no. E478, Switzerland. Plants were placed to receive 600 to 680 $\mu mol.m^{-2}.s^{-1}$ PFD from the side, provided by a high pressure sodium lamp (400 watt Poot Elektra, type PC 1078/N lamp, with a General Electric Lucalox LU 400/40 bulb). Room temperature (°C) and pressure (mmHg) were recorded during these measurements.

Since the volume of the measuring circuit is known, the CO_2 exchange rates can be determined by calculating the rate of decrease in $[CO_2]$ from the closed system volume when the plant is in light (for P_N), and rate of increase in $[CO_2]$ when the plant is in complete darkness (for R_D). The values of $[CO_2]$ ppm versus time were used (after standardizing for pressure and temperature differences) for determining photosynthesis and dark respiration rates.

Dark respiration (R_D) was measured following photosynthesis measurements, using the same system by covering the cuvette to create complete dark conditions.

CO_2 exchange data were expressed on the basis of leaf dry weight (mg $CO_2.h^{-1}.mg\ odw^{-1}$), leaf area (mg $CO_2.h^{-1}.dm^{-2}$) and sF_o of F_{var} fluorescence (mg $CO_2.h^{-1}.(0.01)sF_o^{-1}$).

To further assess seasonal changes in photosynthetic activity and F_{var} fluorescence, periodic measurements were

made on the same trees (non-destructive samples) (Fig. 7). Beginning May, 1991, five representatives of 1-year-old seedlings were randomly selected from each treatment, and periodically measured for photosynthesis and F_{var} fluorescence over the experimental period. Since these seedlings could not be oven-dried, photosynthetic rates were only expressed per unit sF_o.

To determine the photosynthetic light saturation curve responses of the seedlings, PFD during P_N measurements was varied by changing the distance between the light source and the plant. For low PFD (50 - 200 $\mu mol.m^{-2}.s^{-1}$), several layers of cheese cloth were placed between the light source and measured seedlings. Plants were allowed to acclimate to each light intensity for about 30 min, and then checked for a constant rate of CO_2 uptake as displayed by the chart recorder. Light intensities were measured inside at the center of the Plexiglass cuvette.

d. Chlorophyll and carotenoid analyses

Pigment analysis for March and June 1990 data were obtained from five samples of 100 mg of foliage tissue taken from each shade treatment. Foliage tissue of about

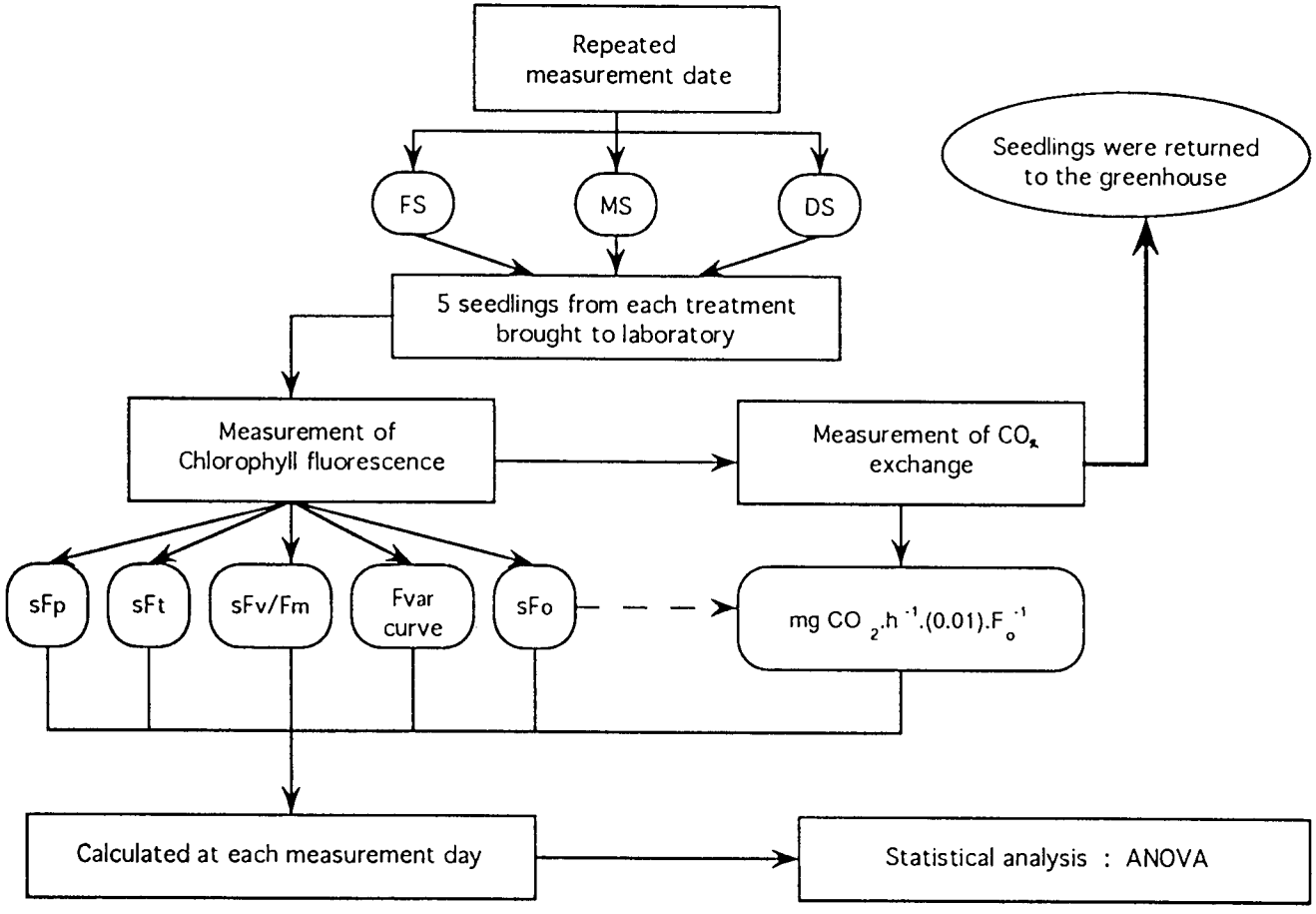


Fig. 7. Flow diagram of repeated measurements

50 mg was ground in 10 ml of 100% ethanol for 30-60 s by using a Polytron® homogenizer, model PT 10-20-3500, Switzerland. The brei was centrifuged at 500 g for 10 min, and the supernatant was filtered into glass tubes wrapped in aluminum foil and stored on dry-ice in dark to prevent the pigment solution from photo-oxidation (Sesták, 1971). Determinations of absorbance at 661.6, 644.8 and 470 nm wavelength ($A_{661.6}$, $A_{644.8}$ and A_{470}) were made on a Model 210, Varian®, CA, USA recording spectrophotometer.

For the August 1991 and April 1992 data, pigment analysis was done separately for foliage from the previous growing period (*i.e.*, summer 1990 for August 1991 data, and summer 1991 for April 1992 data) and from the current growing season (lighter green in color). Three samples of 100 mg foliage tissue of each age category from each shade treatment was analyzed as outlined above. However, due to a technical problem with the first spectrophotometer, absorbance determinations for the 1991 and 1992 data were done on a Model 3000 Milton Roy Spectronic® NY, USA spectrophotometer.

All of the procedures described for pigment analysis were done under a green-safe light to minimize pigment photo-oxidation. The chlorophyll and carotenoid content ($mg.l^{-1}$) were calculated by substituting the absorbance values into the following equations (Lichtenthaler, 1987) :

$$\text{Chl-}a = 11.24\ A_{661.6} - 2.04\ A_{644.8}$$

$$\text{Chl-}b = 20.13\ A_{644.8} - 4.19\ A_{661.6}$$

$$\text{Chl}(a+b) = 7.05\ A_{661.6} - 18.09\ A_{644.8}$$

$$Car = (1000\ A_{470} - 1.90\text{Chl-}a - 63.14\text{Chl-}b)/214$$

Dry weight values were obtained by oven-drying 50 mg foliage samples at 80 ^{o}C for 48 *h*.

The influence of different excitation PFD and different combinations of pre-treatment light and excitation PFD on chlorophyll fluorescence of western redcedar seedlings

Materials and Methods

Two-year-old western redcedar seedlings grown under three different light conditions as described previously were used for these experiments. The experiment was conducted from 6 - 23 October 1992, using five randomly selected seedlings from each shade treatment (*i.e.*, Full sun (FS), Moderate shade (MS), and Deep shade (DS)). The same amount of plant tissue would be measured for each successive chlorophyll fluorescence measurement. Seedlings were marked to indicate the amount of the leaf tissue that was placed into the fluorescence chamber.

There were two series of chlorophyll fluorescence measurements in this experiment. In the first series, the same excitation PFD as the pre-treatment PFD *i.e.*, 25,25; 50,50; 100,100; 200,200; 400,400 $\mu mol.m^{-2}.s^{-1}$ was used. The second series used different light intensities for the measurement of chlorophyll fluorescence of seedlings that were pre-treated with a single light intensity of 300 $\mu mol.m^{-2}.s^{-1}$. The combinations used were 300,25; 300,50; 300,100; 300,200; 300,400 $\mu mol.m^{-2}.s^{-1}$.

To avoid stress on seedlings during this experiment, only one series of light combinations for five trees from each shade treatment (15 trees) were measured each day.

The effect of drought on chlorophyll fluorescence and CO_2 exchange of western redcedar seedlings

Materials and Methods

Plant materials in this experiment were one-year-old western redcedar seedlings, grown under three different light conditions (*i.e.*, 100%, 49% and 27% of ambient light), as described previously.

Beginning 8 August, 1991, five seedlings were randomly selected from each shade treatment, and the soils were saturated and brought to field capacity following the

addition of approximately 300 ml of water. Soil field capacity (percentage of water remaining in a soil after saturation and after free drainage has practically ceased (Brady, 1990), was determined following free drainage for 24 hours.

Drought conditions were induced by withholding water and allowing soil water to be depleted. CO_2 exchange and chlorophyll fluorescence were measured at different times for plants in each shade treatment, dependent on the soil moisture content.

Weight of tube, soil and plant at field capacity level was used as a reference weight (equal to 100% water content) to determine a relative soil moisture conditions during this drought experiment. Percent water loss from soil field capacity at certain times after water withholding was initiated was calculated using the formula:

$$\% WL = \frac{Ws - Wdn}{Wdn} \times 100$$

where:

%WL : Percent water loss

Ws : Total weight of tube, plant and soil at soil field capacity

Wdn : The above weight at (1,2, ..., n) days after water was withheld.

At the end of the drought experiment, seedlings were carefully removed from the tubes, and the soil was oven-dried at a temperature of 100-110 °C for 48 *h* or to a constant weight (Brady, 1990). Percent soil moisture content (SMC) was determined using the formula (Brady, 1990):

$$\% \text{ SMC} = \frac{W_f - W_d}{W_d} \times 100$$

where:

% SMC : percent soil moisture content

W_f : soil weight (g)

W_d : soil oven-dry weight (g)

Chlorophyll fluorescence and CO_2 gas exchange were measured according to the procedure previously described. Since these two parameters were measured on the same seedlings for the entire experiment, CO_2 exchange rates are expressed as mg $CO_2.h^{-1}.(0.01)\ F_o^{-1}$.

Statistical Analyses

All statistical analyses were done on the mainframe computer at Simon Fraser University using SAS (SAS Institute Inc. 1988)[3].

Effects of shade on plant weight (root, shoot and total weight), CO_2 exchange rates and F_{var} components of harvest data were analyzed using two-way ANOVA (SAS Institute Inc. 1988). Tests of normality were performed by an ANOVA of the residuals on all data including CO_2 exchange rates and components of F_{var} transients.

To ensure a normal distribution, the dry weight data were transformed to natural logs (*ln*-transformation), whereas the ratio data, *i.e.*, RWR, R/S ratio, LWR, SLA, LAR and sF_v/F_m were transformed to square-roots.

Post-ANOVA analysis for detecting differences due to shade treatments and harvest time employed the Student-Newman-Keuls test. An overall α of 0.05 was used to detect significant differences.

Some experiments in this research used a repeated measures technique, namely: (1) effects of shade on CO_2 exchange rates and F_{var} components measured periodically over time using the same seedlings (see Fig. 8 for detail on randomized design of each group), (2) effect of different

[3] Most of the statistical analyses applied in this research are based on the recommendation by the statistics consultant at SFU.

light acclimation and excitation intensities on the components of F_{var} transients, and (3) effects of drought stress on CO_2 exchange and F_{var} transients. These data were analyzed by repeated measures analysis of variance using multivariate tests for the repeated measures (Moser *et al.* 1990; Meredith & Stehman, 1991). Post-ANOVA analyses were done by using linear and quadratic orthogonal contrasts (Mize & Schultz, 1985).

A different analysis was used for comparison between RGRs and NARs. As pointed out by Causton (1991), one problem with the classical growth analysis method is that a large within sample variation (calculated as variance or standard deviation) is often obtained from derived data such as RGR and NAR (Evans, 1972). This problem is caused by the way RGR or NAR is calculated, *i.e.*, from two samples obtained at two harvests separated in time, t_2 and t_3 (Causton, 1991). As a result, differences in growth rates between treatments must be large to be statistically significant. Therefore, for RGR and NAR data, a statistical analysis based on an ANOVA with *ln*-transformed plant weight or leaf area data as dependent variable was used, as proposed by Cain & Ormrod (1984) and described by Poorter & Lewis (1986). A significant Group x Time interaction indicates significant differences in relative growth rates between groups (Poorter & Lewis 1986). Some of the advantages of

Plant 1	Plant 3	Plant 5	Plant 2	Plant 4
FS	FS	FS	FS	FS
H1, H2, ..., Hn	H1, H2, ..., Hn	H1, H2, ..., Hn	H1, H2, ..., Hn	H1, H2, ..., Hn
Plant 2	Plant 5	Plant 3	Plant 1	Plant 4
MS	MS	MS	MS	MS
H1, H2, ..., Hn	H1, H2, ..., Hn	H1, H2, ..., Hn	H1, H2, ..., Hn	H1, H2, ..., Hn
Plant 3	Plant 4	Plant 2	Plant 1	Plant 5
DS	DS	DS	DS	DS
H1, H2, ..., Hn	H1, H2, ..., Hn	H1, H2, ..., Hn	H1, H2, ..., Hn	H1, H2, ..., Hn

Randomized block design :

Five trees from each shade treatment were randomly selected every harvest period.

Repeated measures :

Five trees from each shade treatment were randomly selected at the beginning and used subsequently for each measurement .

Notes:

1. FS, MS and DS are the shade treatments
2. Plant 1, ..., Plant n, are the experimental units
3. H1, ..., Hn, are the harvest measurement times

Fig. 8. Comparison of the randomized block and corresponding repeated measurement experimental design

this method over both classical and functional growth analysis are : (1) there is no need for pairing procedure, (2) an analysis can be done to evaluate more than two groups of RGR, and (3) no decision is required concerning the polynomial equation used to fit the curve to the data (Poorter & Lewis 1986).

RESULTS

Growth Environment

For the shade treatments, the below/above screen ratio of light intensity was found to be very constant for MS (single layer) and DS (double layers of screen) measured under both clear sunny and cloudy overcast skies (Fig. 9; Appendix I, Table 1 & 2).

Greenhouse roof construction and air mixing ducts (Fig. 2) reduced the amount of light reaching the shade treatments especially DS. Depending on solar position (time of measurement in a day or month in a year), the light conditions (PFD) received by each shade treatment changed (Appendix I, Table 2). In the morning until about 11:00, the light conditions above the screen were almost identical between the three shade treatments. Only when the sun at the position between 12:00 to 16:00 hours, PFD reaching above screen for DS seedlings changed. Between June and December 1993, the average light PFD above screen measured around 12:00 on clear sunny sky showed that FS had a 36% higher PFD than DS (Fig. 10). This difference was much smaller when measurements were taken on cloudy overcast

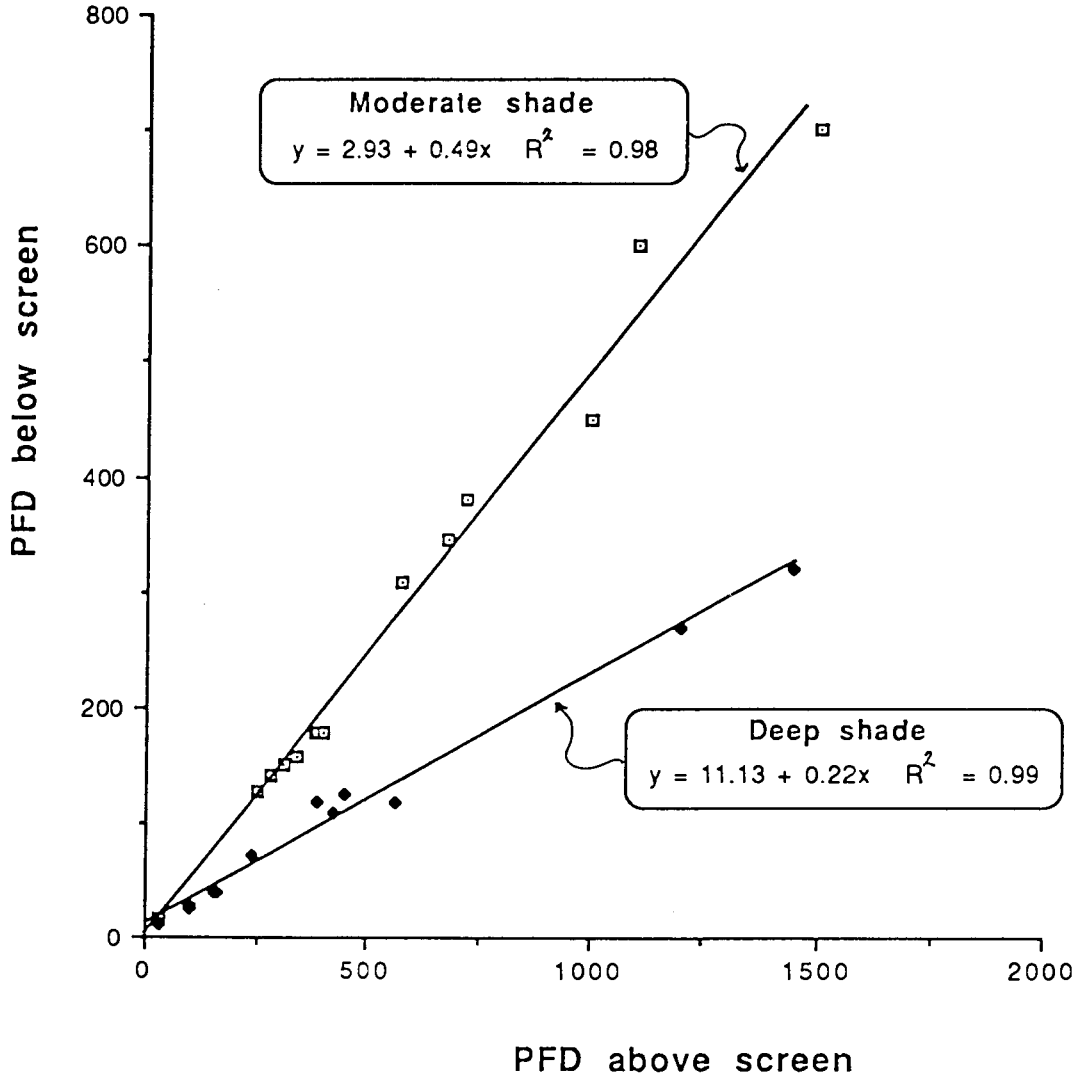


Figure 9. Mean PFD ($\mu mol.m^2.s^{-1}$) above screen plots against PFD below screen. Light data were recorded under both clear sunny and cloudy overcast skies at different times of the year (n=5).

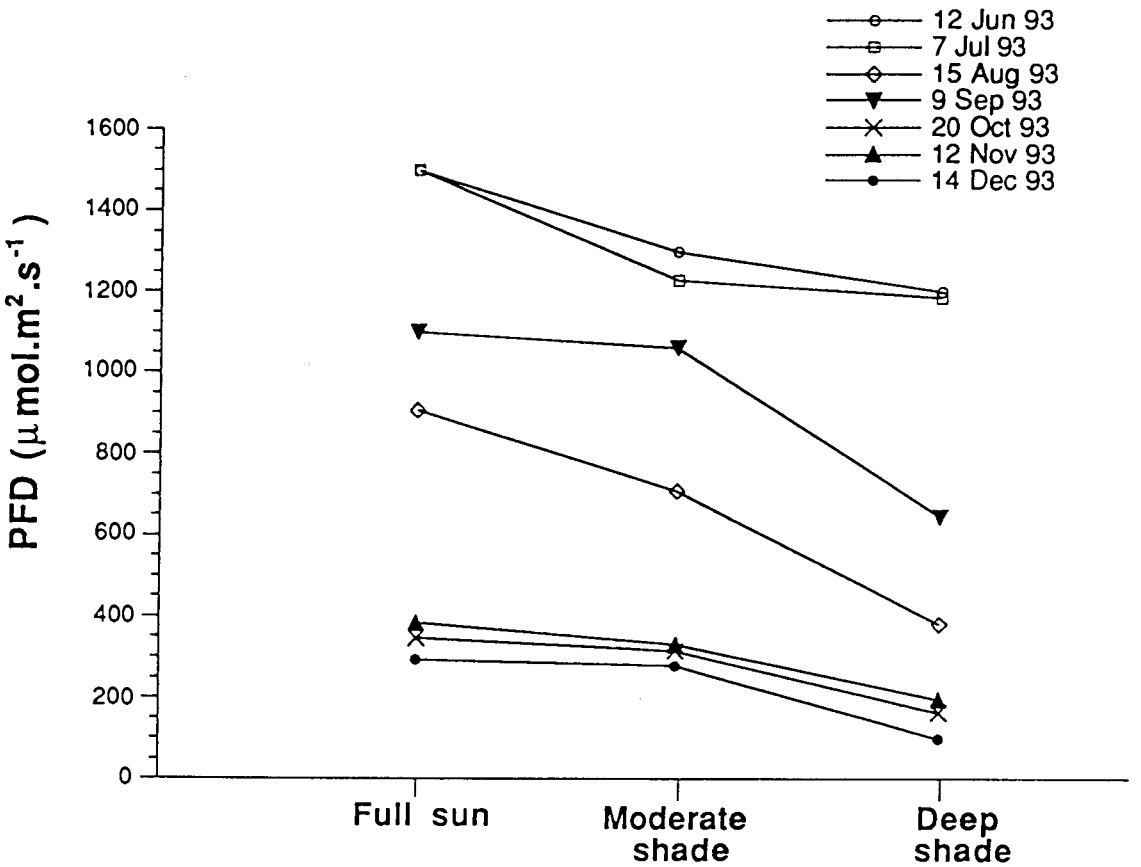


Figure 10. Mean PFD ($\mu mol.m^2.s^{-1}$) at each shade treatment site, measured around 12:00 with clear sunny sky conditions at different times of the year (n=5).

days, *i.e.*, DS received only about 19% lower PFD than FS treatments (Appendix I, Table 2).

Single and double layers of screen had little effect on red/far-red (R/Fr) ratio. This ratio measured from the absorption at each maximum wavelength (Red: λ = 660; Far-red : λ = 730) indicated that one layer of fiberglass screen had a R/Fr ratio of 1.01 and double layers of fiberglass screen had a 0.96 ratio.

From the minimum/maximum temperatures located in each treatment, there were differences in ambient temperature (Fig. 11). The FS treatment had an average maximum temperature of approximately 3.8 and 5.2 °C higher than MS and DS treatments respectively. Little difference was recorded in the average minimum temperature between treatments, *i.e.*, FS had an average of about 0.8 and 0.9 °C higher than MS and DS treatments respectively. The highest maximum temperature was recorded in July 1991, *i.e.*, 44, 38.5 and 36 °C for FS, MS and DS treatments respectively, and the lowest minimum temperature in January, *i.e.*, 0.0, -1.0 and -1.0 °C for FS, MS and DS respectively. The overall minimum and maximum greenhouse temperature will be shown with the Photosynthesis and F_{var} fluorescence data (Fig. 26, p. 87A & B).

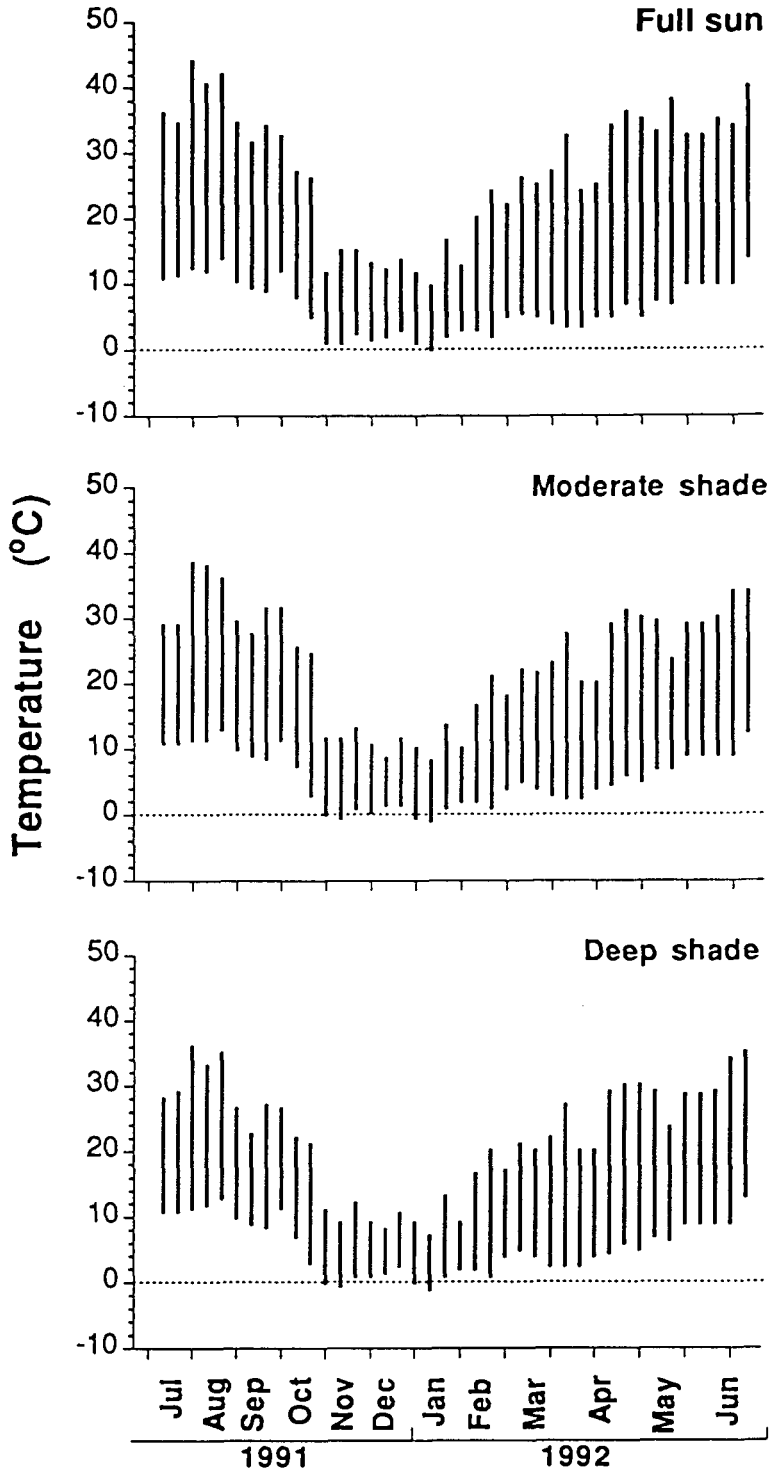


Fig. 11. Weekly minimum and maximum ambient temperatures (°C) for each shade treatment.

Part I. Growth Analysis

To simplify the comparison of growth components for the western redcedar seedlings, the duration of this research is divided into three periods : (1) May to November 1990, *first year*, (2) November 1990 to November 1991, *second year* and (3) November 1991 to November 1992, *third year*. After the second year, it was realized that limitation in rooting space (tube size) might influence results obtained in this research. However, regular watering and fertilization may offset in part this space limiting constraint.

The effect of shade on western redcedar seedling morphology

General appearance of seedlings

About two months after germination (July 1990), the upper surface of FS leaves started showing symptoms of a 'bronzy' or reddish brown color, whereas the leaf color of shaded seedlings, both MS and DS, were still green. Interestingly, while the top surface of the leaf branches of these seedlings was bronzy, the under surface was still green (Fig. 12). This bronzy color, then gradually

Figure 12. Nine-month-old (March 1991) western redcedar seedling grown under Full sun (FS) light treatment. The upper surface of leaves were bronzy while the under surface was still green.

disappeared in late August and totally vanished in mid-September when temperature were cooler in late summer. In winter, however, it appeared again following high light-low temperature conditions, particularly from 3-6 January 1991 (Fig. 13). This bronzy color was also observed on the leaves of some MS seedlings, although it was not as bronzy as those of FS seedlings. DS seedlings did not show any color change.

The branches of western redcedar seedlings grown under FS conditions had a tendency to grow in a vertically oriented position as opposed to the more horizontal oriented leaf growth found in shaded seedlings.

Pigment content

In general, chl-*a*,*b*, and total chl (*a*+*b*) contents were higher in shade grown seedlings than in FS grown seedlings (Table 1). Most of the differences were not statistically significant ($\alpha<0.05$), except for the June and September 1991 data for chl-*a* of MS and DS which were significantly higher than that of FS seedlings. Significantly higher chl-*b* in DS than in FS was found in September 1991 and April 1992 (for older foliage only).

Carotenoid content was significantly higher in FS and MS seedlings than in DS seedlings in March 1991.

Figure 13. Bronzy color developed by 9-month-old (March 1991) western redcedar seedlings grown under Full sun (100%) ambient light.

Significantly lower carotenoid contents in both shaded seedlings were found in April 1992 data (Table 1).

Significantly higher chl *a/b* ratios in FS seedlings than in seedlings from both shade treatments were found in April 1992. As compared to DS seedlings, *car/chl*(*a*+*b*) ratio was generally higher in FS seedlings except in September for older foliage only, and significantly higher in March 1991 and April 1992 for both old and new foliage (Table 1).

No consistent pattern was found in old and new leaf's pigment content. Chlorophyll seemed to be higher in old leaves than in new leaves in September 1991. In April 1992, however, except for DS seedlings, *chl-a* and *b* and *car* contents were higher in new leaves than in old leaves.

Growth pattern of western redcedar seedlings

Seed germination occurred 5 to 10 days after sowing and was completed within a month. Normally, two but sometimes three linear cotyledons which were flat in cross section emerged following germination (Fig. 14). Cotyledons were persistent but generally died after the first season.

Juvenile leaves were subulate and flattened, mostly in whorls of four, although individuals with whorls of three were also found (Fig. 14). Scale-like leaves (Fig. 14) were

Table 1. Chlorophyll and carotenoid content (mg.g odw^{-1}) from one- (March 1991), two- (June, September 1991) and three- (April 1992) year-old western redcedar foliage grown under three shade conditions. (Mean ± SE, n=5, except for September 1991 and April 1992, n=3). O = Old leaves, N = New leaves.

Treat-ment	Date	Pigment				a/b ratio	Car/Chl ratio
		Chl-a	*Chl-b*	*Chl(a+b)*	*Car*		
FS	23-Mar	1.85 ± 0.12 *a*	1.47 ± 0.11 *a*	3.32 ± 0.23 *a*	1.19 ± 0.08 *a*	1.26 *a*	0.36 *a*
	12-Jun	1.38 ± 0.15 *b*	1.05 ± 0.13 *a*	2.43 ± 0.28 *a*	1.12 ± 0.14 *a*	1.31 *a*	0.46 *a*
	25-Sep O	0.12 ± 0.04 *b*	0.12 ± 0.08 *b*	0.24 ± 0.13 *b*	0.02 ± 0.00 *a*	1.00 *a*	0.08 *a*
	N	0.09 ± 0.02 *b*	0.08 ± 0.04 *b*	0.17 ± 0.07 *b*	0.02 ± 0.00 *a*	1.13 *a*	0.12 *a*
	16-Apr O	0.80 ± 0.37 *a*	0.39 ± 0.17 *b*	1.19 ± 0.54 *a*	0.31 ± 0.11 *a*	2.05 *a*	0.26 *a*
	1992 N	1.20 ± 0.57 *a*	0.68 ± 0.33 *a*	1.88 ± 0.90 *a*	0.60 ± 0.21 *a*	1.76 *a*	0.32 *a*
MS	23-Mar	2.01 ± 0.11 *a*	1.42 ± 0.44 *a*	3.43 ± 0.52 *a*	1.29 ± 0.17 *a*	1.41 *a*	0.38 *a*
	12-Jun	2.70 ± 0.21 *a*	1.35 ± 0.12 *a*	4.05 ± 0.31 *a*	1.50 ± 0.09 *a*	2.00 *a*	0.37 *b*
	25-Sep O	0.25 ± 0.04 *a*	0.24 ± 0.06 *a*	0.49 ± 0.10 *a*	0.03 ± 0.00 *a*	1.04 *a*	0.06 *a*
	N	0.21 ± 0.02 *a*	0.20 ± 0.04 *a*	0.41 ± 0.06 *a*	0.04 ± 0.01 *a*	1.05 *a*	0.10 *a*
	16-Apr O	0.56 ± 0.05 *a*	0.48 ± 0.04 *b*	1.04 ± 0.08 *a*	0.08 ± 0.02 *b*	1.17 *b*	0.08 *b*
	1992 N N	1.53 ± 0.66 *a*	1.34 ± 0.60 *a*	2.87 ± 1.25 *a*	0.26 ± 0.12 *b*	1.14 *b*	0.09 *b*
DS	23-Mar	1.91 ± 0.17 *a*	1.53 ± 0.27 *a*	3.44 ± 0.43 *a*	0.72 ± 0.10 *b*	1.25 *a*	0.21 *b*
	12-Jun	2.82 ± 0.43 *a*	1.23 ± 0.28 *a*	4.00 ± 0.63 *a*	1.31 ± 0.20 *a*	2.29 *a*	0.33 *b*
	25-Sep O	0.24 ± 0.03 *a*	0.18 ± 0.05 *ab*	0.42 ± 0.08 *a*	0.04 ± 0.01 *a*	1.33 *a*	0.10 *a*
	N	0.16 ± 0.01 *a*	0.14 ± 0.03 *a*	0.30 ± 0.04 *a*	0.03 ± 0.01 *a*	1.14 *a*	0.10 *a*
	16-Apr O	1.23 ± 0.31 *a*	1.07 ± 0.25 *a*	2.30 ± 0.55 *a*	0.19 ± 0.06 *b*	1.15 *b*	0.08 *b*
	1992 N	0.78 ± 0.18 *a*	0.73 ± 0.14 *a*	1.51 ± 0.31 *a*	0.09 ± 0.05 *b*	1.07 *b*	0.06 *b*

Means with the same letter are not significantly different between treatment (α<0.05, Student-Newman-Keuls test) for the same date and age of foliage.

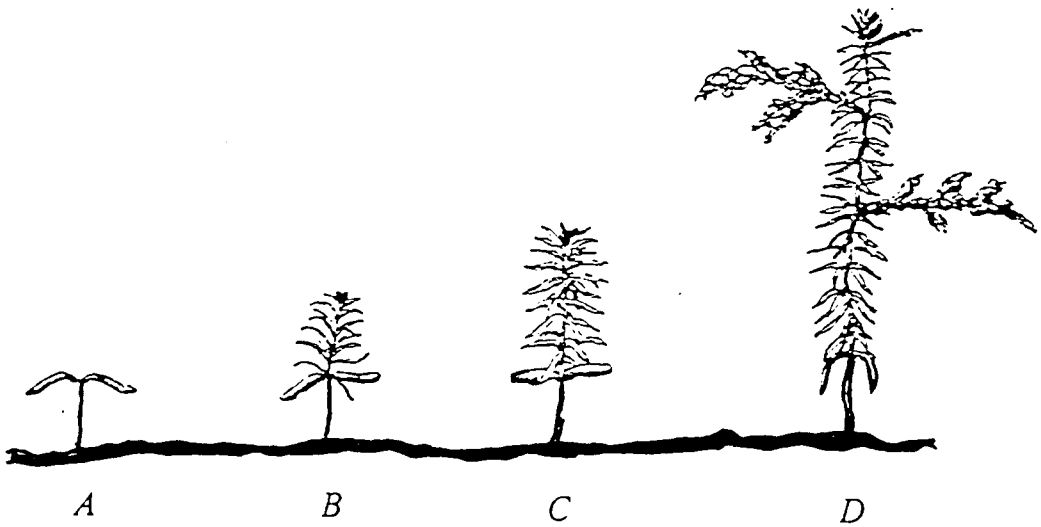


Figure 14. Seedling development in western redcedar. A = cotyledons, B,C = subulate juvenile leaves, D = branches with scale-like leaves.

first observed in FS grown seedlings (31 July 1990, 77 days after sowing), followed by those of MS (5 days later) and DS grown seedlings, 10 days later. On 11 August 1990, out of 182 seedlings in each treatment, 3%, 11% and 1% of FS, MS and DS seedlings respectively had a branch with scale-like leaves. On 20 August 1990, 38%, 72% and 15% of FS, MS and DS seedlings had at least one branch with scale-like leaves.

At the end of the first year, all seedlings generally had two or more branches with scale-like leaves. Spring leaf growth in the second year commenced first in DS seedlings (03 March 1991), followed by MS seedlings a week later and FS seedlings 26 days later.

Percentage mortality of seedlings at the end of the first year was found to be the highest in FS seedlings (16%), followed by DS (14%) and MS (4%) seedlings. The main cause of seedling mortality in FS was probably high soil temperature and in the DS seedlings pathogens.

Growth of most morphological components of seedlings from germination until dormancy, regardless of the shade treatments, followed a sigmoid curve (Appendix I, Table 4 for detail of individual weight of each harvest). First year growth began with a slow phase from germination until July, followed by a rapid increase in August before it again slowed in November.

Leaf area

The moderate light and temperature growing conditions in the MS treatment had a distinct impact on the leaf growth of western redcedar. MS grown seedlings had a consistently higher leaf area in November each year than leaf area of FS and DS grown seedlings (Table 2; see Appendix I, Table 3 for

differences at each harvest date). At the end of the first year, MS seedlings had 15% and 45% higher leaf area than FS and DS seedlings respectively (Table 2). Here, leaf areas of MS and FS seedlings were significantly ($\alpha<0.05$) higher than leaf area of DS seedlings. In the last two years, MS grown seedlings had significantly higher ($\alpha<0.05$) leaf area than DS and FS seedlings (Appendix I, Table 3). In the second year, MS seedlings had 28% and 42% higher leaf area than FS and DS seedlings respectively, and in the third year, 54% and 39% higher leaf area than FS and DS seedlings respectively (Table 2).

Shoot length

Except for April 1991, significantly longer shoots ($\alpha<0.05$) in MS seedlings were observed beginning October 1990 (Fig. 15; see Appendix I, Table 5 for statistical analysis for each harvest). At the last harvest (November 1992), shoot length of the FS and DS seedlings were 81% and 70% as tall respectively as the MS seedlings (Fig. 15; Table 2).

DS grown seedlings generally had longer shoots than FS grown seedlings until October of the second year. From October 1991, FS seedlings had longer shoots than DS grown

Table 2. End of season growth data for first, second, and third year growth periods of western redcedar seedlings grown under three shade treatments (mean ± SE, n=5, except on November 1991 for FS (n=4)).

Variable	Treatment / Date	**Full sun**	**Moderate Shade**	**Deep Shade**	% difference from the highest value (FS ;MS ;DS)
Leaf area	*Nov'90*	348 ± 33 *a*	412 ± 29 *a*	225 ± 14 *b*	15; 0; 45
(mm2)	*Nov'91*	5037 ± 600 *b*	7013 ± 326 *a*	4064 ± 248 *b*	28; 0; 42
	Nov'92	7020 ± 903 *b*	15326 ± 1154 *a*	9310 ± 2239 *b*	54; 0; 39
Shoot length	*Nov'90*	6 ± 0.5 *b*	8 ± 0.5 *a*	6 ± 0.3 *b*	23; 0; 24
(cm)	*Nov'91*	23 ± 1.7 *b*	32 ± 0.9 *a*	22 ± 1.9 *b*	27; 0; 32
	Nov'92	32 ± 1.4 *b*	40 ± 1.5 *a*	28 ± 1.5 *b*	19; 0; 30
Stem weight	*Nov'90*	18 ± 2 *b*	25 ± 2 *a*	10 ± 1 *c*	30; 0; 60
(mg)	*Nov'91*	325 ± 35 *b*	423 ± 29 *a*	178 ± 14 *c*	23; 0; 58
	Nov'92	885 ± 112 *b*	1591 ± 65 *a*	498 ± 55 *c*	44; 0; 69
Leaf weight	*Nov'90*	69 ± 8 *a*	91 ± 7 *a*	34 ± 4 *b*	24; 0; 62
(mg)	*Nov'91*	970 ± 91 *a*	1105 ± 110 *a*	478 ± 55 *b*	12; 0; 57
	Nov'92	1554 ± 249 *b*	3005 ± 186 *a*	980 ± 210 *c*	48; 0; 67
Shoot weight	*Nov'90*	86 ± 10 *a*	116 ± 8 *a*	45 ± 5 *b*	26; 0; 62
(mg)	*Nov'91*	1296 ± 123 *a*	1528 ± 138 *a*	656 ± 67 *b*	15; 0; 57
	Nov'92	2439 ± 340 *b*	4596 ± 240 *a*	1477 ± 189 *c*	47; 0; 68

Table 2. Continued

Variable	Date	**Full sun**		**Moderate Shade**		**Deep Shade**		% difference
Root weight	*Nov'90*	60 ± 6	*a*	43 ± 3	*b*	10 ± 0.8	*c*	0; 28; 83
(mg)	*Nov'91*	551 ± 40	*a*	365 ± 41	*a*	169 ± 36	*b*	0; 34; 69
	Nov'92	1502 ± 232	*a*	1662 ± 286	*a*	556 ± 108	*b*	10; 0; 66
Total weight	*Nov'90*	146 ± 16	*a*	159 ± 10	*a*	55 ± 5	*b*	8; 0; 66
(mg)	*Nov'91*	1847 ± 143	*a*	1893 ± 171	*a*	825 ± 98	*b*	2; 0; 56
	Nov'92	3941 ± 552	*b*	6258 ± 457	*a*	2034 ± 208	*c*	37; 0; 67

Notes : Means with the same letter are not significantly different between treatment (α<0.05, Student-Newman-Keuls test).

seedlings. In both comparisons, however, the differences were generally not statistically significant (Fig. 15, Table 2).

There was an interesting relationship observed between shoot height and shoot biomass of shaded and unshaded grown seedlings of western redcedar (Fig. 16). FS and MS developed stronger supporting structures by having significantly greater shoot and stem biomass than DS seedlings (Fig. 16). DS grown seedlings had shorter shoots and less shoot biomass than MS and FS seedlings. This indicates that DS seedlings developed a weaker supporting structure by having less leaf biomass than either FS and MS grown seedlings.

Seasonal variation in shoot growth was observed between the treatments (Fig. 15; Appendix I, Table 5). MS seedlings showed faster shoot growth in the first year with the main growth occurring in August 1990. In the second year, MS and DS seedlings started most rapid shoot growth earlier (July 1991) than FS (August 1991). In September 1990 and 1991, shoot extension of DS seedlings stopped with another period of shoot extension in October before a second cessation in November. FS and MS seedlings, in contrast, stopped shoot extension by October 1990 and MS seedlings by October 1991. FS seedlings appeared to maintain shoot extension throughout

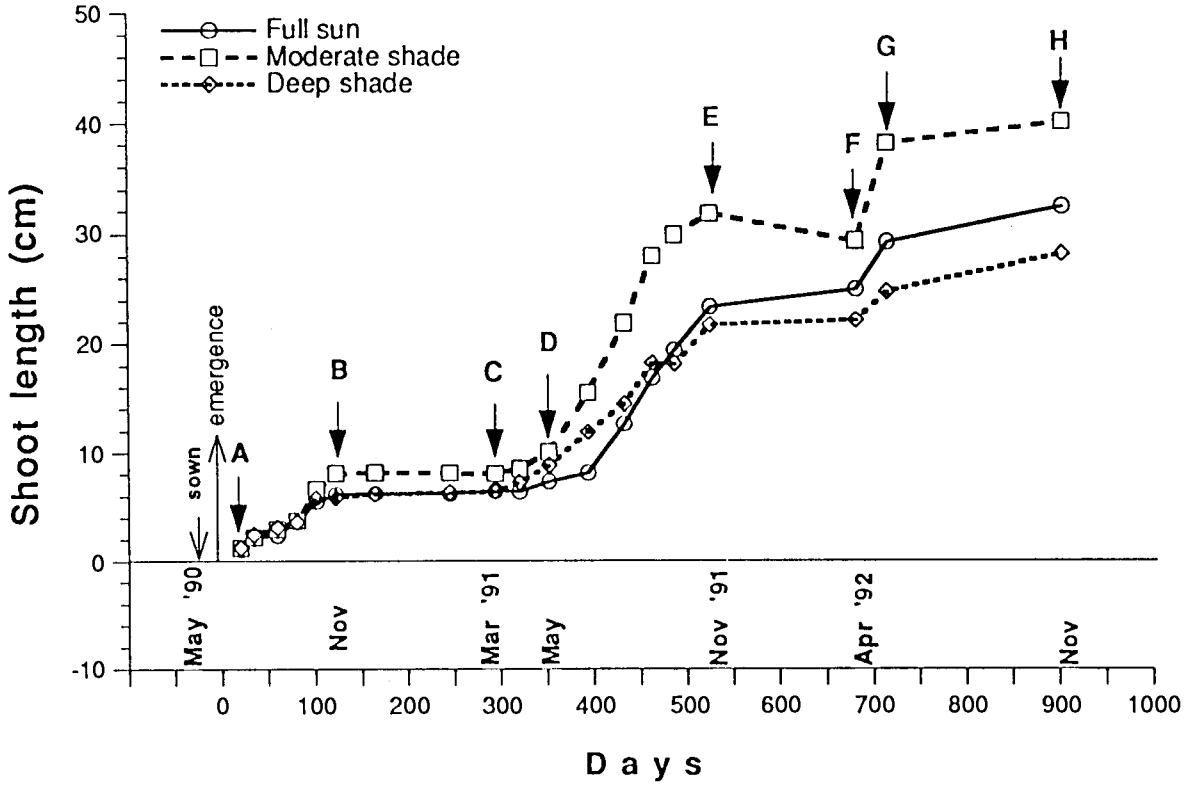


Figure 5. Changes with time in the mean shoot length (n=5) of western redcedar seedlings grown under three shade treatments. The letters demarcate the author's interpretation of the stages of growth, as follows: 1990: A-B = expansion of the summer shoot; 1991: C-D = expansion of the spring shoot; D-E = expansion of the summer shoot; 1992: F-G = expansion of the spring shoot; and G-H = expansion of summer shoot.

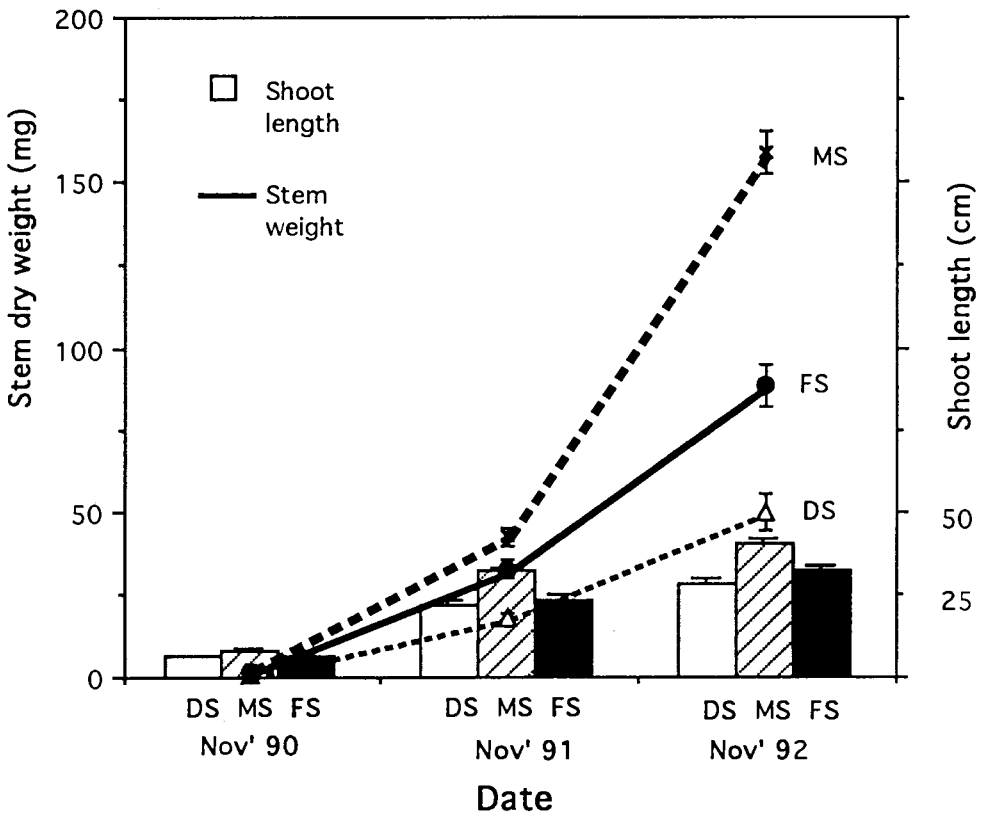


Figure 16. Relationships between mean stem weight and shoot length for three years of western redcedar grown under three shade treatments. Each point represents 5 replicates ± SE.

the winter in 1991/1992. In 1991, shoot extension began about 1 month earlier in DS and MS grown seedlings than those grown in FS (Appendix I, Table 5).

Dry weight of growth components

Stem, leaf, shoot, root as well as total dry weights of western redcedar were significantly affected by shade treatment during seedling growth.

Stem weights were significantly different ($\alpha<0.05$) between all shade treatments at the end of each years' growth period (Table 2). MS grown seedlings had the largest stem weights at the end of each year and DS seedlings the lowest. After 3 years, FS grown seedlings attained only 56% and DS seedlings only 31% of the stem weight of the MS grown seedlings (Table 2).

At the end of each year, the highest leaf weights were attained by MS grown seedlings (Table 2). Leaf weights of both FS and MS seedlings were significantly higher ($\alpha<0.05$) than DS in the first and second year, but this was not significant between each other. At the end of the third year, differences in leaf weight between all treatments were significant ($\alpha<0.05$) (Table 2). MS seedlings had 48% and 67% higher leaf weight than FS and DS seedlings respectively.

During the first year, significant differences ($\alpha<0.05$) in shoot weight between the three shade treatments were first observed in August 1990 or about 2 months after the shade treatments were applied to the seedlings (Appendix I, Table 4). At this time, largest shoot weight was found in FS seedlings which had 33% and 57% higher weight than that of MS and DS respectively. Differences in shoot weights between the shade treatments changed in September 1990 when both MS and FS seedlings had significantly higher shoot weights ($\alpha<0.05$) than that of DS. These differences remained the same until May 1991. No significant difference between FS and MS seedlings was observed. During the second year, significant differences ($\alpha<0.05$) in shoot weight between MS and both FS and DS occurred again in July 1991 (Appendix I, Table 4). In August and September 1991, shoot weights of all treatments were significantly different. At the end of each year, shoot weight of MS grown seedlings was the highest and DS grown seedlings the lowest (Table 2). At the end of the third year, however, differences in shoot weight of all treatments were significantly different ($\alpha<0.05$). At this time, MS seedlings had 47% and 68% higher shoot weights than FS and DS respectively, and FS seedlings had about 39% higher weight than DS seedlings (Table 2).

Seasonally, there was a significant increase ($\alpha<0.05$) in shoot weight of all seedlings of the three treatments from July to September 1990 (the first three months of their growth) (Appendix I, Table 4), before growth slowed in October 1990 for FS and DS seedlings and November 1990 for MS seedlings. Little increase in shoot weight occurred during winter until April 1991.

The first significant difference in root weight occurred in August 1990 (about two months after treatments were applied). Except for November 1992, root dry weights of FS grown seedlings were always 2 to 5 times greater than root dry weight of DS seedlings which were always the lowest (Appendix I, Table 4). Root weights appeared to be responsive in biomass allocation to the shade treatments with significant differences between all treatments on 10 out of 17 harvest dates (Appendix, I Table 4).

At the end of the first year, FS seedlings had 28% and 83% higher root weight and 34% and 69% higher at the end of the second year than MS and DS seedlings respectively (Table 2). FS seedlings had about 63% higher root weights than DS at the end of the third year, both MS and FS were significantly higher ($\alpha<0.05$) than DS seedlings (Table 2).

Seasonal variation in root growth was observed between the three shade treatments (Appendix I, Table 4). Little root growth occurred in FS and MS seedlings from November

1990 to March 1991 and September through November 1992. In DS grown seedlings, less root growth occurred in February through April 1991, and August to October 1991.

For total dry weights (Appendix I, Table 4), there were significant differences ($\alpha<0.05$) between the three shade treatments for the August to October 1990 harvests, February and July 1991 harvests and the November 1992 harvest. At the August 1990 harvest FS seedlings had already attained a 32%, and 57% higher total dry weight than MS and DS seedlings respectively with MS 37% higher than DS seedlings. Except for the July 1990 harvest, FS and MS grown seedlings had significantly higher total dry weights than the DS grown seedlings (Appendix I, Table 4).

Allocation of dry matter within plant

The allocation of dry matter to the shoot and root was clearly affected by the shade treatments (Fig. 17 & 18). At the end of the first year, FS allocated 41% of the total biomass to the root, while MS and DS only contributed about 27% and 18% respectively. At the end of the second year, FS seedlings allocated 30% of their total biomass to the root, followed by DS (20%) and MS seedlings (19%), and at the end of the third year: 38%, 27% and 27% for FS, MS, and DS seedlings respectively.

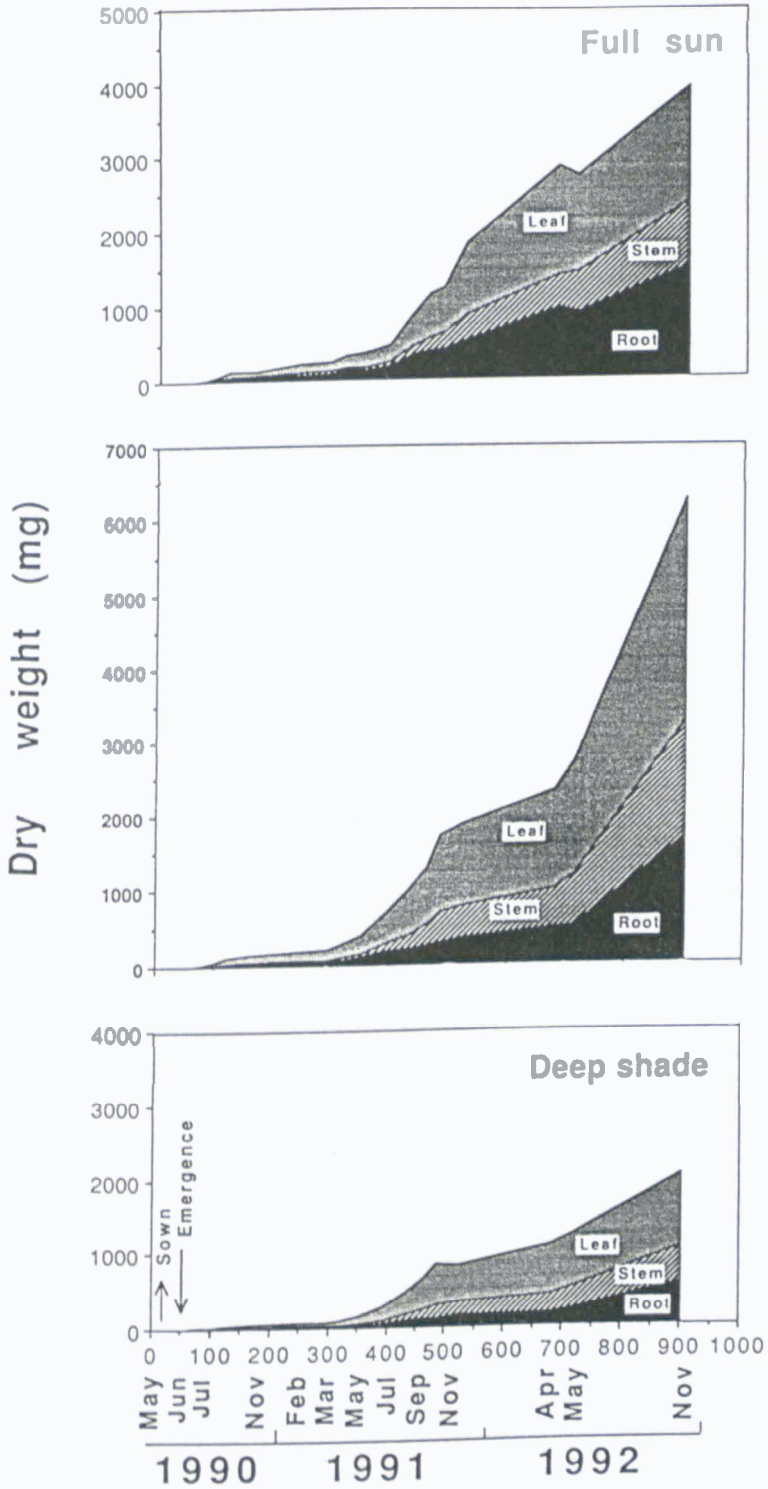


Figure 17. The pattern of dry matter allocation in western redcedar seedlings grown under three shade treatments.

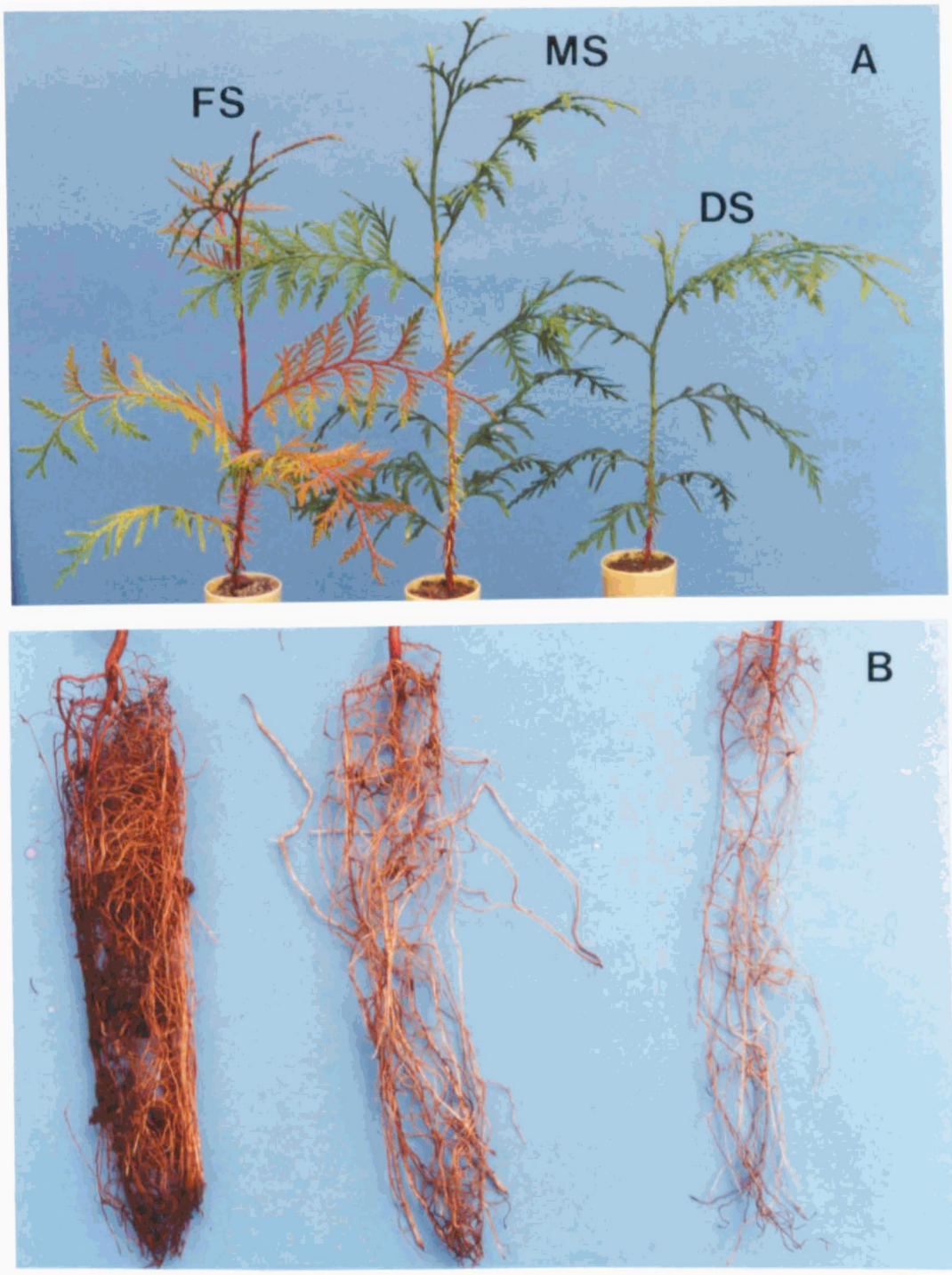


Figure 18. Shoots (A) and roots (B) of 2-year-old (May 1992) western redcedar grown under Full sun, Moderate shade and Deep shade growing conditions.

Derived growth components (R/S ratio, RWR, LWR, SLA, LAR)

Root/shoot (R/S) ratio

Between shade treatments, the first significant differences in R/S ratio occurred in September 1990 when FS seedlings had 45% and 55% higher R/S ratio than MS and DS seedlings respectively. After October 1990, FS seedlings always had a higher R/S ratio compared to MS and DS seedlings for the remaining growth periods (Fig. 19; Appendix I, Table 6 for statistical analysis of each harvest). The mean R/S ratios for 1990 (n=5), 1991 (n=9) and 1992 (n=3), were 0.46, 0.62, 0.54 for FS, 0.31, 0.32 and 0.28 for MS, and 0.25, 0.26, and 0.28 for DS seedlings respectively. Percent differences in R/S ratio between FS, MS and DS seedlings gradually decreased at the end of each year, with the smallest differences occurring in the third year (Table 3).

Root weight ratio (RWR)

RWRs were consistently highest in FS grown seedlings as compared to the MS and DS grown seedlings (Fig. 20; Appendix I, Table 6). At the end of the first year, FS seedlings had significantly higher RWR (34% and 54%) than MS and DS respectively (Table 3). Higher RWR in FS seedlings

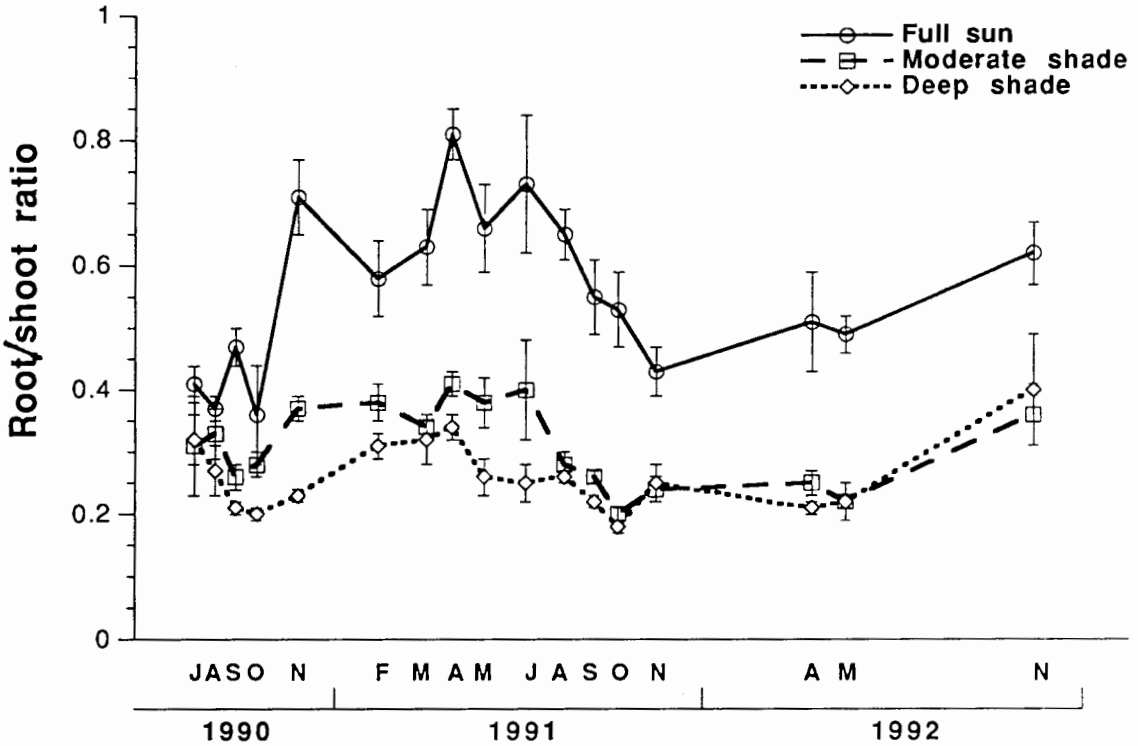


Figure 19. The seasonal course of root/shoot ratio of western redcedar seedlings grown under three shade treatments (mean ± SE, n=5, except November 1991 for FS n=4).

Table 3. Derived growth data for the end of the first (1990), second (1991) and third (1992) year growth periods of western redcedar seedlings grown under three shade treatments (mean ± SE, n=5, except November 1991 for FS (n=4)).

Index of Performance	Treatment / Date	**Full sun**	**Moderate Shade**	**Deep Shade**	% difference from the highest value FS;MS;DS
R/S	*Nov'90*	0.71 ± 0.06a	0.37 ± 0.02b	0.23 ± 0.01c	0; 48; 68
	Nov'91	0.43 ± 0.04a	0.24 ± 0.02b	0.25 ± 0.03b	0; 44; 42
	Nov'92	0.62 ± 0.05a	0.36 ± 0.05b	0.40 ± 0.09b	0; 42; 35
RWR	*Nov'90*	0.41 ± 0.02a	0.27 ± 0.01b	0.19 ± 0.01c	0; 34; 54
	Nov'91	0.30 ± 0.02a	0.19 ± 0.01b	0.20 ± 0.02b	0; 37; 33
	Nov'92	0.38 ± 0.02a	0.26 ± 0.03a	0.29 ± 0.04a	0; 32; 24
LWR	*Nov'90*	0.46 ± 0.01c	0.57 ± 0.02a	0.62 ± 0.01a	26; 8; 0
	Nov'91	0.52 ± 0.02b	0.58 ± 0.01a	0.58 ± 0.01a	10; 0; 0
	Nov'92	0.39 ± 0.01a	0.48 ± 0.02a	0.41 ± 0.04a	19; 0;14
SLA	*Nov'90*	5.19 ± 0.34b	4.56 ± 0.13b	6.65 ± 0.30a	22; 31; 0
	Nov'91	5.20 ± 0.39b	6.48 ± 0.35b	8.89 ± 1.01a	41; 27; 0
	Nov'92	4.63 ± 0.28b	5.14 ± 0.16b	11.62 ± 2.19a	60; 56; 0
LAR	*Nov'90*	2.42 ± 0.14b	2.60 ± 0.11b	4.16 ± 0.16a	42; 38; 0
	Nov'91	2.71 ± 0.15c	3.76 ± 0.18b	5.14 ± 0.56a	47; 27; 0
	Nov'92	1.80 ± 0.09b	2.48 ± 0.13b	4.92 ± 1.12a	63; 50; 0

Table 3. Continued.

Variables	Date	Full sun	Moderate Shade	Deep Shade
NAR*				
	Nov'91	187 ± 6	143 ± 9	112 ± 11
	Nov'92	62 ± 12	76 ± 6	38 ± 7
RGR**				
Shoot	*Nov'90*	257 ± 6a	272 ± 3a	225 ± 4a
	Nov'91	52 ± 1a	50 ± 1a	52 ± 2a
	Nov'92	11 ± 2a	20 ± 1a	14 ± 2a
Root	*Nov'90*	295 ± 5a	280 ± 3a	211 ± 4b
	Nov'91	43 ± 1a	41 ± 2a	53 ± 3a
	Nov'92	18 ± 2a	27 ± 3a	21 ± 3a
Total	*Nov'90*	265 ± 5a	274 ± 3a	222 ± 4a
	Nov'91	49 ± 1a	48 ± 1a	52 ± 2a
	Nov'92	13 ± 2a	21 ± 1a	16 ± 2a

Notes: Means with the same letter are not significantly different between treatment ($\alpha<0.05$, Student-Newman-Keuls test).
RGR was analysed by using the method by Cain & Ormrod (1984).

* Calculated from the base harvest of Nov' 90 for year 2 and Nov' 91 for year 3.
** Mean data (n=5) calculated from the base harvest June'90 for year 1, Nov' 90 for year 2 and Nov' 91 for year 3.

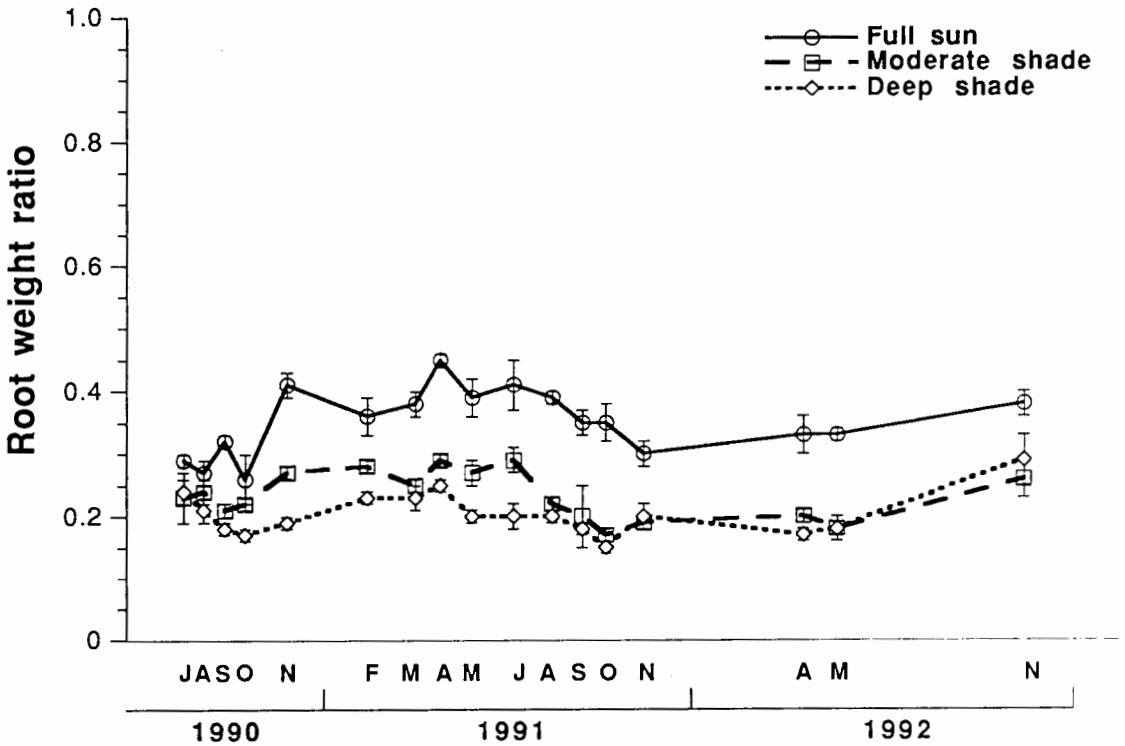


Figure 20. The seasonal course of root weight ratio of western redcedar seedlings grown under three shade treatments (mean ± SE, n=5, except November 1991 for FS n = 4).

than in MS and DS seedlings were maintained throughout the second year until at least the middle of the third year (Appendix I, Table 6). At the end of the second year, FS seedlings had 37% and 33% higher RWR than MS and DS seedlings respectively (Table 3). There was no significant difference in RWR between MS and DS seedlings at the end of the second and third years (Table 3).

Leaf weight ratio (LWR)

Except in July and August 1990, LWR of FS grown seedlings was consistently lower than LWR of both MS and DS seedlings, where DS seedlings were generally the highest (Fig. 21). At the end of the first year, significantly higher LWR ($\alpha<0.05$) was found in both shaded treatments compared to FS seedlings (Table 3). DS seedlings had the highest LWR, 8% and 26% higher than MS and FS respectively (Table 3). In the second year, seedlings from both shade treatments had significantly higher LWR (except for February) than that of FS seedlings, while no significant difference was observed between MS and DS seedlings (Appendix I, Table 6). At the end of the third year, there were no significant differences between the three shade treatments (Table 3).

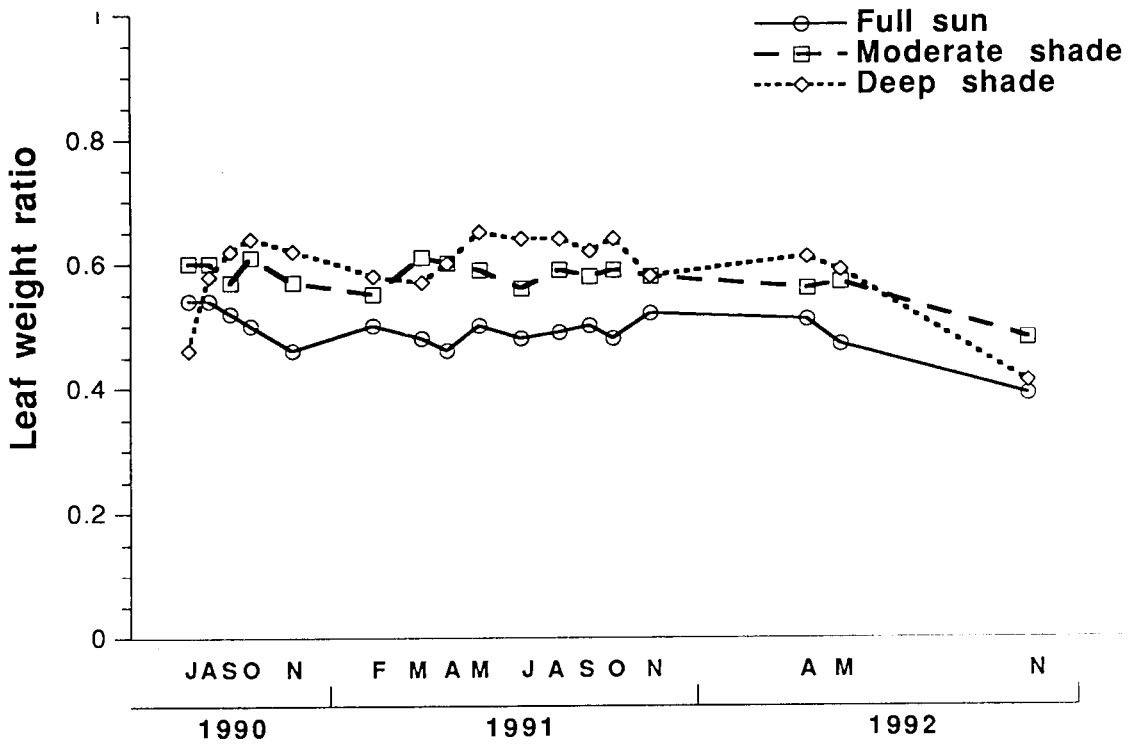


Figure 21. The seasonal course of leaf weight ratio of western redcedar seedlings grown under three shade treatments (mean ± SE, n=5, except November 1991 for FS n=4).

Leaf area ratio (LAR)

Leaf area ratio (LAR), the amount of leaf area per unit total plant dry weight, represents a morphological index of plant leafiness. It is the product of the leaf weight ratio (LWR) and specific leaf area (SLA) (the amount of leaf area per unit leaf dry weight which provides a measure of leaf density or relative thinness) (Hunt, 1990). As is expected from the dry weight and leaf area data (Appendix I, Table 6), shading treatments during growth contributed to higher SLA and LAR in western redcedar seedlings (Fig. 22 and 23).

At the end of the first year, SLA and LAR were in the order of DS>MS>FS where the mean SLA and LAR of DS seedlings were about 31% and 38% higher respectively than that of MS seedlings, and 22% and 42% higher than that of FS seedlings (Table 3). This pattern of higher SLA and LAR in DS seedlings was maintained over 3 years of this research.

At the end of each year, DS grown seedlings had a significantly higher SLA and LAR ($\alpha<0.05$) than MS and FS seedlings. Overall , LAR and SLA parameters of DS grown seedlings were always significantly higher than FS seedlings. Compared to MS seedlings, FS seedlings had lower LAR although the differences were not always significant.

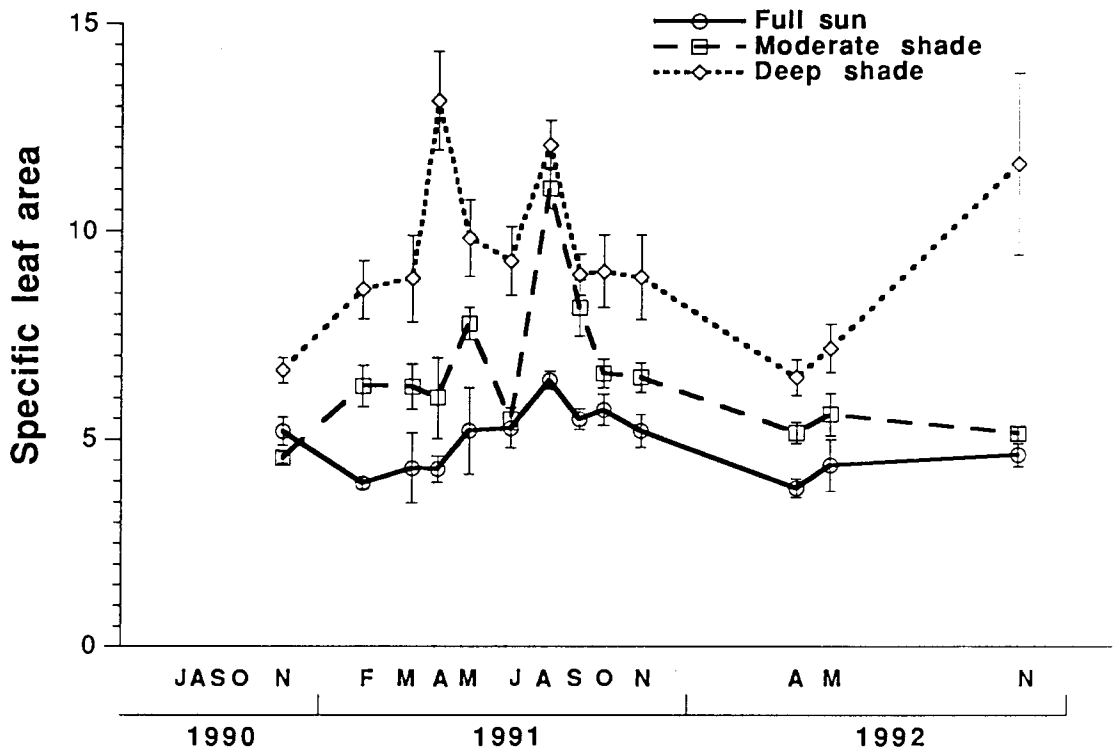


Figure 22. The seasonal course of specific leaf area of western redcedar seedlings grown under three shade treatments (mean ± SE, n=5, except November 1991 for FS n=4).

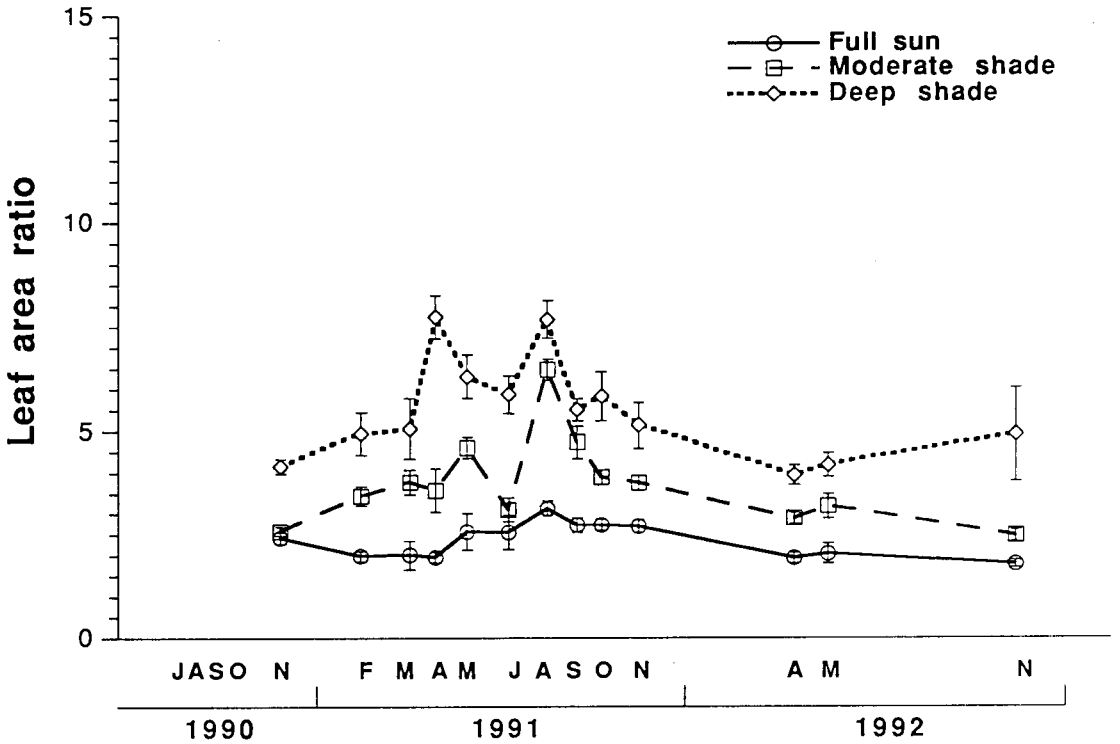


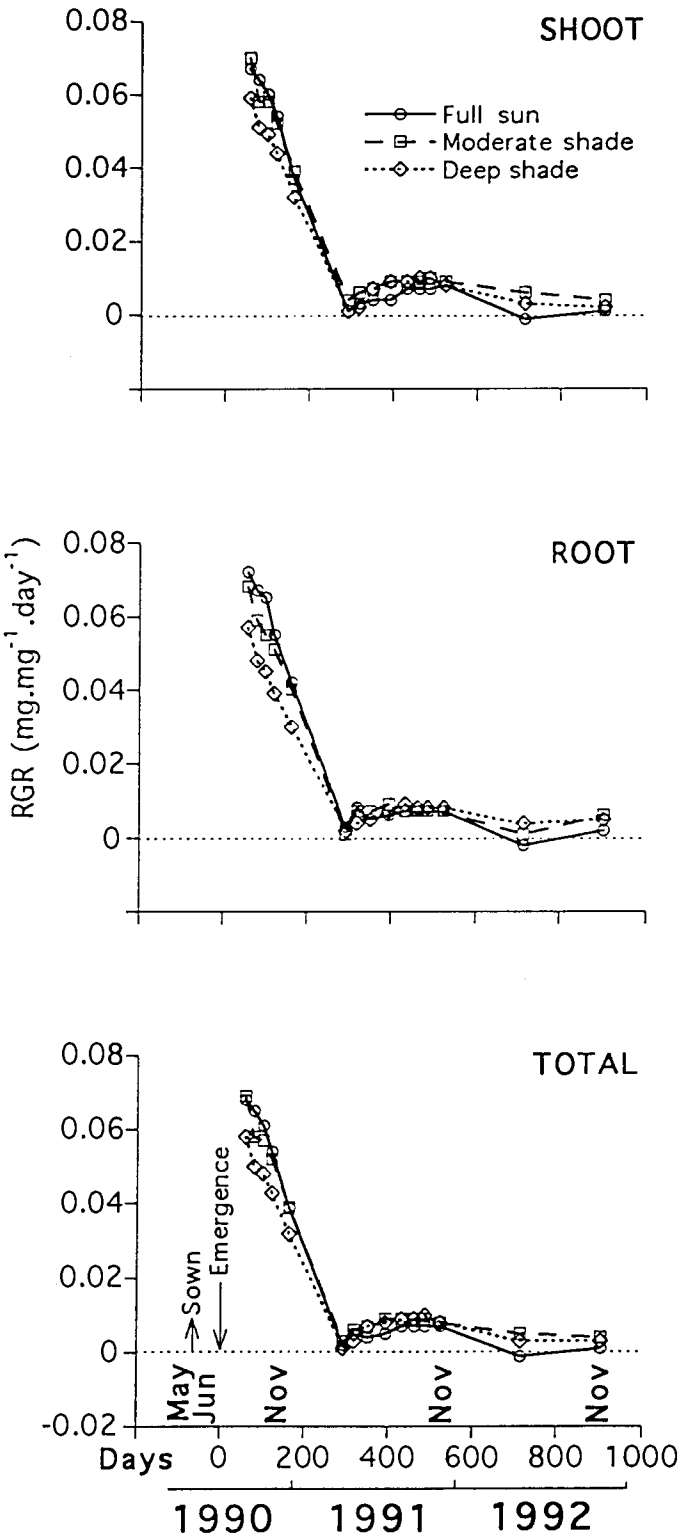
Figure 23. The seasonal course of leaf area ratio of western redcedar seedlings grown under three shade treatments (mean ± SE, n=5, except November 1991 for FS n=4).

Growth analysis parameters (RGR and NAR)

RGR, a measure of the rate at which the existing plant material produces new plant material (*i.e.*, the rate of increase in plant dry weight per unit plant dry weight already produced at the base harvest) was calculated using a base harvest at the end of each year, except for RGR 1990 which used the first harvest (June 1990) as the base harvest.

RGR calculated at the end of each year growth (Table 3, Fig. 24) shows that at the end of the first year, MS seedlings had both higher RGR-shoot and RGR-total, followed by FS and DS seedlings. RGR-root for 1990 was found to be the highest in FS seedlings, followed by MS and DS seedlings (Table 3). In the second year, however, this rank was reversed with DS seedlings having the highest RGR-root and RGR total, followed by FS and MS seedlings. In the third year, MS grown seedlings had higher values of all RGRs (root, shoot and total), followed by DS and FS seedlings (Table 3). Overall, all RGR values from the three treatments

Figure 24. Relative growth rates of root, shoot and total plant of western redcedar seedlings grown under three shade treatments (mean ± SE, n=5). RGR was calculated based on the mean data from the base harvest of June 1990 for year 1, November 1990 for year 2 and November 1991 for year 3.

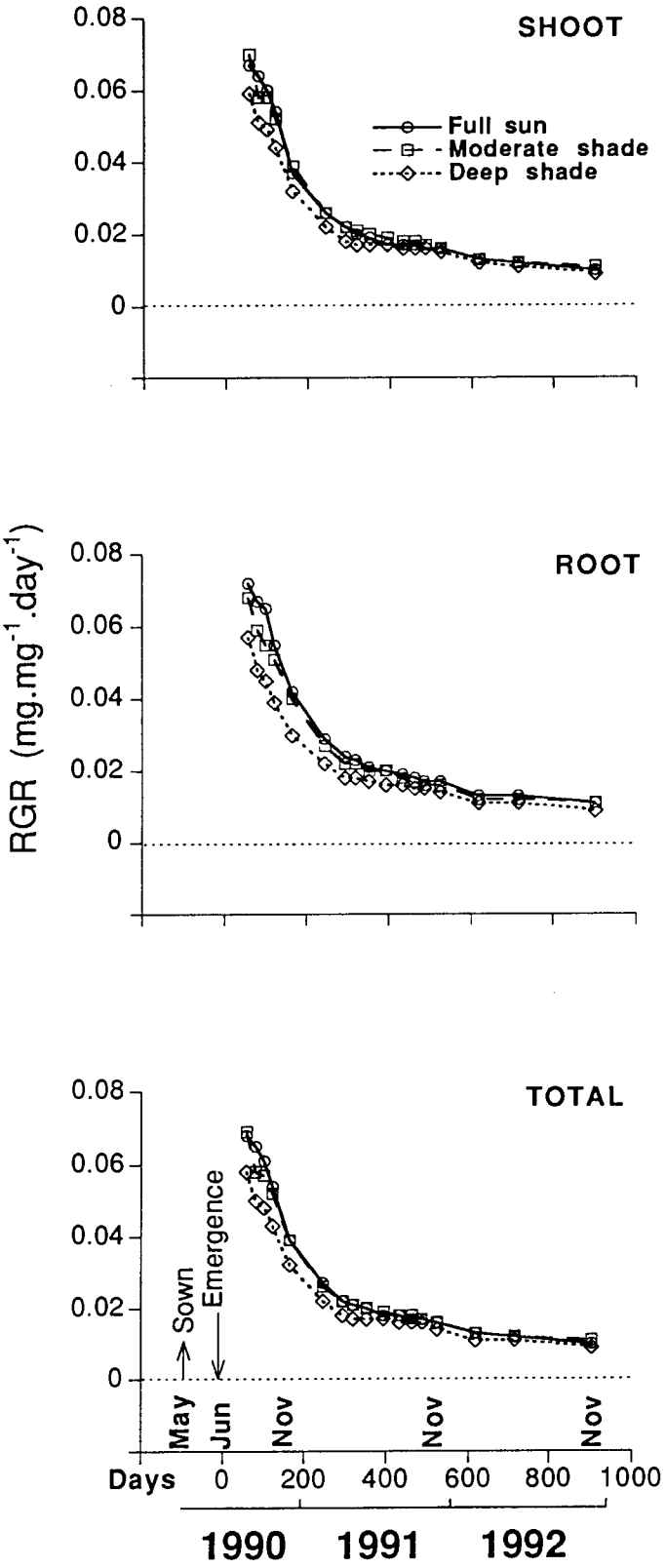

SHOOT
ROOT
TOTAL
Full sun
Moderate shade
Deep shade
RGR (mg.mg-1.day-1)
0.08
0.06
0.04
0.02
0
-0.02
Sown
Emergence
May
Jun
Nov
Nov
Nov
Days
0
200
400
600
800
1000
1990
1991
1992

decreased with each successive year of the experiment, as is normally found for RGR of trees.

Similar results were also found when the calculation of RGR used only the first harvest (June 1990) as the base harvest. Differences in RGR between shade treatments mainly occurred during the first year, these differences then became smaller in the second and third year (Fig. 25; see Appendix I, Table 8).

NAR was only calculated for the second and third year since there were no leaf area data available prior to November 1990. In the second year, FS seedling had the highest NAR (187 $mg.m^{-2}.week^{-1}$) followed by MS (143 $mg.m^{-2}.week^{-1}$) and DS seedlings (112 $mg.m^{-2}.week^{-1}$) (Table 3). This rank changed in the third year with MS having the highest NAR (76 $mg.m^{-2}.\ week^{-1}$) followed by FS and DS, at 62 and 38 $mg.m^{-2}.\ week^{-1}$ respectively.

Figure 25. Relative growth rates of root, shoot and total plant of western redcedar seedlings grown under three shade treatments (mean ± SE, n=5). RGR was calculated based on the mean data from the base harvest of June 1990 for each growth component.


SHOOT
ROOT
TOTAL
Full sun
Moderate shade
Deep shade
RGR (mg.mg-1.day-1)
0.08
0.06
0.04
0.02
0
Sown
Emergence
May
Jun
Nov
Nov
Nov
Days
0
200
400
600
800
1000
1990
1991
1992

Part II. Effect of shade treatments on CO_2 exchange rates and chlorophyll-a fluorescence

CO_2 exchange

Daily maximum and minimum greenhouse temperatures, rates of apparent photosynthesis (sF_o basis) and variable fluorescence of both harvest and repeated measures of western redcedar seedlings (Fig. 26) show changes in these physiological activities as a response to seasonal changes in temperature and the growth of western redcedar seedlings over time. P_N rates declined toward winter, reached its minimum in February 1991 and increased toward summer as temperature increased. The F_{var} fluorescence transients, especially sF_p and sF_t, regardless of the shade treatments, had an almost identical pattern to P_N rates in response to the seasonal temperature changes (Fig. 26).

Strong relationships were found between foliage dry weight (odw) and leaf area, R^2 = 0.99, 0.97, 0.99 for FS, MS and DS grown seedlings respectively (based on mean values) (Fig. 27) and between foliage odw and sF_o (based on mean values), R^2 = 0.97, 0.96, 0.98 for FS, MS and DS grown seedlings respectively (Fig. 28). These relationships, however, were established without the 1992 data, since only

Figure 26. Seasonal changes in rates of apparent photosynthesis (P_N) and in variable fluorescence (sF_{var}) for western redcedar seedlings grown under three shade treatments. (Mean data are shown for P_N and sF_{var}, n=5 except February, n=3 and November for FS n=4). Δ data from the non-destructive samples (repeated measures). Note change in P_N scale between page 87A and 87B.

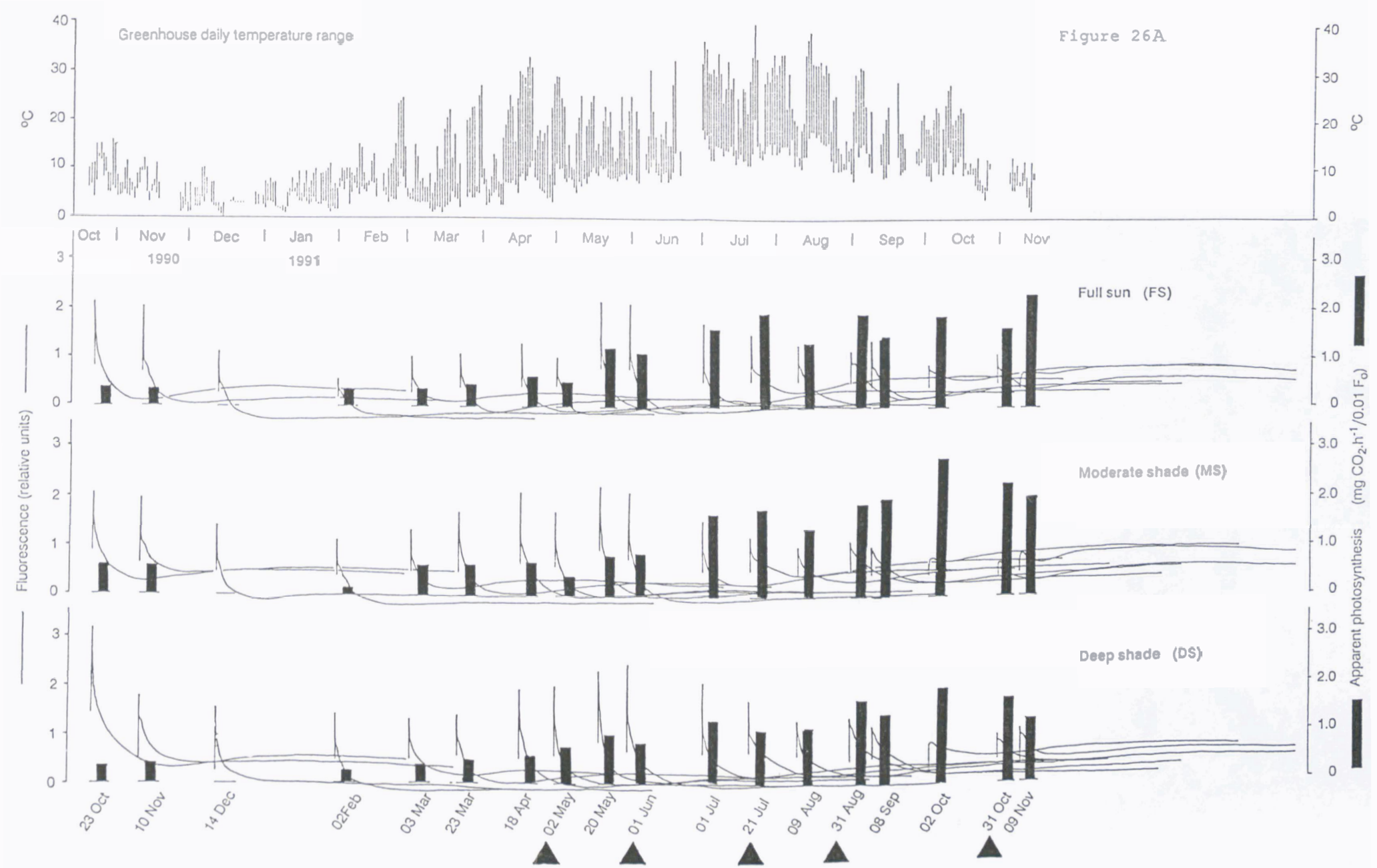
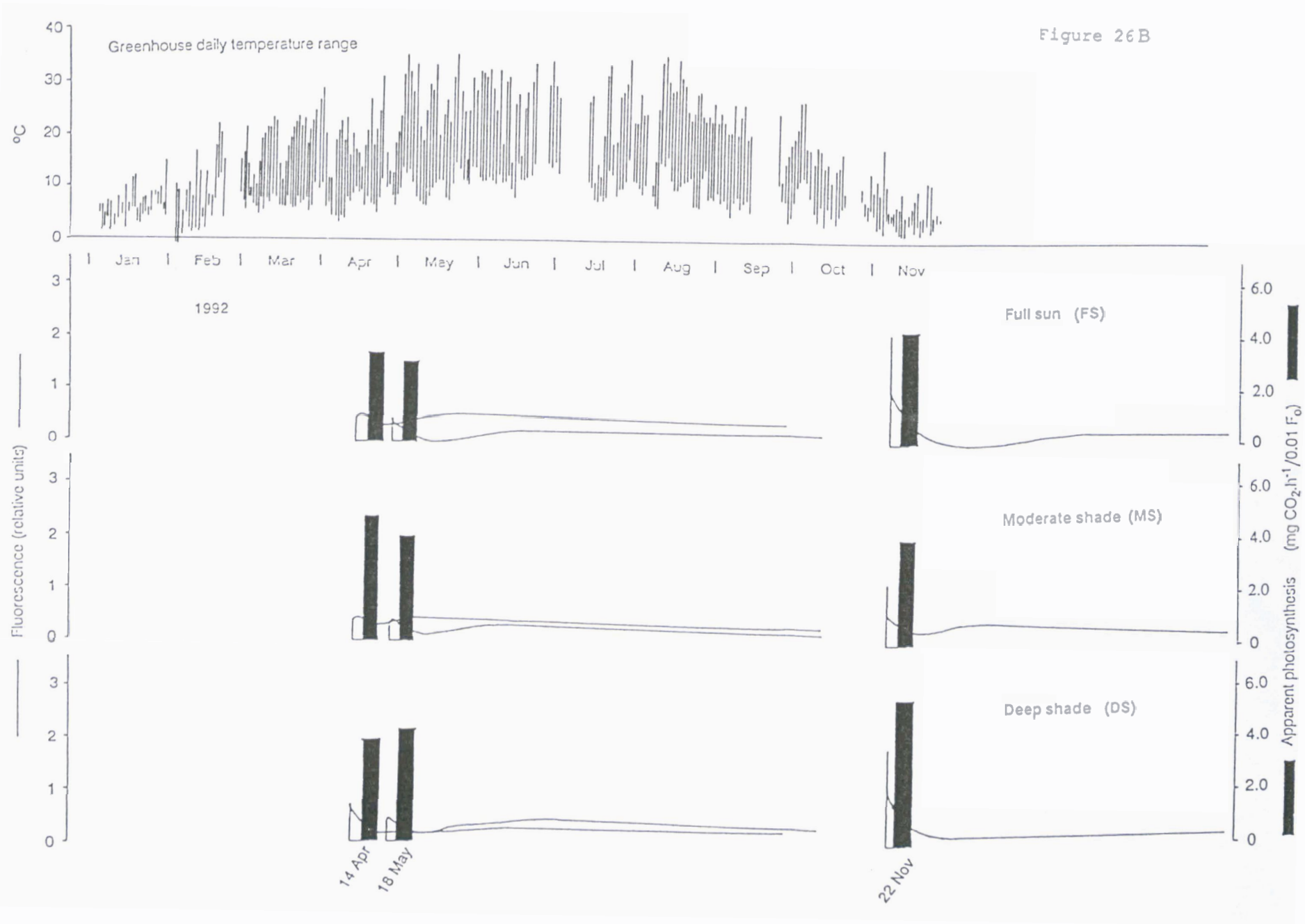


Figure 26A
Greenhouse daily temperature range
°C
Oct
Nov
1990
Dec
Jan
1991
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Full sun (FS)
Moderate shade (MS)
Deep shade (DS)
Fluorescence (relative units)
Apparent photosynthesis (mg $CO_2.h^{-1}/0.01\ F_o$)
23 Oct
10 Nov
14 Dec
02Feb
03 Mar
23 Mar
18 Apr
02 May
20 May
01 Jun
01 Jul
21 Jul
09 Aug
31 Aug
08 Sep
02 Oct
31 Oct
09 Nov

Figure 26B


Greenhouse daily temperature range
°C
40
30
20
10
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
1992
Full sun (FS)
Moderate shade (MS)
Deep shade (DS)
Fluorescence (relative units)
Apparent photosynthesis (mg $CO_2.h^{-1}/0.01\ F_o$)
14 Apr
18 May
22 Nov

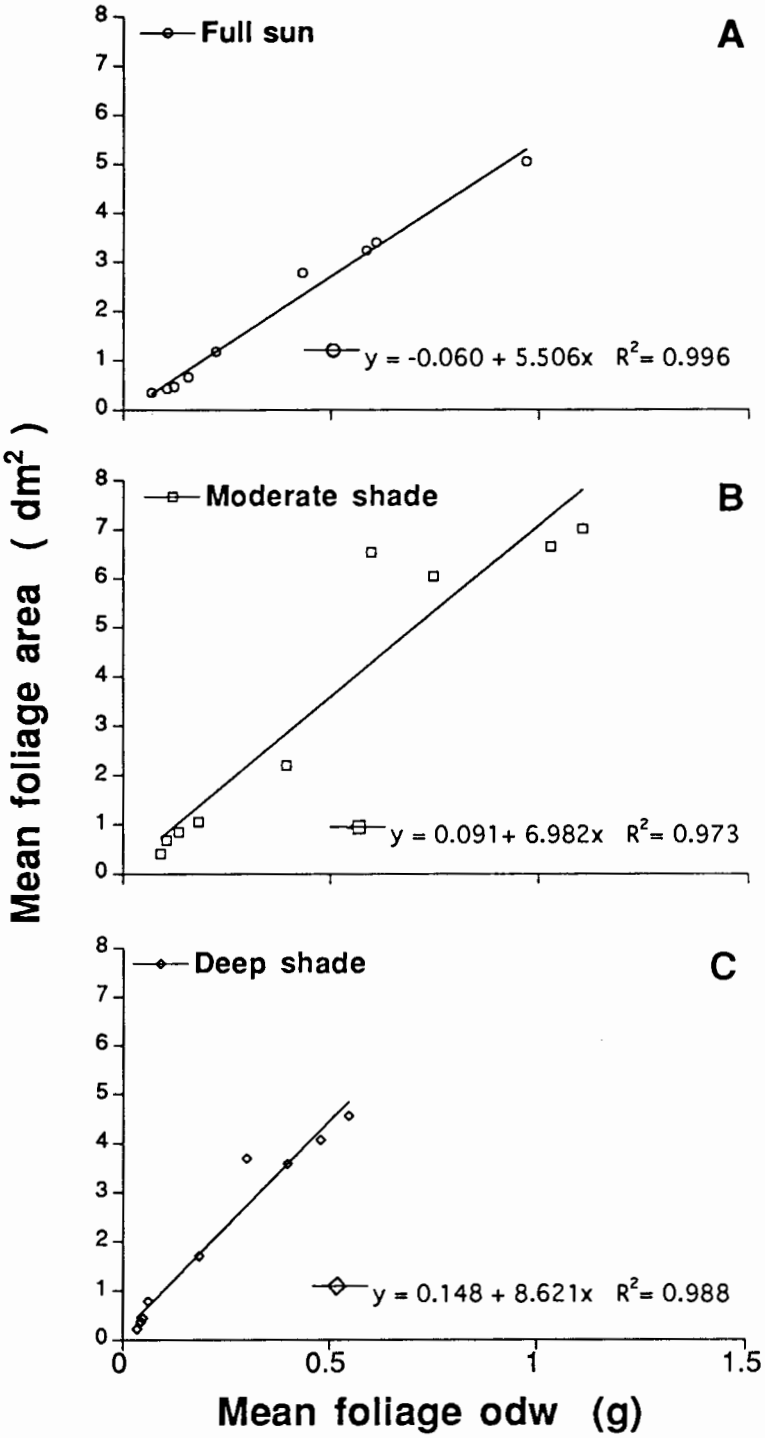


Figure 27. Relationship between foliage odw and leaf area of western redcedar seedlings growing under (**A**) Full sun, (**B**) Moderate shade and (**C**) Deep shade treatments. (n=5).

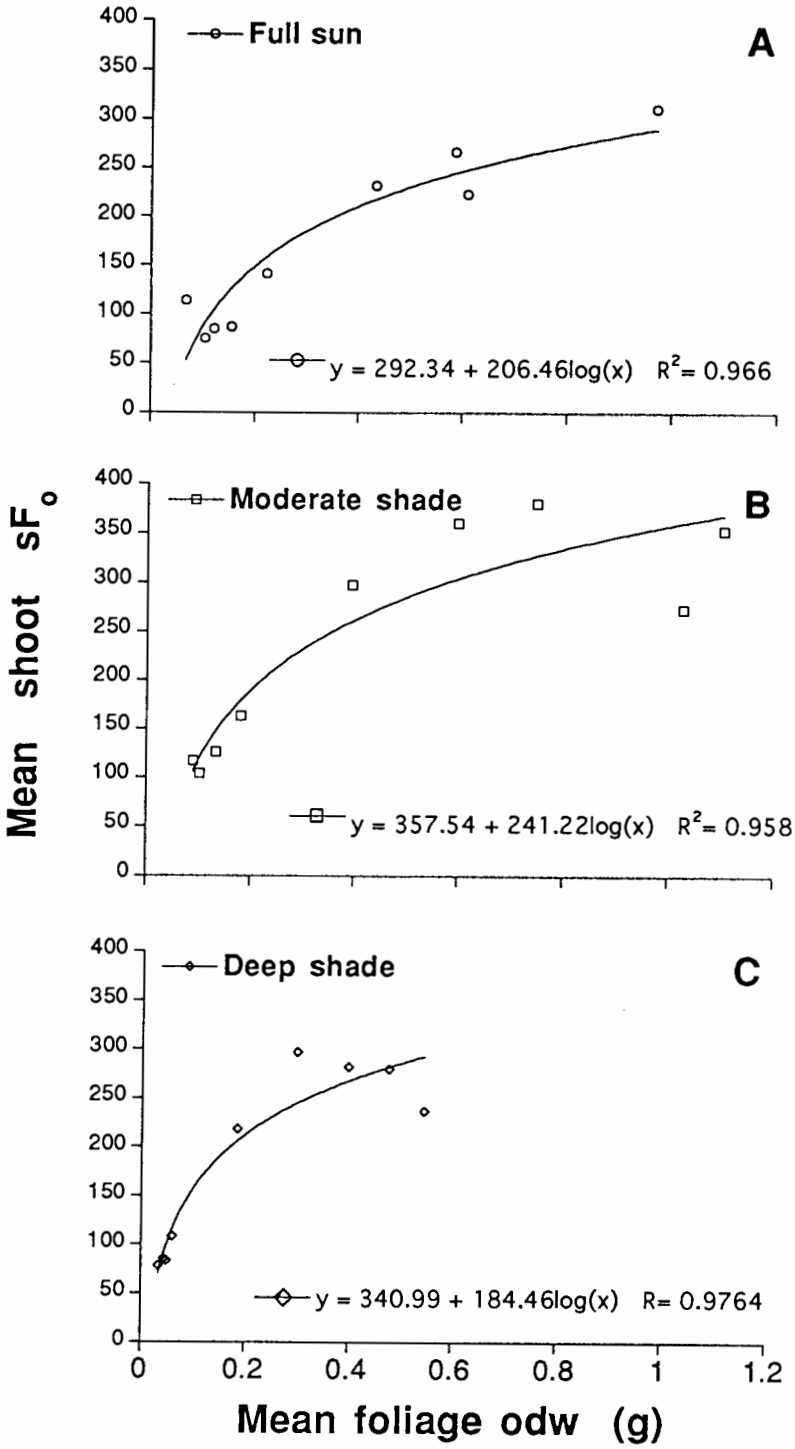


Figure 28. Relationship between foliage odw and sF_o of western redcedar seedlings growing under: (A) Full sun, (B) Moderate shade, and (C) Deep shade. (n=5).

about 2/3 of the entire shoot fit in the cuvette for CO_2 measurements especially for MS grown seedlings.

P_N (odw basis) rates decreased significantly ($\alpha<0.05$) regardless of the shade treatments in winter (1990-1991), (see Appendix II, Table 1, for statistics on seasonal differences), and reached their minima in February. Photosynthetic rates then significantly increased to maxima in July before they again decreased in winter 1991-1992 toward the following spring.

A similar seasonal pattern to that of odw basis was also found when P_N was expressed per unit leaf area, except in August and November 1991 where FS seedlings had an increase in P_N rates while MS and DS decreased.

P_N rates (sF_O basis) (Fig. 26A&B) also decreased from October 1990 to the lowest value in February 1991 for all shade treatments. From February 1991, the P_N rates increased to the first peak in July 1991 as a mid-growing season maximum. There was a decrease in P_N rates in August for all shade treatments due probably to drought stress in July (see Fig. 26A and also Fig. 11 for ambient temperature differences between treatments), then increased again in October 1991 after which both shaded seedlings declined in P_N, but FS seedlings did not (Fig. 26A).

Due to different software and equipment used between the measurement of chlorophyll fluorescence in 1991 and in

1992, and the large size of seedlings in which entire shoots no longer fit the cuvette, the 1992 data will not be discussed in great detail.

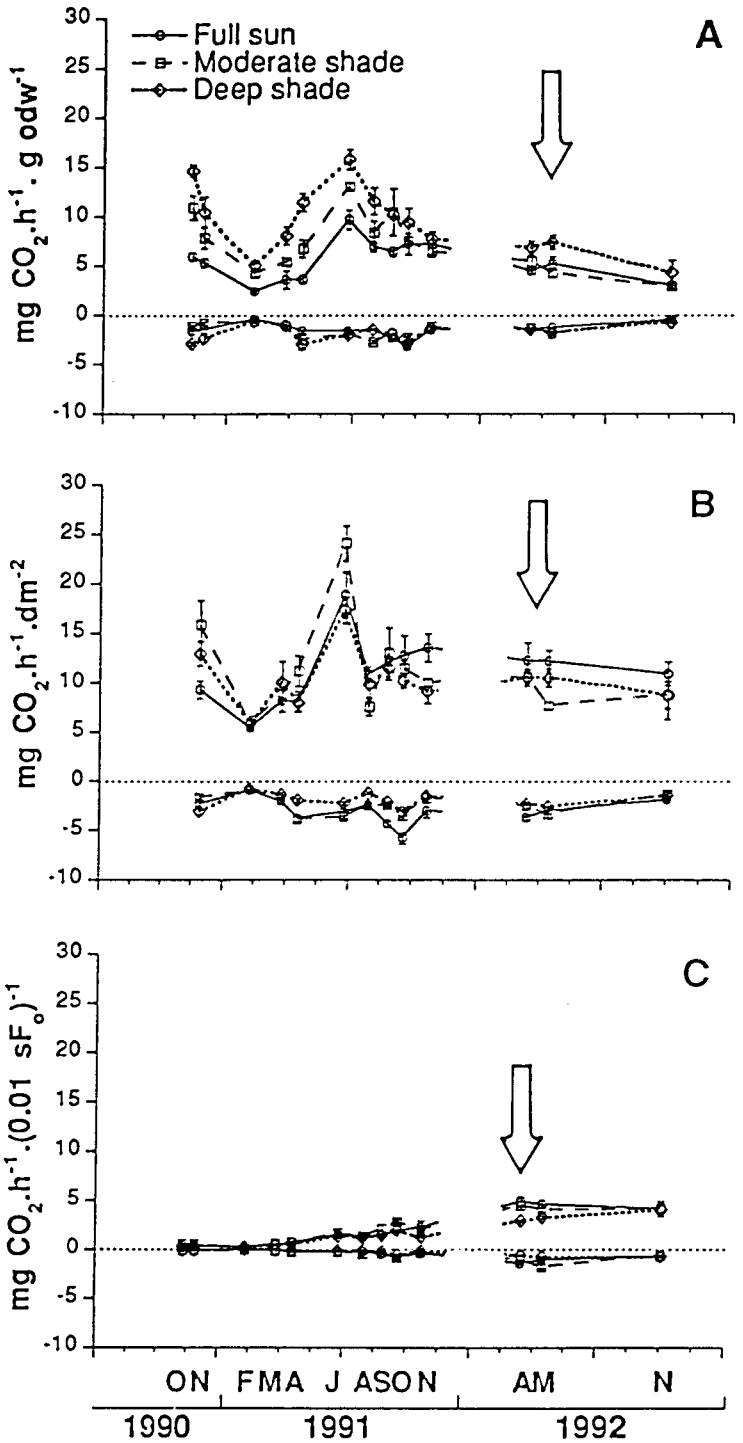
FS seedlings had significantly lower P_N (odw basis) than DS grown seedlings from October 1990 to August 1991 (Fig. 29A; Appendix II, Table 1). During this period, the P_N rates were highest for DS seedlings and lowest for FS seedlings. From October 1991 to November 1992, highest P_N rates were maintained by DS seedlings with rates for MS and FS seedlings being quite similar. P_N rates for DS grown seedlings were significantly higher than those for FS seedlings in April and May 1992 (Fig. 29A).

When expressed per unit leaf area (Fig. 29B), P_N rates were highest in MS, between November 1990 to July 1991. Different order was found from October to November 1991, with FS seedlings having the highest P_N, followed by MS and DS (Appendix II, Table 1).

P_N (sF_O basis) of MS seedlings generally had the highest P_N rates (significantly higher in October 1990, September and October 1991) and DS seedlings had generally lowest rates (Fig. 29C).

Unlike P_N, R_D rates showed much less fluctuation compared to P_N rates. R_D (odw basis) of all shade treatments decreased from October/November 1990 to a minimum

Figure 29. Net photosynthesis (P_N) and dark respiration (R_D) rates of western redcedar seedlings expressed per (**A**) mg leaf odw, (**B**) leaf area, and (**C**) 0.01 sF_o basis. (Mean ± SE, n=5 except February n=3, and November 1991 for FS n=4). For statistical analyses see Appendix II, Table 1. Arrow (⇓) indicates that only part of seedling shoot was measured in 1992 because of seedling size.


A
Full sun
Moderate shade
Deep shade
mg $CO_2.h^{-1}$. g odw^{-1}
B
mg $CO_2.h^{-1}.dm^{-2}$
C
mg $CO_2.h^{-1}.(0.01\ sF_o)^{-1}$
30
25
20
15
10
5
0
-5
-10
ON FMA J ASON AM N
1990 1991 1992

in February, then increased to a first maximum in April 1991 and a second maximum in October 1991 before declining in November 1991 (Fig. 29A). A similar pattern was found in R_D expressed on a leaf area basis (Fig. 29B).

R_D rates (sF_o basis) had a mirror-image pattern to the P_N rates (Fig. 29C). For all shade treatments, R_D decreased from October 1990 to February 1991, then increased to a first maximum in April 1991, and reached a second maximum in October 1991 (Fig. 29; Appendix II, Table 1).

No consistent pattern in treatment effects on R_D (sF_o basis) from October 1990 to March 1991 was observed. R_D rates were significantly higher in FS than in DS grown seedlings from August 1991 to May 1992. Between shade treatments, FS generally had highest R_D rates, and DS lowest rates in 1991 (Fig. 29C).

Measurements of P_N and F_{var} fluorescence of the same seedlings (repeated measurements over time) (Table 4) had a very similar pattern to seedlings destructively sampled for the harvest data (Appendix II, Table 1). As in the harvest data, the P_N and R_D rates significantly increased ($\alpha<0.05$) during the summer (May to September), with the first marked increase in July, then they continually increased to reach their maxima in late September. In July, P_N and R_D rates were significantly different between the three treatments,

Table 4. CO_2 exchange rate (sF_o basis) measured during the 1991 growing season from the same seedlings of western redcedar grown under three shade treatments (mean ± SE, n=5).

DATE	Shade Treatment		
	Full sun [100%]	Moderate shade [49%]	Deep shade [27%]
Photosynthetic rate (sFo basis)			
1991			
2-May	0.85 ± 0.07 a	0.78 ± 0.10 a	0.66 ± 0.05 a
1-Jun	1.10 ± 0.03 a	0.89 ± 0.09 a	0.78 ± 0.12 b
21-Jul	1.91 ± 0.07 a	1.74 ± 0.08 a	1.11 ± 0.14 b
31-Aug	1.91 ± 0.07 a	1.36 ± 0.10 b	1.44 ± 0.17 b
30-Sep	2.73 ± 0.44 a	2.83 ± 0.28 a	2.34 ± 0.22 a
31-Oct	1.40 ± 0.15 a	2.26 ± 0.26 a	1.71 ± 0.08 a
Dark respiration (sFo basis)			
1991			
2-May	0.44 ± 0.02 a	0.40 ± 0.04 a	0.25 ± 0.01 b
1-Jun	0.37 ± 0.05 a	0.28 ± 0.03 ab	0.20 ± 0.04 b
21-Jul	0.51 ± 0.04 a	0.31 ± 0.02 b	0.17 ± 0.01 c
31-Aug	0.32 ± 0.03 a	0.18 ± 0.01 b	0.13 ± 0.01 b
30-Sep	0.69 ± 0.08 a	0.44 ± 0.05 b	0.38 ± 0.03 b
31-Oct	0.33 ± 0.04 a	0.34 ± 0.06 a	0.25 ± 0.03 a

Means with the same letter are not significantly different between treatments for a particular date ($\alpha<0.05$, Student-Newman-Keuls test).

with FS grown seedlings having the highest P_N and R_D rates (1.91 and 0.51 mg.CO_2.h^{-1}.0.01 sF_o^{-1}), followed by MS (1.74 and 0.31 mg.CO_2.h^{-1}.0.01 sF_o^{-1}) and DS seedlings (1.11 and 0.17 mg.CO_2.h^{-1}.0.01 sF_o^{-1}). In September, seedlings from all treatments experienced maximum P_N and R_D rates, however there were no significant differences in P_N rates. R_D values were significantly different between FS seedlings and both MS and DS grown seedlings ($\alpha<0.05$) (Table 4). These variables declined in October, and started to increase again in April for the next growing season.

P_N/R_D ratios showed very similar seasonal patterns regardless of the unit in which CO_2 exchange was expressed, *i.e.*, leaf odw, leaf area, and sF_o (Fig. 30 and 31). This, in fact, shows that sF_o as well as leaf area and dry weight can be useful measures for the expression of CO_2 exchange.

Changes in P_N/R_D ratio generally corresponded to changes in seasonal variation of photosynthesis (Fig. 32) in FS and MS grown seedlings. But the ratio in DS seedlings more closely follows the R_D rate. MS seedlings also experienced decrease in P_N rates in February. However, a much higher P_N rate compared to R_D in November and October 1990 resulted in a decline in P_N/R_D ratio in MS grown seedlings. P_N/R_D ratios then increased as P_N rates increased in the summer and reached maximum in July 1991 for FS and MS, and August 1991 for DS grown seedlings (Fig. 32).

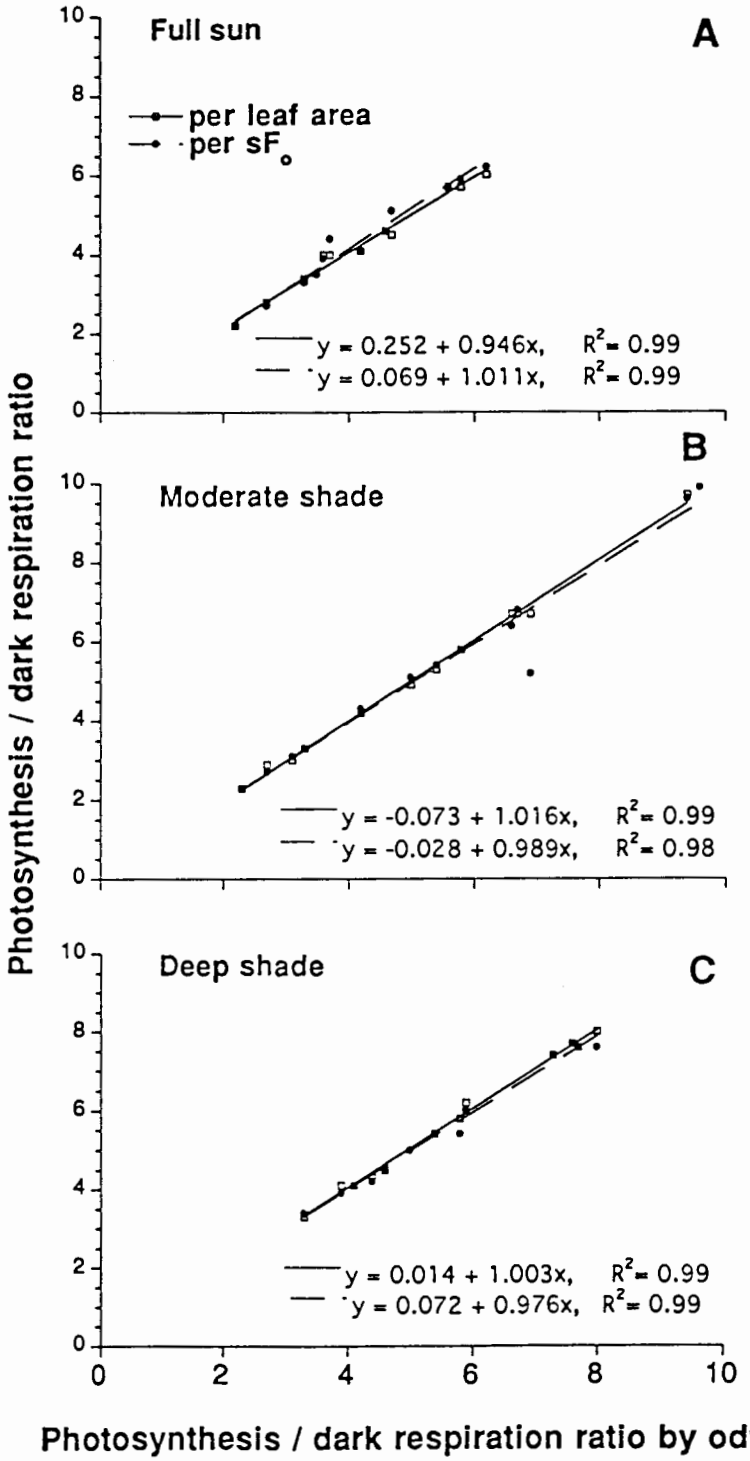


Figure 30. Relationship between P_N/R_D ratio expressed per g leaf odw basis *vs* leaf area and sF_O basis of western redcedar seedlings grown under three shade treatments (n=5).

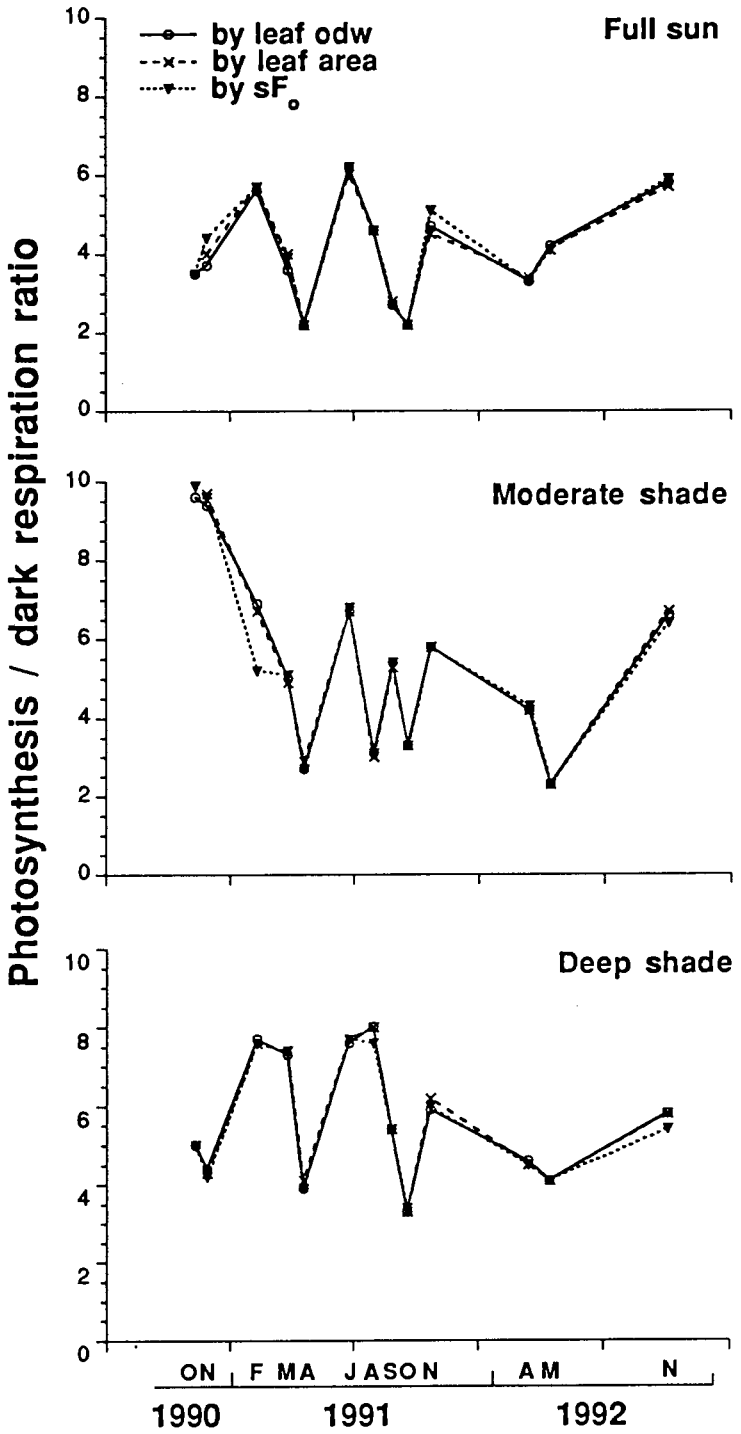


Figure 31. Ratio of photosynthesis and dark respiration of western redcedar seedlings expressed per g leaf odw, leaf area (dm^2) and sF_o. (Mean, n=5 except February n=3, and November 1991 for FS n=4).

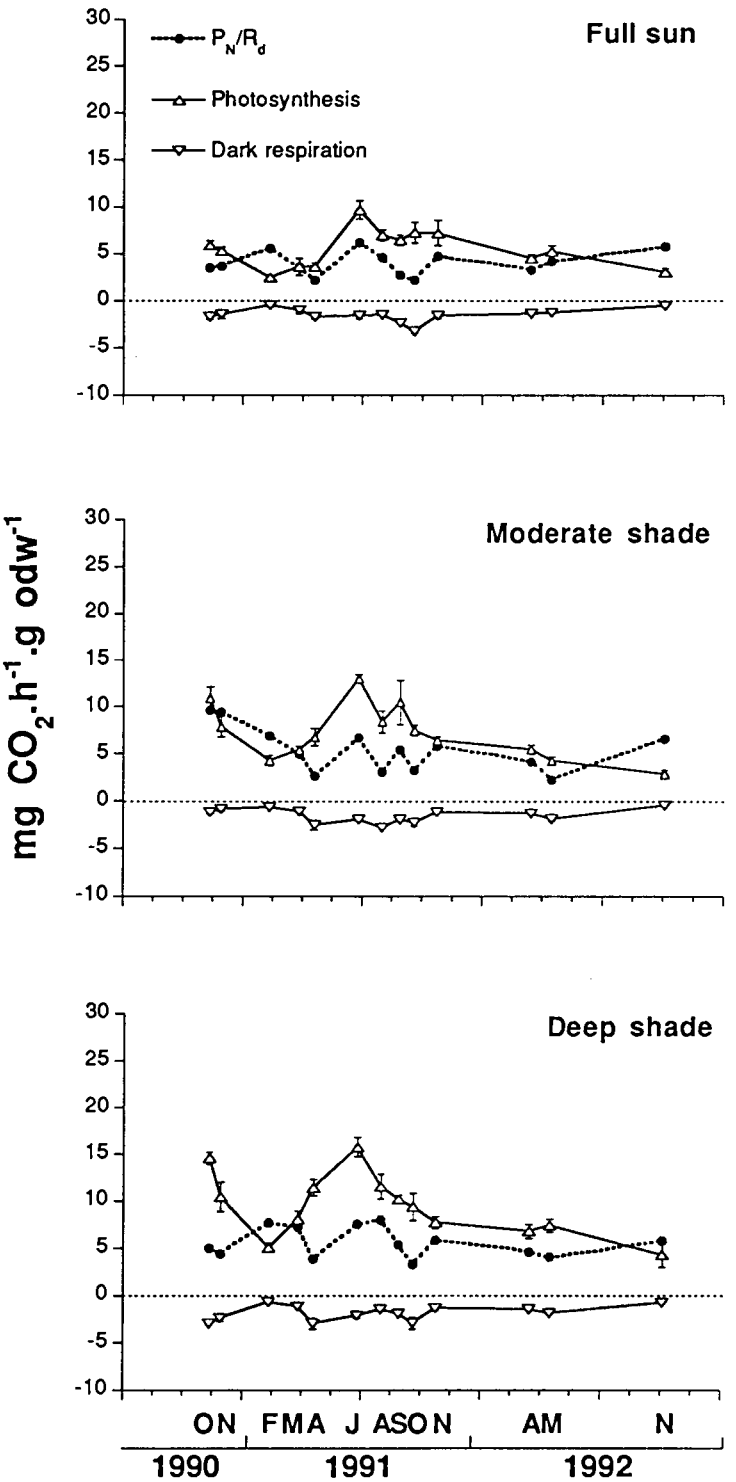


Figure 32. Seasonal changes in P_N/R_D ratios following seasonal variation in photosynthesis and dark respiration. (Mean ± SE, n=5 except February n=3, and November 1991 for FS n=4).

Different light growing environments induced different physiological responses to the seasonal changes. Shade grown seedlings (MS and DS) responded earlier than FS seedlings to shortening day length and temperature changes as winter approached. It was found that only a 10% reduction in P_N rate (odw basis) occurred in FS seedlings from October to November 1990, while a 28% decline occurred in both MS and DS seedlings (Appendix II, Table 1). These rates then significantly ($\alpha<0.05$) decreased in all treatments from November 1990 to February 1991 with FS having the highest decline, and DS seedlings the lowest. A similar decline occurred from October to November 1991, where P_N rates decreased about 13% and 18% (MS and DS seedlings respectively), but only about 0.4% for FS seedlings. P_N rates (leaf area basis) had a similar pattern. The rates of MS and DS seedlings declined as much as 12% and 10% respectively, while FS seedlings had 6% increase from October to November 1991. The generally smaller decrease in P_N rate (leaf area and odw basis) in November 1991 may indicate that FS seedlings had experienced a slightly longer growing season than for seedlings that were shaded.

In February 1991, the highest percent reduction in P_N rate as well as the lowest P_N rates (both odw and leaf area basis) was found in FS grown seedlings (Appendix II, Table

1). This coincided with "the high light-low temperature" stress experienced by FS seedlings which started early in January 1991 and induced changes in the color of the upper leaves of FS seedlings. The low rate of CO_2 exchange in FS seedlings in February might be an indication that these seedlings, as compared to MS and DS seedlings, experienced a deeper inactivation of physiological activity during winter.

Similar to P_N rates, R_D rates (odw basis) also decreased from October to November 1990, with the largest decline occurring in MS seedlings (28%), followed by DS and FS seedlings (18% and 14% respectively) (Fig. 29A; see Appendix II, Table 1).

Chlorophyll-a fluorescence

The initial fluorescence, sF_o, significantly increased from November 1990 to September 1991 in all three treatments (Fig. 33 A; Appendix II, Table 2). The highest sF_o occurred at different times in 1991 dependent on the shade treatment. DS seedlings were the earliest (August), followed by MS (September) and FS (November 1991).

Overall, MS seedlings had consistently higher sF_o's than FS and DS seedlings in 1990 and 1991 (Fig. 33A; Appendix II, Table 2). Except for November 1990, this difference was significant ($\alpha<0.05$).

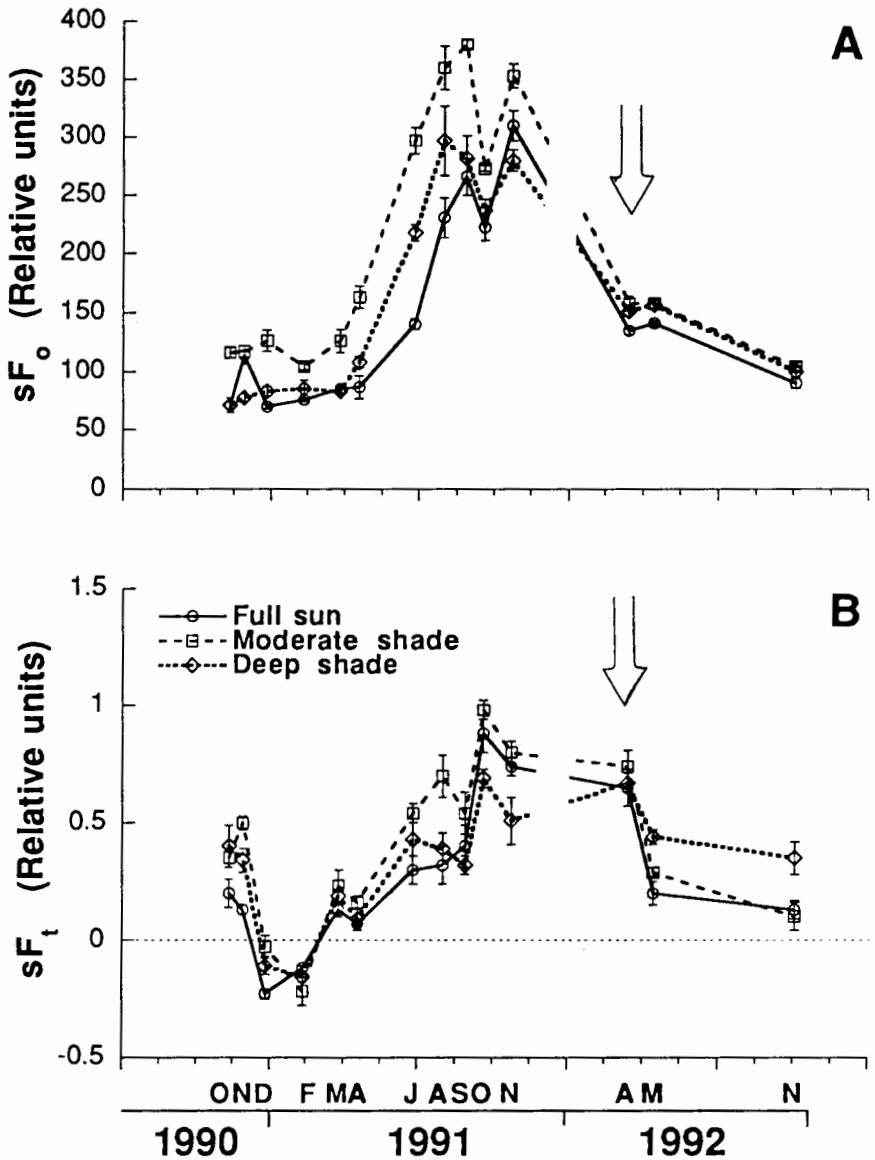


Figure 33. Seasonal changes in components of variable chlorophyll fluorescence: (A) sF_o, and (B) sF_t of western redcedar grown under three shade treatments. Arrow (⇓) indicates that only the top part of the seedling shoot was measured because of seedling size.

A different fluorometer and software were used for the 1992 data. In addition, the entire shoots of the seedlings could not be measured due to their size . These factors may account for the lower sF_o's and decrease measured from April to November 1992 (Fig. 33A).

Steady state fluorescence, sF_t, of seedlings from the three shade treatments decreased significantly ($\alpha<0.05$) from October to December 1990 (Fig. 33B; Appendix II, Table 2), and significantly increased from February 1991 to October 1991. In December 1990, FS seedlings had a significantly lower sF_t than either the MS or DS seedlings. The lowest sF_t occurred in February 1991 and was found in MS (-0.22), followed by DS (-0.16) and FS (-0.12). Differences in sF_t between the three shade treatments in February were not significant (Appendix II, Table 2). Highest sF_t from October 1990 to November 1991 was measured from seedlings grown in moderate shade although they were not always significantly higher than seedlings grown in FS and DS treatments. The sF_t of all treatments declined after October in both 1990 and 1991 (Fig. 33B).

P_N data expressed per sF_o basis (1991 data only) also had a strong relationship with sF_t (R^2 = 0.83 for mean values from the three shade treatments) (Fig. 34). Thus, this component of F_{var} fluorescence may be useful in predicting the P_N rates of western redcedar seedlings.

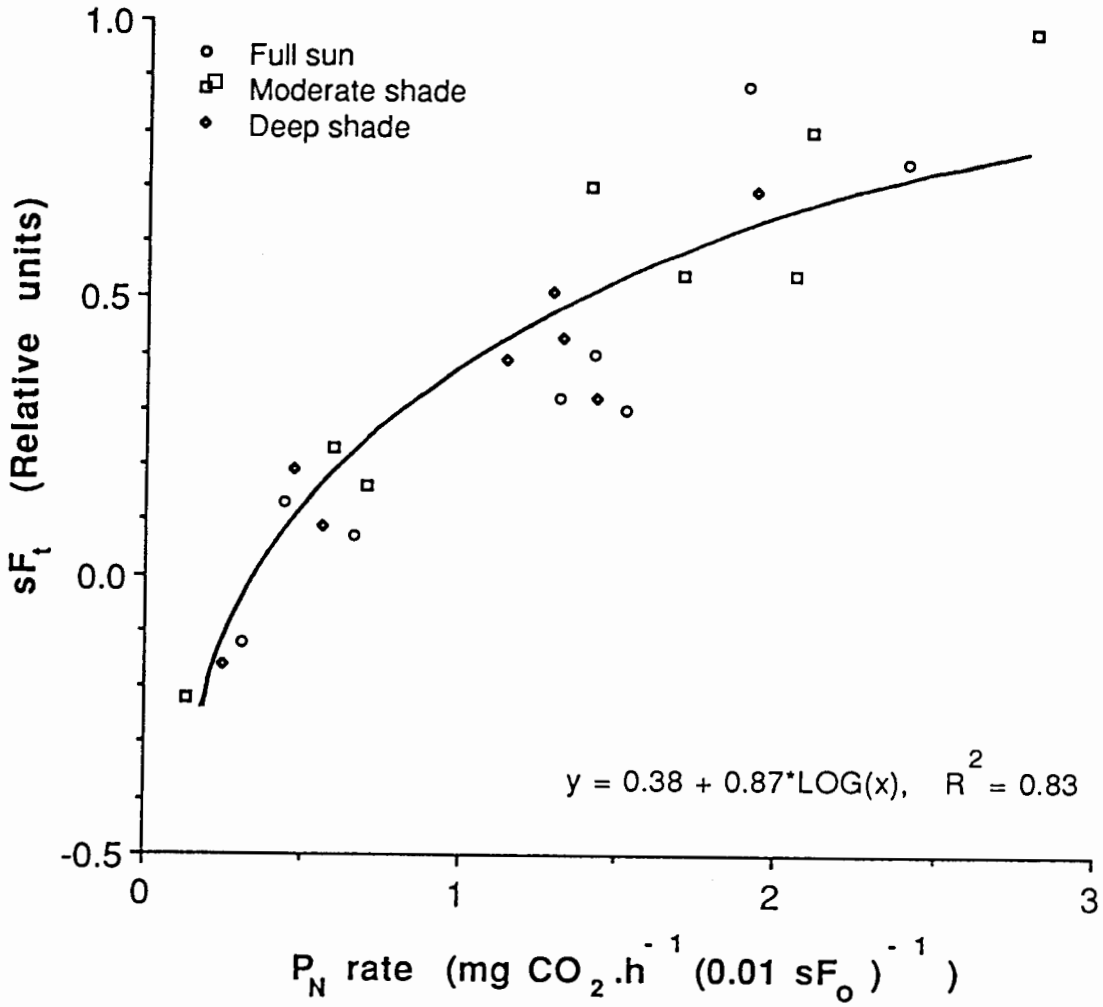


Figure 34. Relationship between P_N rates (sF_o basis) and the steady state fluorescence (sF_t), based on 1990 and 1991 data only. Mean values, (n=5) except February n=3, and November 1991 for FS n=4.

The ratio of variable to maximum chlorophyll fluorescence, sF_v/F_m, also decreased from November 1990 to February 1991 for all treatments (Fig. 35A; see Appendix II Table 2). Except for the period December 1990 to April 1991 inclusive when FS grown seedlings had lower sF_v/F_m ratios than either MS or DS seedlings, there was no consistent difference in the ratios between the shade treatments.

Fluorescence quenching, $sF_{(p-t)}$, of FS and MS seedlings decreased significantly ($\alpha<0.05$) from November 1990 to February 1991 (Fig. 35B; Appendix II, Table 2). For this period, the largest decline was found in FS seedlings (57%), followed by MS (23%) and DS (2%). The lowest $sF_{(p-t)}$, as for the sF_v/F_m ratio, occurred in October 1991 for MS and DS grown seedlings, and November for FS seedlings. Differences in $sF_{(p-t)}$ between treatments were generally not significant (Fig. 35B; Appendix II, Table 2).

Response of leaf photosynthesis to changes in PFD

Light response curves were measured several times at different seedling age *i.e.*, 1-year-old (14 May and 13 July 1991), and 2-year-old (20 August 1992) (Appendix II, Table 3-5). The light intensity at which photosynthesis becomes saturated was lower in shade treated seedlings compared to FS grown seedlings (Fig. 36). DS seedlings become light

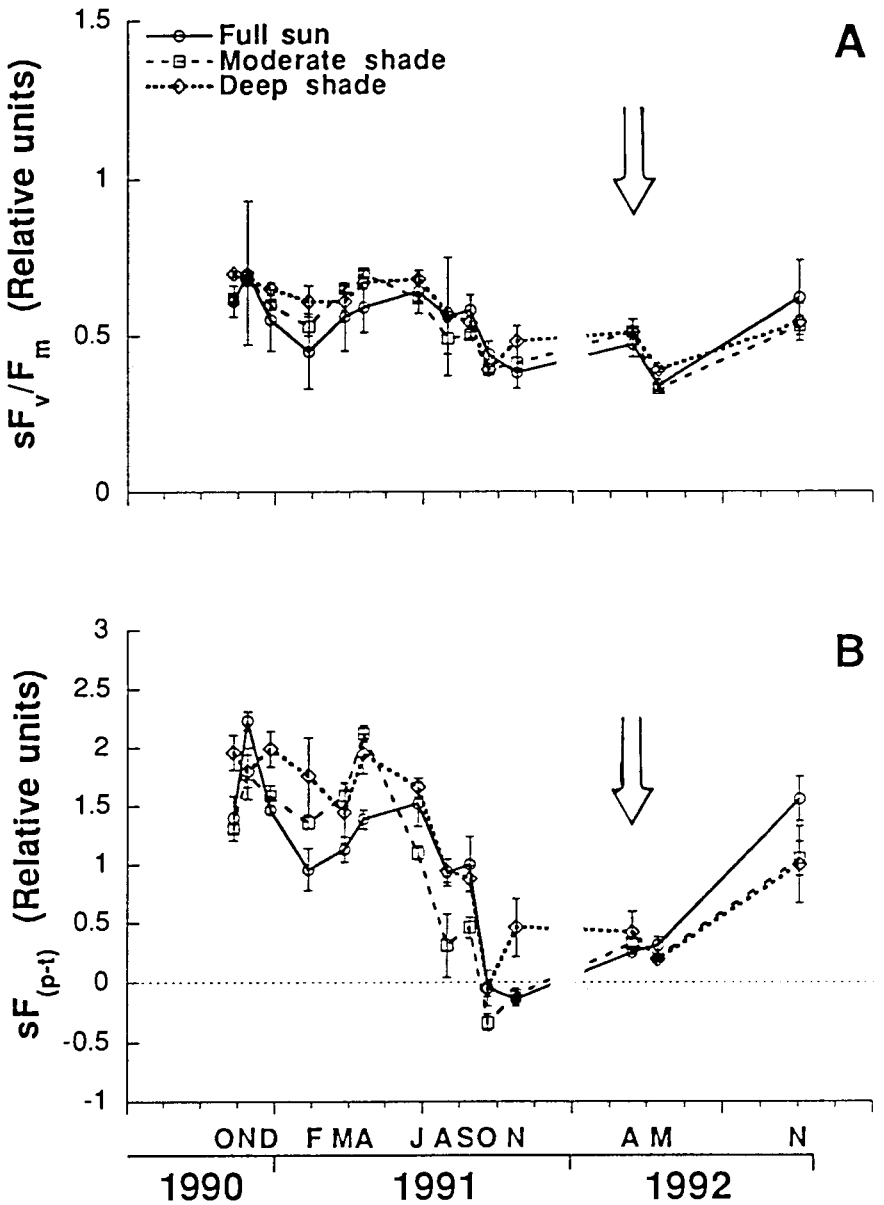


Figure 35. Seasonal changes in components of variable chlorophyll fluorescence (A) sF_v/F_m, and (B) $sF_{(p-t)}$ for western redcedar seedlings grown under three shade treatments (mean ± SE, n=5, except February n=3, and November 1991 for FS n=4). Arrow (⇓) indicates that only the top part of seedling shoot was measured in 1992 because of seedling size.

saturated at about 500 to 600 $\mu mol.m^{-2}.s^{-1}$ PFD and, MS at about 800 to 1000 $\mu mol.m^{-2}.s^{-1}$, whereas FS seedlings had not reached a light saturated state at 1500 $\mu mol.m^{-2}.s^{-1}$ (Fig. 36).

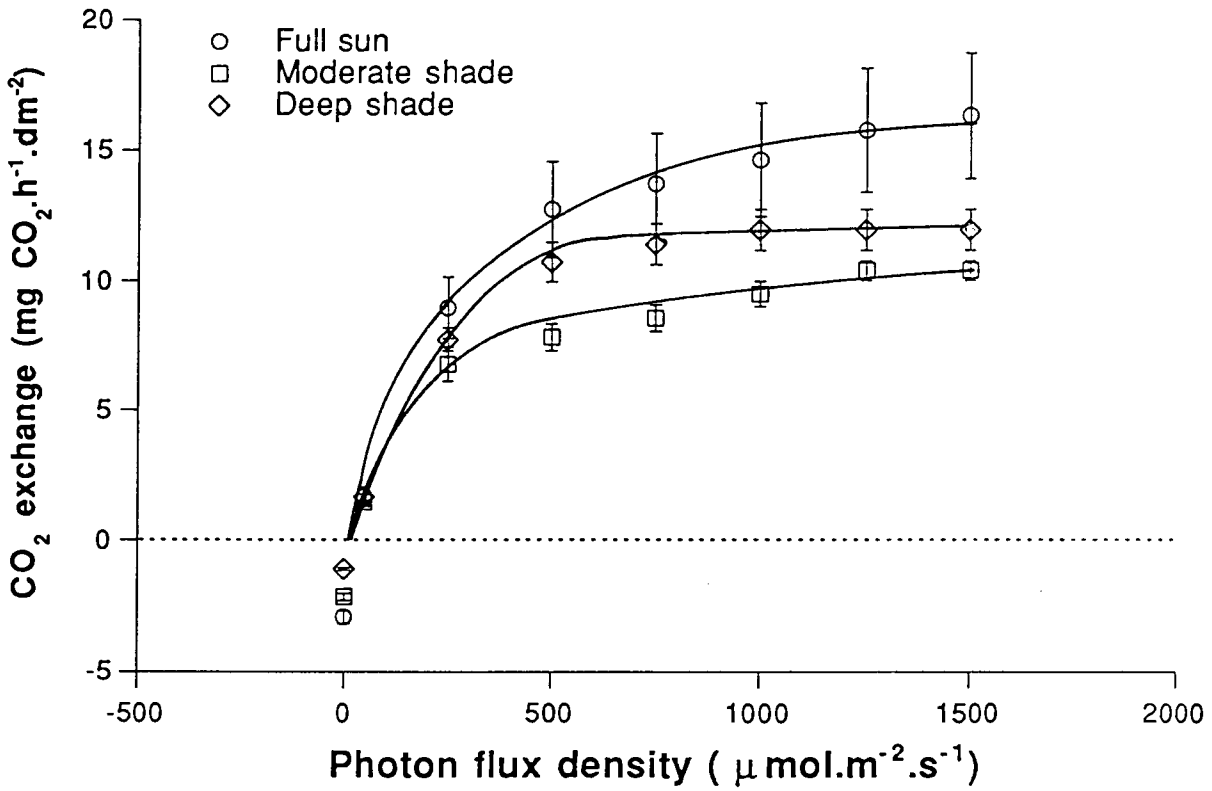


Figure 36. Light response curve of apparent photosynthesis of 2-year-old (August 1992) western redcedar seedlings grown under three shade treatments. (Mean ± SE, n=3).

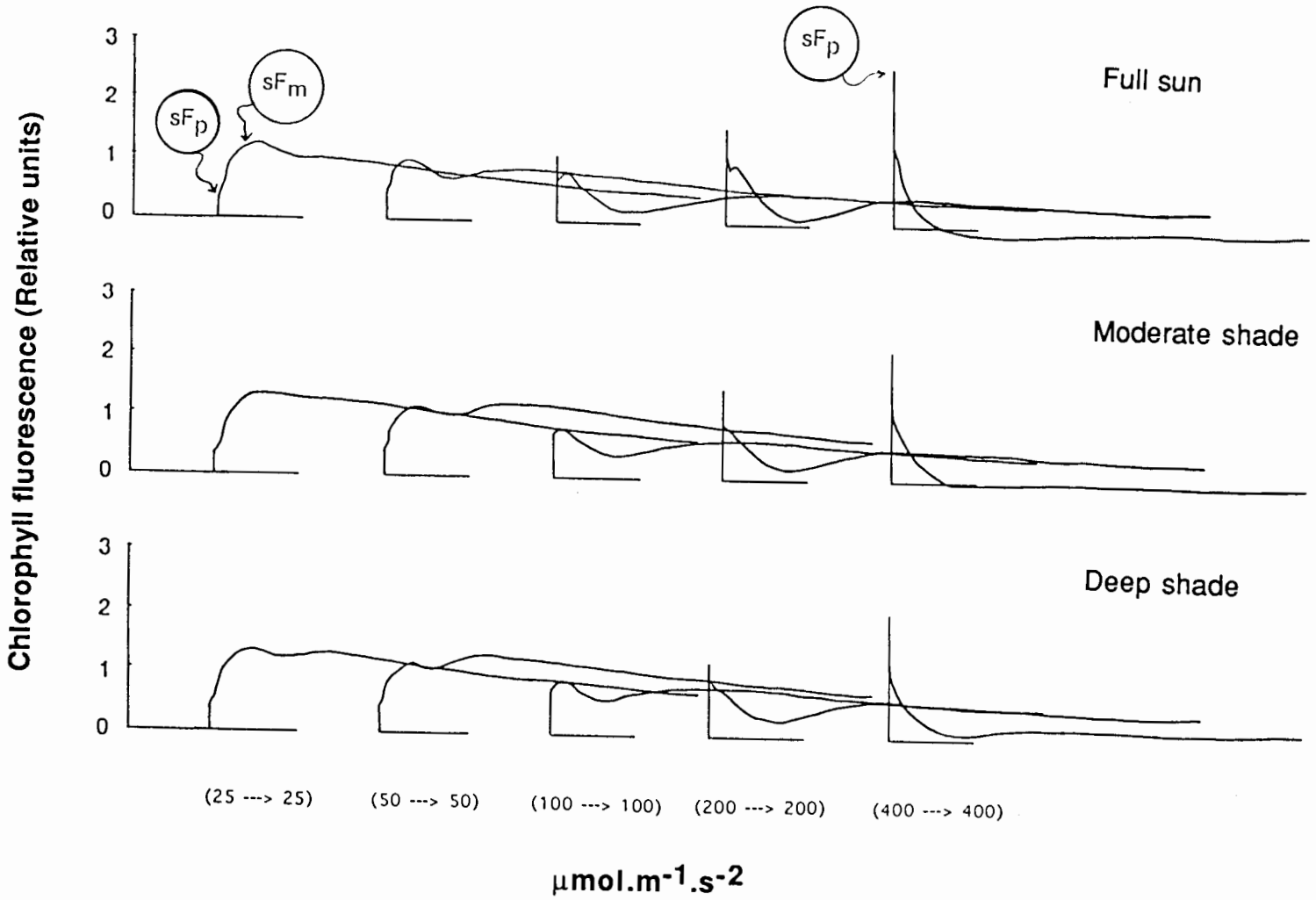
Part III. Effect of different photon flux density (PFD) on chlorophyll-a fluorescence

A. Effect of using the same PFD during the 30 min light acclimation period and for the excitation light used for chl-a fluorescence induction

Chlorophyll fluorescence induction curves of western redcedar seedlings, which were acclimated for 30 min at the same PFD as used for the excitation light, showed a consistent change in fluorescence components between shade treatments (Fig. 37). An increase in light intensity resulted in a change in sF_p of the F_{var} transient from a rounded shoulder to a spike-like feature (Fig. 37). This spike-like feature appeared in FS grown seedlings at a lower PFD than that of the shade treatments. Other consistent changes between all treatments include sF_m, sF_s, and sF_t.

Significant increases ($\alpha<0.05$) in sF_o, sF_p, and sF_v/F_m of the seedlings from three shade treatments were consistently observed as the PFD increased (Appendix III, Table 1). The lowest values for each F_{var} component were found when the lowest combination of PFD (25 $\mu mol.m^{-2}.s^{-1}$) was used. These values then gradually increased as PFD increased, and reached a maximum at 400 $\mu mol.m^{-2}.s^{-1}$ (the highest PFD used). Regression of F_{var} components *vs* PFD had

Figure 37 Changes in F_{var} fluorescence of 2-year-old western redcedar seedlings grown under three shade treatments. Seedlings were acclimated at the same PFD as the excitation light for chlorophyll-*a* induction: 25, 50, 100, 200, and 400 $\mu mol.m^{-2}.s^{-1}$. Each curve represents the average of five seedlings.


Chlorophyll fluorescence (Relative units)
3
2
1
0
sFp
sFm
sFp
Full sun
Moderate shade
Deep shade
(25 ---> 25)
(50 ---> 50)
(100 ---> 100)
(200 ---> 200)
(400 ---> 400)
µmol.m-1.s-2

R^2 values of 0.98, 0.97, 0.79, 0.96 (for FS seedlings), 0.98, 0.77, 0.74, and 0.96 (for MS seedlings) and 0.98, 0.90, 0.85, 0.96 (for DS seedlings). Each value represents sF_o, sF_p, sF_t, and sF_v/F_m respectively Fig. 38,39,40 and 41). sF_v/F_m was calculated based on the sF_p value, which is not necessarily sF_{max} or the highest point in the entire F_{var} fluorescence transient (Fig. 37).

Between treatments, sF_o was found always significantly higher in MS and DS seedlings than in FS seedlings (Appendix III, Table 1).

The steady state fluorescence, sF_t, steadily decreased as the PFD increased and reached lowest value at 400 $\mu mol.m^{-2}.s^{-1}$. At this PFD level, sF_t of FS and MS seedlings were below sF_o level (Fig. 37; Appendix III, Table 1). Between treatments, the sF_t of DS grown seedlings was always higher than FS seedlings.

The sF_v/F_m ratio based on the highest point (F_{max}) in the F_{var} transient showed little or no changes for the comparison between measurement using 25 $\mu mol.m^{-2}.s^{-1}$ and 400 $\mu mol.m^{-2}.s^{-1}$ (Appendix III, Table 1).

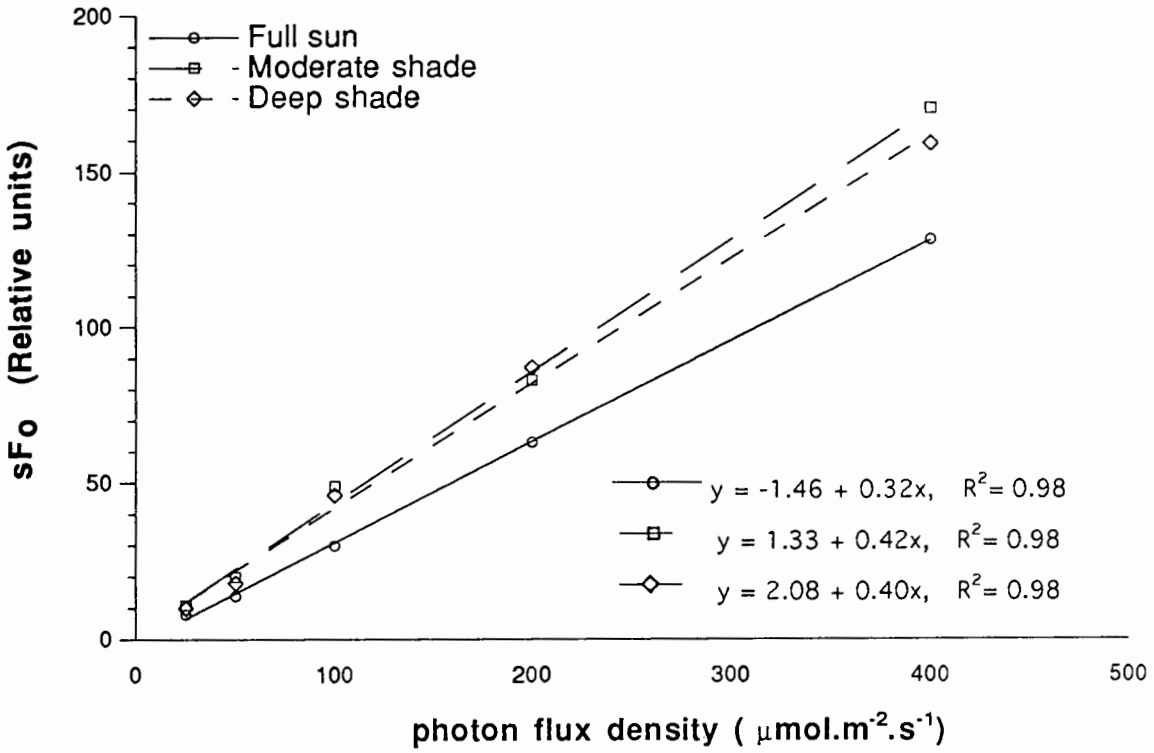


Figure 38. Relationship between PFD ($\mu mol.m^{-2}.s^{-1}$) and the initial fluorescence (sF_o) of 2-year-old western redcedar seedlings grown under three different shade treatments. Each point represents the average of five seedlings.

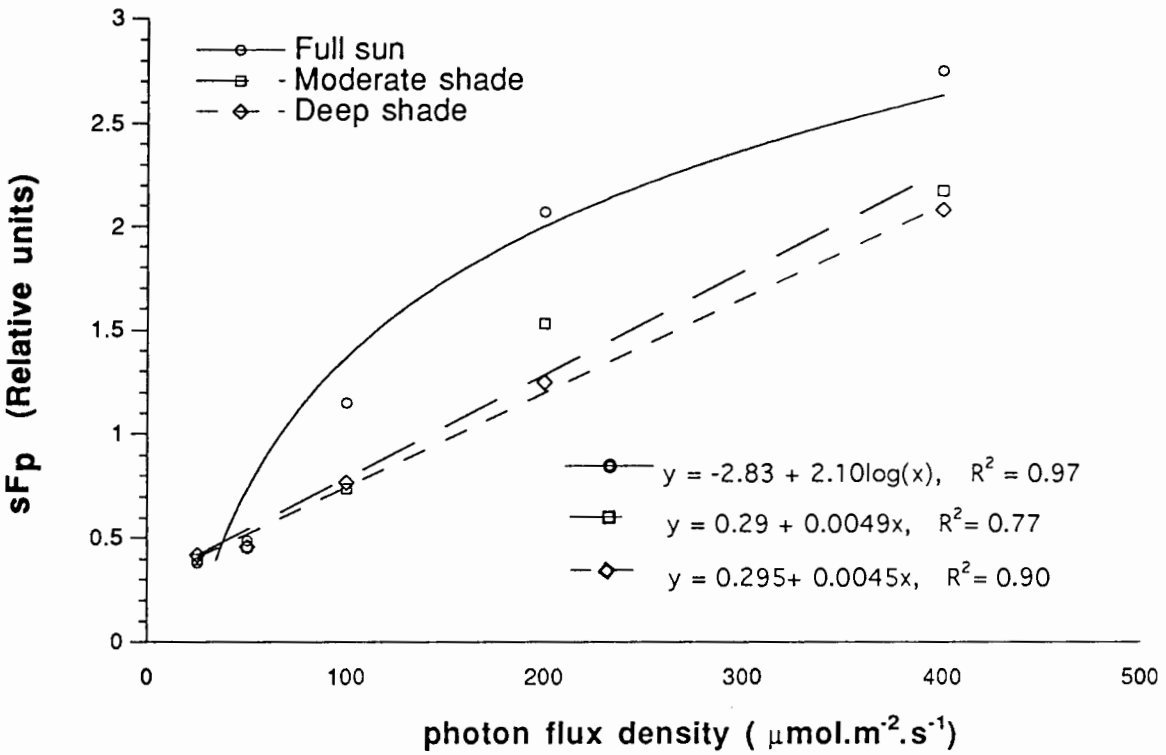


Figure 39. Relationship between PFD ($\mu mol.m^{-2}.s^{-1}$) and the sF_p component of F_{var} fluorescence of 2-year-old western redcedar seedlings grown under three shade treatments. Each point represents the average of five seedlings.

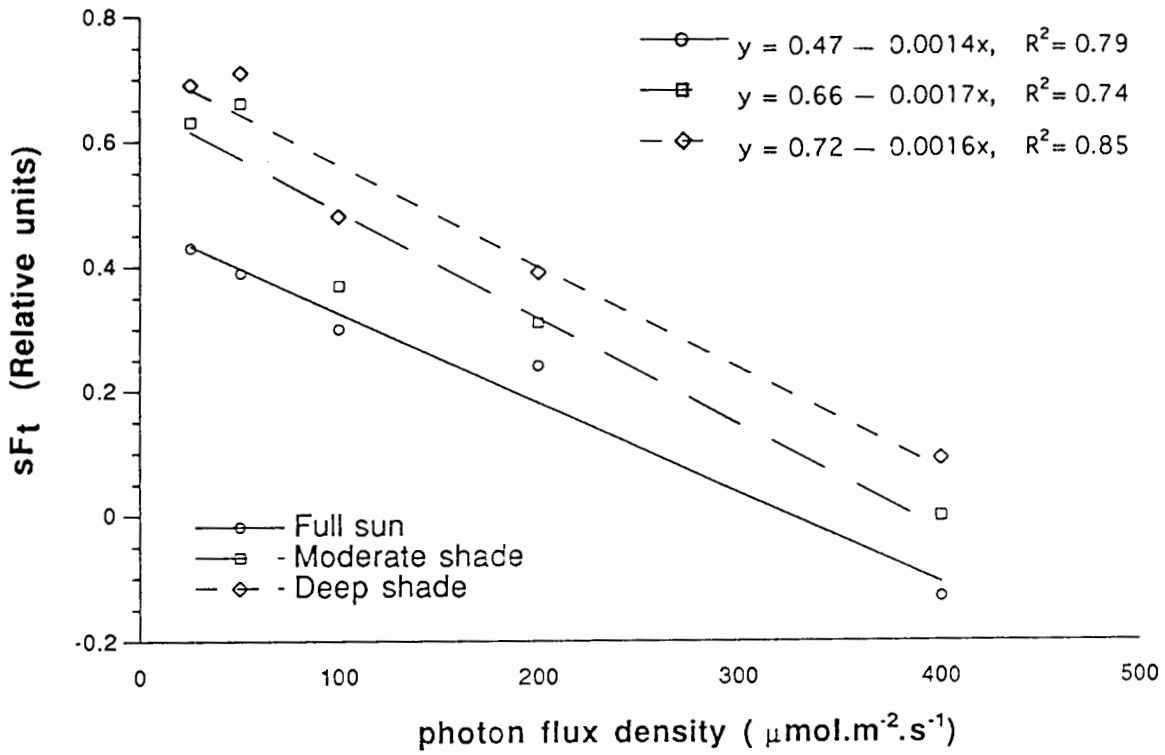


Figure 40. Relationship between PFD ($\mu mol.m^{-2}.s^{-1}$) and the steady state fluorescence (sF_t) of 2-year-old western redcedar grown under three shade treatments. Each point represents the average of five seedlings.

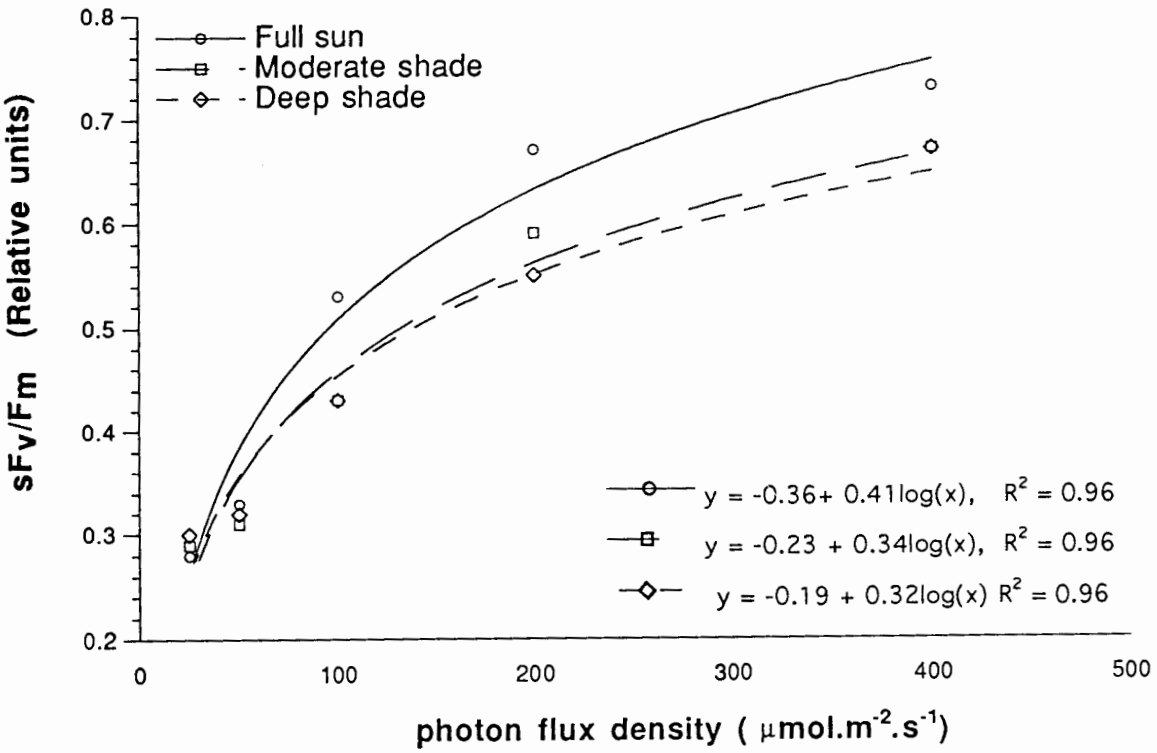


Figure 41. Relationship between PFD ($\mu mol.m^{-2}.s^{-1}$) and the ratio of variable to maximum fluorescence (sF_v/F_m) of 2-year-old western redcedar seedlings grown under three shade treatments. Each point represents the average of five seedlings.

B. Effect of using a fixed PFD (300 $\mu mol.m^{-2}.s^{-1}$) for light acclimation and different excitation PFD for fluorescence measurement.

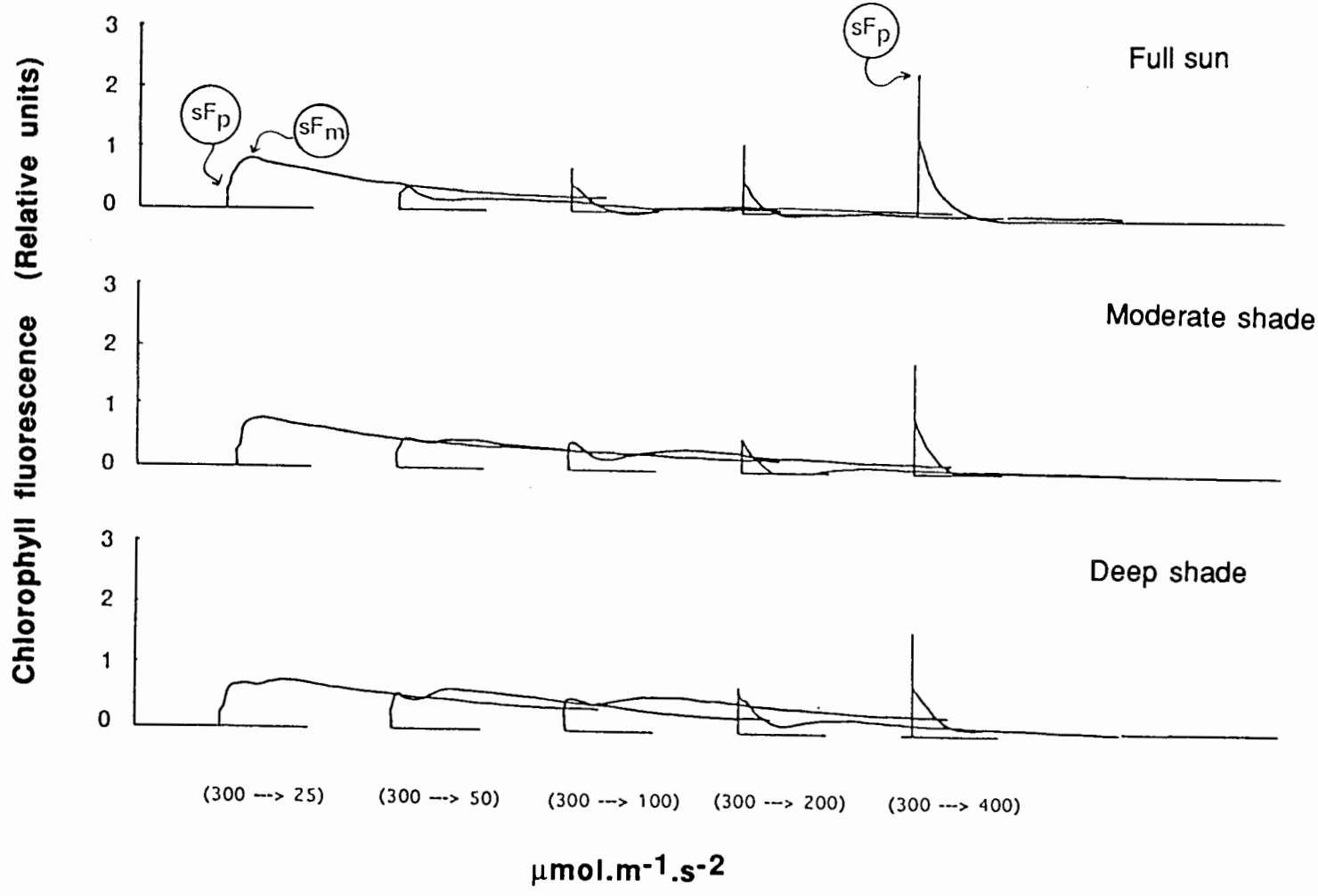
The F_{var} transient curves obtained in this experiment (B) were similar to those found in the previous experiment (A) (Fig. 37 and 42). sF_o, sF_p, and sF_v/F_m significantly increased with increasing excitation PFD and reached maximum values at 400 $\mu mol.m^{-2}.s^{-1}$ (Appendix III, Table 2). The relationship between F_{var} components *vs.* PFD had R^2 values of 0.98, 0.96, 0.89, 0.96 (for FS seedlings), 0.98, 0.88, 0.97, 0.94, (for MS seedlings) 0.98, 0.88, 0.88, and 0.98 (for DS seedlings), each value represents sF_o, sF_p, sF_t and sF_v/F_m respectively (Fig. 43,44,45,46). sF_v/F_m was calculated based on the sF_p point (not necessarily the highest point in the F_{var} transient).

The relationship between PFD *vs.* sF_t changed from linear (Fig. 40) to curvilinear (Fig. 45) when PFD during acclimation was lower than light excitation PFD during F_{var} fluorescence measurement.

Between shade treatments, sF_o of shaded seedlings were always significantly higher ($\alpha<0.05$) than FS seedlings, with MS seedlings having the highest sF_o (Appendix III, Table 2).

The sF_t for all treatments gradually decreased as

Figure 42. Changes in F_{var} fluorescence of 2-year-old western redcedar seedlings grown under three shade conditions. Seedlings were acclimated at 300 $\mu mol.m^{-2}.s^{-1}$ and measured at different excitation PFDs. Each point represents the average of five seedlings.


Chlorophyll fluorescence (Relative units)
3
2
1
0
sFp
sFm
sFp
Full sun
Moderate shade
Deep shade
(300 ---> 25)
(300 ---> 50)
(300 ---> 100)
(300 ---> 200)
(300 ---> 400)
µmol.m-1.s-2

excitation PFD increased, and reached lowest values at 400 $\mu mol.m^{-2}.s^{-1}$ (FS= -0.03, MS = 0.002, and DS = 0.07 relative units).

The same pattern of change in sF_p also occurred in this experiment (Fig. 37 and 42). As excitation PFD increased, sF_p became a pronounced spike-like feature in the F_{var} transient. This parameter was significantly higher in FS seedlings than both MS and DS seedlings at the excitation PFD of 100, 200 and 400 $\mu mol.m^{-2}.s^{-1}$ (Appendix III, Table 2).

The sF_v/F_m ratio calculated based on the maximum point (F_{max}) indicates that higher sF_v/F_m was obtained at the highest excitation PFD (Appendix III, Table 2). sF_v/F_m of FS seedlings was significantly higher than MS and DS at an excitation PFD larger than 100 $\mu mol.m^{-2}.s^{-1}$.

Acclimation PFD had little influence on sF_o but doubling excitation PFD also doubled sF_o. Similarly in both experiments, doubling excitation PFD also doubled the absorption value (I_{abs}) of seedlings in the sphere (Fig. 47A & B).

In both experiments, as excitation light intensity increased, sF_o, sF_p and the sF_v/F_m ratio increased whereas sF_t generally decreased irrespective of shade treatments. Acclimation PFD had little or no influence on the F_{var} components measured.

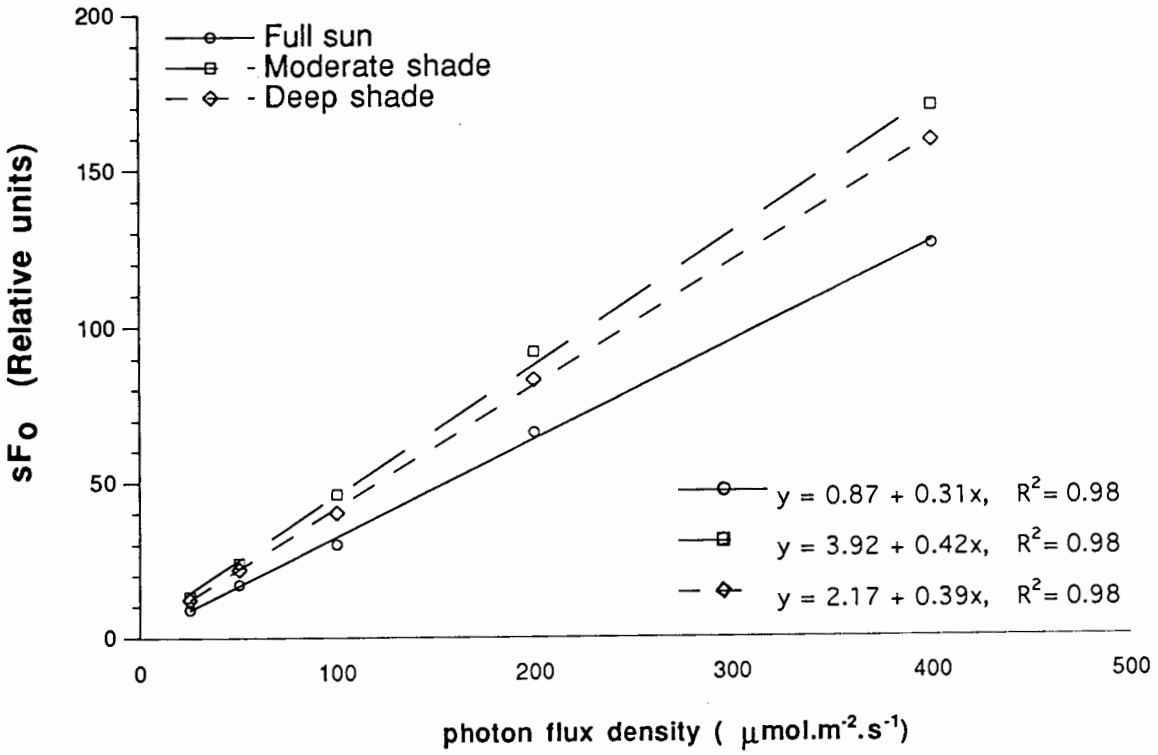


Figure 43. Relationship between PFD ($\mu mol.m^{-2}.s^{-1}$) and the initial fluorescence (sF_o) of 2-year-old western redcedar seedlings grown under three shade treatments. Each point represents the average of five seedlings.

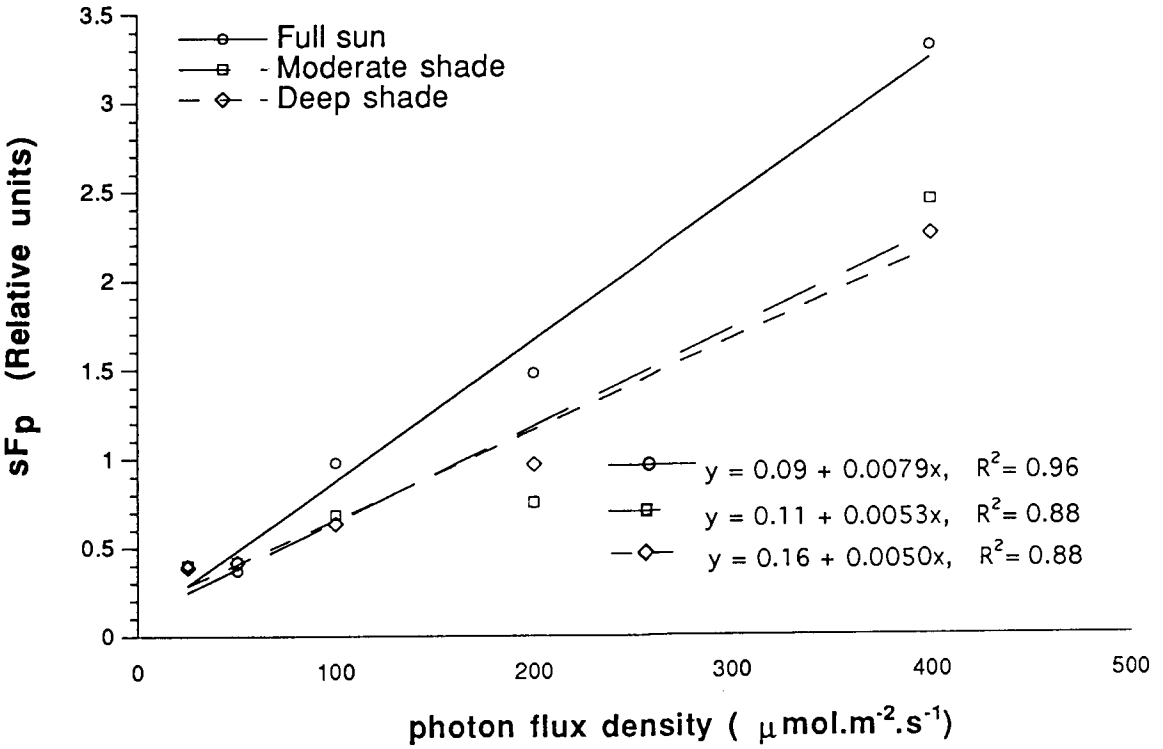


Figure 44. Relationship between PFD ($\mu mol.m^{-2}.s^{-1}$) and the sF_p component of F_{var} fluorescence of 2-year-old western redcedar seedlings grown under three shade treatments. Each point represents the average of five seedlings.

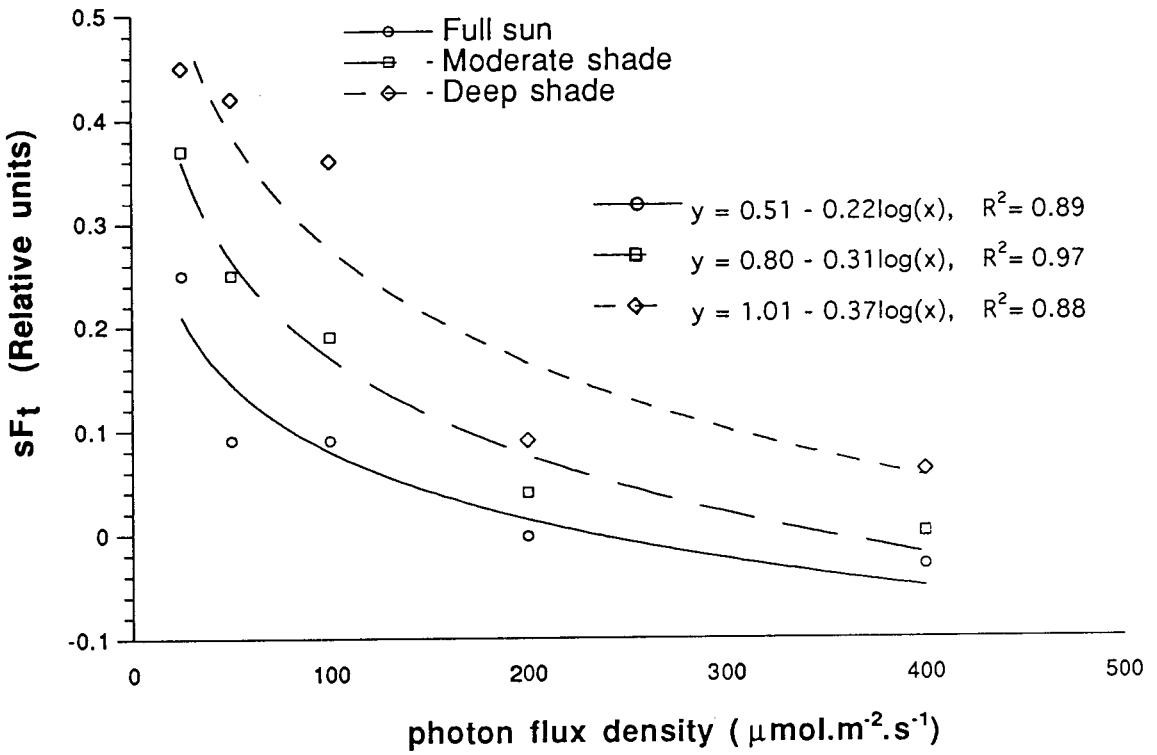


Figure 45. Relationship between PFD ($\mu mol.m^{-2}.s^{-1}$) and the steady state fluorescence (sF_t) of 2-year-old western redcedar grown under three shade treatments. Each point represents the average of five seedlings.

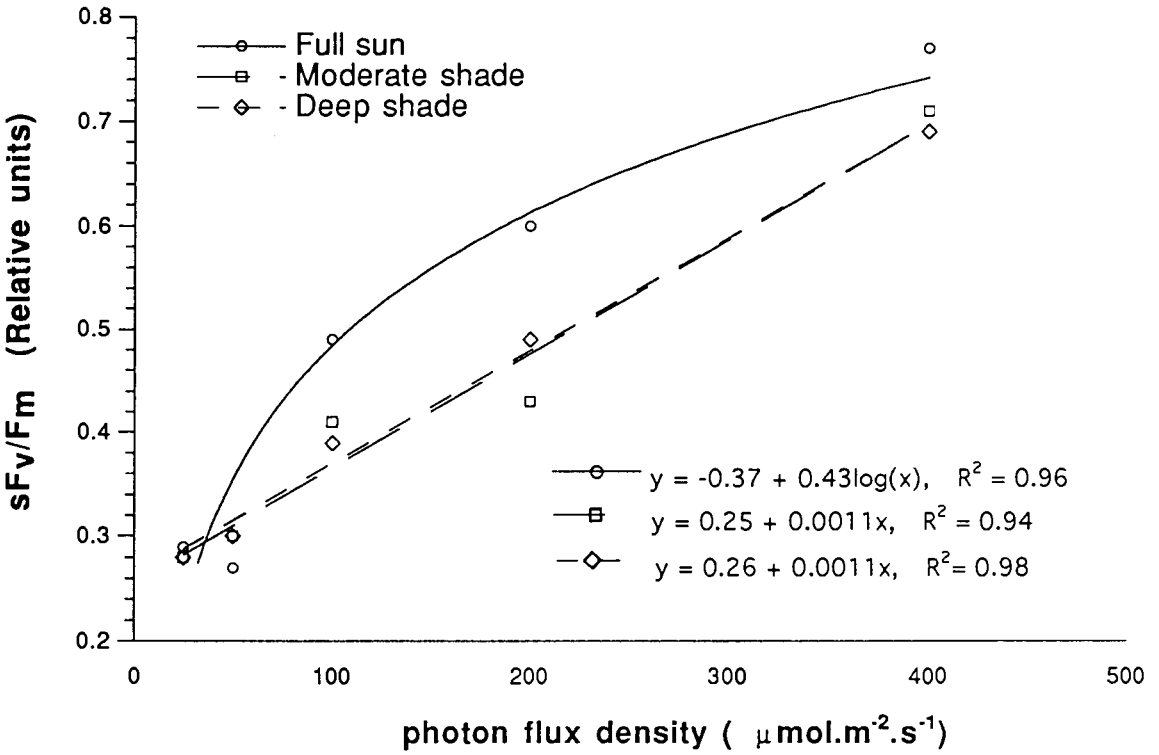


Figure 46. Relationship between PFD ($\mu mol.m^{-2}.s^{-1}$) and the ratio of variable to maximum fluorescence (sF_v/F_m) of 2-year-old western redcedar seedlings grown under three shade treatments. Each point represents the average of five seedlings.

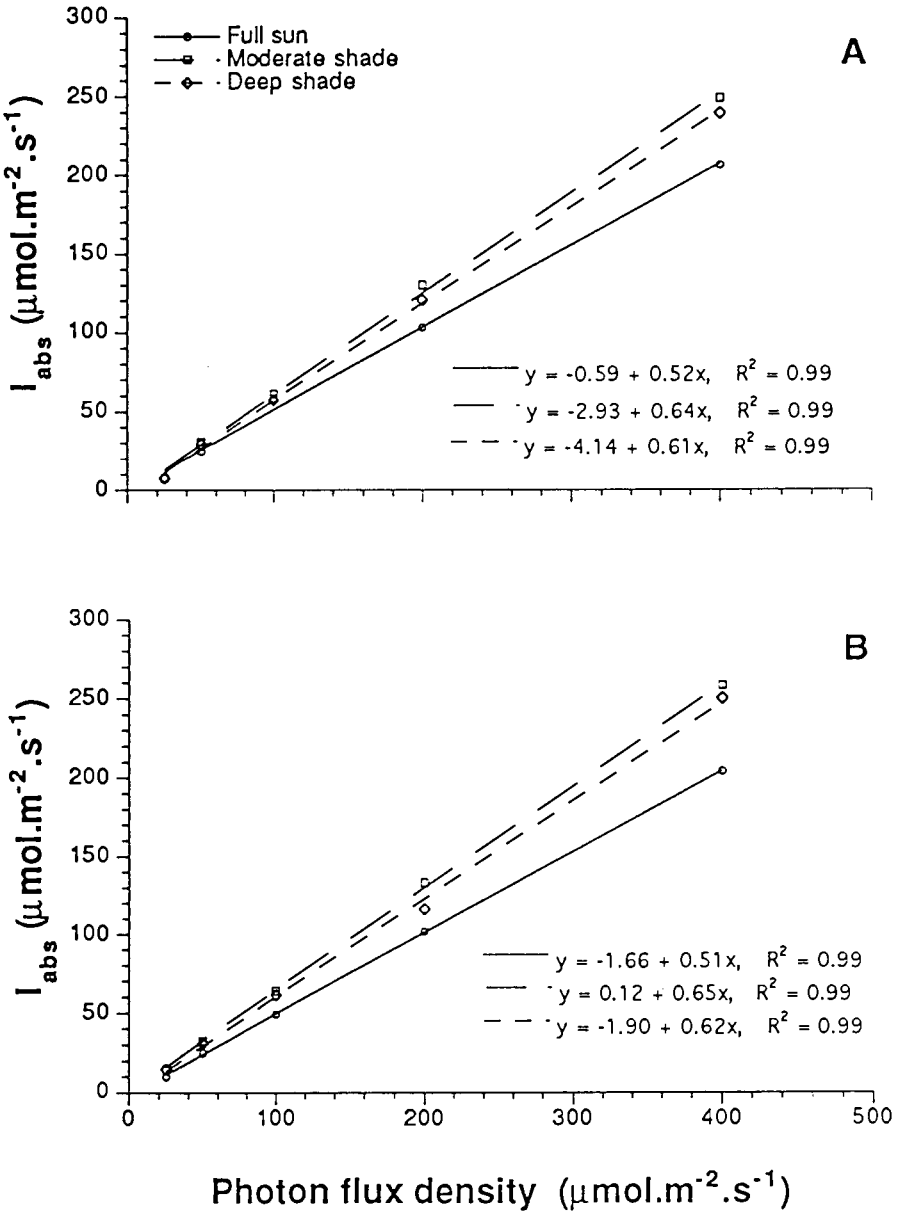


Figure 47. Relationship between PFD (µmol.m^{-2}.s^{-1}) and light absorbed (I_{abs}) by 2-year-old western redcedar seedlings grown under three shade treatments. **(A)** Acclimation PFD same as excitation PFD, **(B)** Acclimation PFD a constant 300 µmol.m^{-2}.s^{-1} , excitation PFDs same as in **(A)**. Each point represents the average of five seedlings.

Part IV. Effect of drought conditions on physiology of western redcedar seedlings grown under three shade treatments

To assess whether shade treatment moderated the effects of drought stress by reducing the rate of soil drying in pots of MS and DS grown seedlings, which in turn, might slow down the decline in their photosynthetic activity compared to that of FS grown seedlings, a drought experiment was conducted during August and September 1991. Daily minimum, maximum and average greenhouse air temperature and humidity during the drought experiment are shown in Appendix IV, Table 1. Maximum temperatures ranged from 12.5 ^{o}C to 38.5 ^{o}C in August and 14.5 ^{o}C to 32.5 ^{o}C in September. There were several days in both months with relative humidity in the 20% range.

P_N rates (sF_o basis) significantly ($\alpha<0.05$) decreased in all treatments as water stress developed and reached the minimum (nontraceable P_N rates) at about 15% to 25% SWC (Appendix IV, Table 2).

The maximum fluorescence, sF_p, measured at soil field capacity (at the beginning of this experiment) was lower than sF_p measured at 15% to 25% SWC, (where P_N rates were zero) except for DS seedlings (Fig. 48; Appendix IV,

Figure 48. Effect of drought stress on chlorophyll-*a* fluorescence and CO_2 exchange of 1-year-old western redcedar seedlings grown under Full sun, Moderate shade and Deep shade conditions. Curves are the mean of n=5 seedlings.

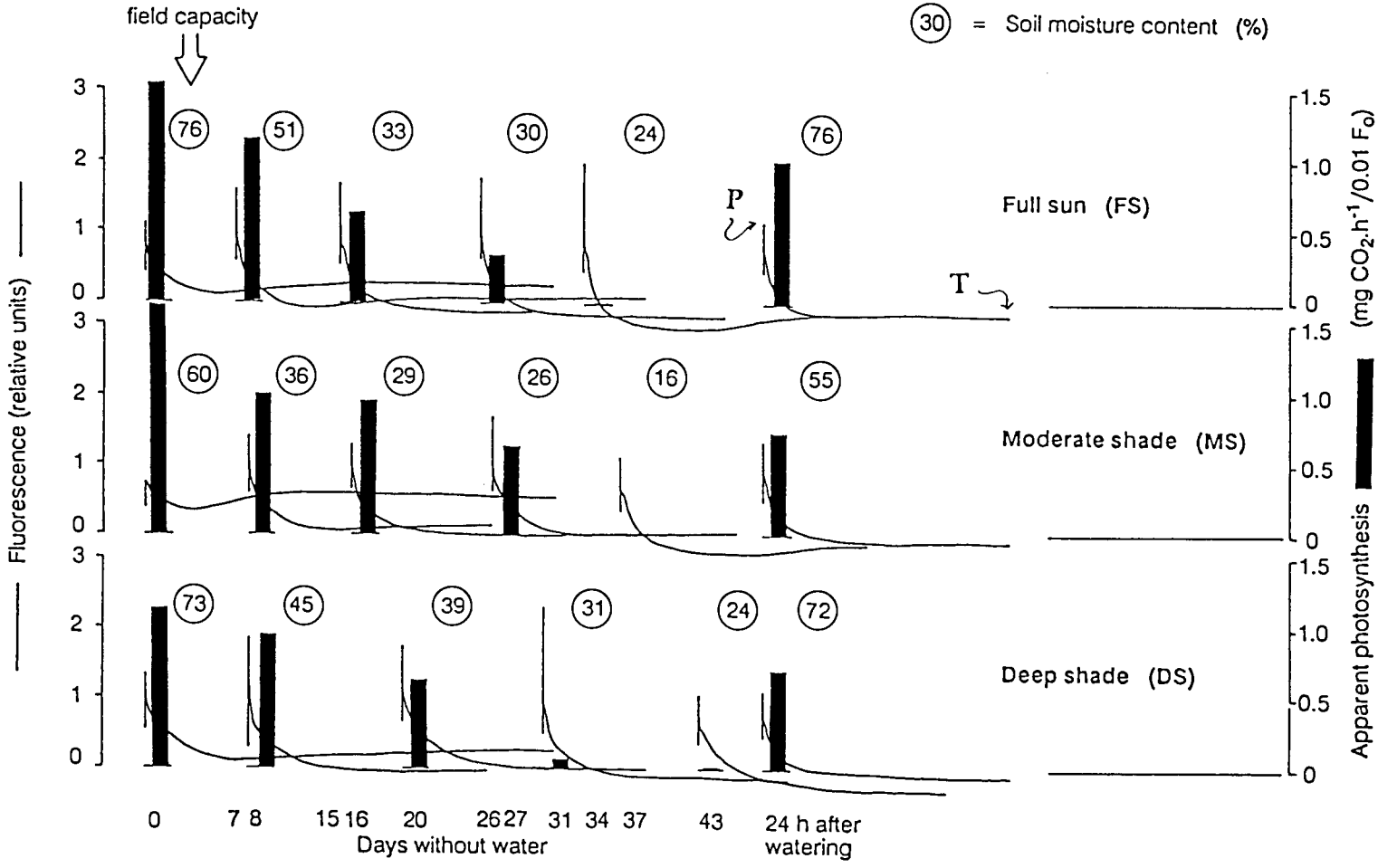

field capacity
30 = Soil moisture content (%)
Fluorescence (relative units)
Apparent photosynthesis (mg CO2.h-1/0.01 Fo)
Full sun (FS)
Moderate shade (MS)
Deep shade (DS)
P
T
76
51
33
30
24
76
60
36
29
26
16
55
73
45
39
31
24
72
0 7 8 15 16 20 26 27 31 34 37 43
Days without water
24 h after watering

Table 2). The increase of sF_p between the two levels of SWC was significant ($\alpha<0.05$) in MS (34%), followed by FS seedlings (24%). For DS seedlings, however, sF_p significantly decreased (Fig. 48).

Steady state fluorescence, sF_t, of all treatments generally declined as drought stress developed, and reached their lowest points at approximately 15% to 25% SWC: -0.27, -0.12, -0.12 for FS, MS and DS respectively (all values were below the sF_o level) (Appendix IV, Table 2). There were significant differences in sF_t between F_{var} measurement at soil field capacity and at the lowest SWC for each treatment with the most pronounced decline occurring in FS seedlings followed by MS and DS seedlings.

The ratio of variable to maximum fluorescence, (sF_v/F_m), for all shade treatments was relatively constant in this experiment with averages of about 0.58, 0.54, and 0.58 for FS, MS and FS respectively (Appendix IV, Table 2).

On re-watering, seedlings from all treatments showed recovery of photochemical and photosynthesis activity within 24 h, indicated by the increase both in their P_N rates and sF_t (Fig. 48). Maximum fluorescence (sF_p) increased after re-watering in all seedlings but FS seedlings.

DISCUSSION

Effects of shade on seedling growth

Growth of a tree requires an ability to maintain a positive carbon balance over time in a continuously changing environment over time. In nature, growth is influenced by many environmental stresses that occur simultaneously (Chapin *et al.* 1987; Osmond *et al.* 1987). Accordingly, there may be different growth strategies and patterns between plant species in response to variation in the environment. For example, shade tolerant species — species that are able to establish, compete, and grow under low photon flux densities (Kimmins, 1987) — may maintain a positive carbon gain by increasing the efficiency of the photosynthetic system (*e.g.*, low respiration or high photosynthesis at low PFD) and through morphological adaptations (Loach, 1970).

Much experimental data indicate that differences between shade and sun grown plants involve differences in their morphology, physiology, biochemistry and leaf anatomy (Björkman *et al.* 1972; Boardman *et al.* 1975; Boardman, 1977; Lichtenthaler *et al.* 1981; Givnish, 1988).

Compared to shade leaves, sun leaves are often characterized by smaller leaf area and thicker leaves

(Björkman *et al.* 1972; Lichtenthaler, 1981), frequently reddish color on the adaxial leaf surface (Hodges & Scott, 1968; Givnish, 1988; Nozzolillo, *et al.* 1990; Weger *et al.* 1993), higher leaf and root weight ratio, decrease in leaf area ratio and specific leaf area (Corré, 1983), higher chlorophyll and carotenoid content on a leaf area basis, but lower on a dry weight basis (Kirk & Tilney-Basset, 1978; Lichtenthaler, 1981).

High light has been shown to influence characteristics of the photosynthetic apparatus (Boardman *et al.* 1975; Boardman, 1977; Lichtenthaler, 1981). Sun type chloroplasts contain less chlorophyll per chloroplast (Goryshina, 1980; Lichtenthaler, 1981), higher ratio of chlorophyll *a/b* (Boardman, 1977; Lichtenthaler, 1981; Givnish, 1987, 1988), and a lower proportion of xanthophyll/ β-carotene ratio (*x/c*) (Lichtenthaler, 1981). The chloroplasts of sun-type leaves also have fewer and smaller grana stacks and a lower amount of chloroplast lamellae per chloroplast, which is probably associated as well with less light harvesting chlorophyll *a/b* protein in sun leaves than in shade leaves (Boardman *et al.* 1975; Lichtenthaler & Buschmann, 1978; Lichtenthaler, 1981; Givnish 1987, 1988). These differences generally result in lower dark respiration and photosynthetic rates, and in turn, lower relative growth

(RGR) and net assimilation rates (NAR) in shade grown plants than sun grown plants (Corré, 1983).

The growth response exhibited by western redcedar in this research (Table 5) generally followed the growth pattern of shade tolerant species grown under different light conditions reported by others. Among these results was the increase in LAR — relative size of the photosynthetic apparatus — of deep shade grown western redcedar seedlings (low light). This fits Blackman and Wilson's (1951) definition of a shade tolerant species and supports the argument that western redcedar is a shade tolerant tree species (Klinka *et al.* 1990).

Changes in LAR with different light growing conditions in western redcedar seedlings may occur through alteration of its components : LWR and SLA (Fig. 21 & 22). A high SLA in DS grown seedlings can be seen as a strategy to maximize light interception. Low light grown plants usually have thinner leaves, a large surface area and a higher LWR which means low non-structural carbohydrate (Alberda, 1965; Thornley & Hurd, 1974). Results of increasing SLA in low light grown woody plants have been widely reported in many genera including: *Betula, Liriodendron, Quercus, Fagus, Pseudotsuga, Coffea, Pentaclethra* and *Castanospermum* (after Kozlowski *et al.* 1991). A lower SLA in high light grown plants, on the other hand, may be caused by the

Table 5. Summary of shade effects on growth of western redcedar at the end of the second year (1991) grown under three shade treatments.

Parameters	Differences between shade treatments
Leaf area	FS = DS < MS*
Shoot length	DS = FS < MS*
Mean seedling biomass	
Stem	DS < FS < MS*
Leaf	DS < FS = MS*
Shoot	DS < FS = MS*
Root	DS < MS = FS*
Total	DS < FS = MS*
Root/shoot ratio (R/S)	DS = MS < FS*
Root weight ratio (RWR)	DS = MS < FS*
Leaf weight ratio (LWR)	FS < DS = MS*
Specific leaf area (SLA)	FS = MS < DS*
Leaf area ratio (LAR)	FS < MS < DS*
Net assimilation rate (NAR) **	DS < MS < FS (1991)
Relative growth rate (RGR) **	
1990	
Shoot	DS = MS = FS
Root	DS < MS = FS
Total	DS = MS = FS
1991	
Shoot	DS = MS = FS
Root	DS = MS = FS
Total	DS = MS = FS

*) significantly different ($\alpha < 0.05$)
**) no statistical analysis

accumulation of sugar and starch in leaves (Blacquière *et al.* 1987), antiherbivore compounds (Coley, 1987) or other leaf components important as a defense mechanism.

Stem elongation (long internodes) is a characteristic plant adaptation to low light environment (Morgan & Smith, 1979; Smith, 1982). But, for western redcedar seedlings in this research, longer stems occurred in FS seedlings with almost similar stem dry weight as DS grown seedlings (Fig. 16). Similar responses were found in some species due to forest canopy closure (*Quercus petraea*, Jarvis, 1964; *Trifolium repens*, Solangaarachchi & Harper, 1987, and Thompson & Harper, 1988; *Eichhornia crassipes*, Mèty *et al.* 1990).

More allocation of biomass to stem than to the root in low light grown plants may be a strategy to conserve carbohydrate due to the usually higher respiration in roots than in stems (Corré, 1983; Lambers & Poorter, 1992).

A more vertical foliage orientation was found in FS grown seedlings, which agrees with the commonly reported vertical orientation of foliage at the upper branches of conifers (Kozlowski *et al.* 1991). Ecologically, this is an adaptation to high light environment by reducing light interception, while at the same time allowing deeper penetration of light into the canopy (Kozlowski *et al.* 1991). Physiologically at the plant level, it plays a role

in controlling the amount of absorbed light hence preventing plants from photodamage (Björkman & Powles, 1982; Powles & Björkman, 1982).

The RGR and NAR analysis of western redcedar show this species' ability for morphological adaptation when grown under different light environments. Except in 1990 for RGR_{root}, there were no significant differences found in RGR_{total} and RGR_{shoot} in FS seedlings compared to the shaded seedlings (Fig. 24A,B,C & 25A,B,C), in spite of approximately five times higher quantity of light received by FS seedlings. The same results have been reported that many species show a relatively constant RGR under a range of light growing conditions if they are grown from seed in different light intensities (Blackman & Wilson, 1951; Evans & Hughes, 1961; Huxley, 1967, Corré, 1983). Factors other than light such as high temperature, water deficit and root space limitation, however, may also contribute at least partly to no significant differences in RGR of western redcedar between the shade treatments. Higher temperatures in the FS block (Table 11) may create increased water stress due to high evapotranspiration compared to the two shaded blocks. FS seedlings may respond by greater allocation of biomass to root than to the shoot (Fig. 17 & 18).

An increase in root biomass and hence RWR in water deficit conditions has been explained by Brouwer (1968) as an alteration in the competitive ability of roots and shoots for resources leading to a functional equilibrium. Root space limitations in the tubes used in this research may have increased the severity of a drought effect especially in the second and third year resulting in the consistently highest RWR and R/S ratio of FS seedlings compared to MS and DS grown seedlings (Fig. 19 & 20).

The well known decrease in root/shoot ratio as light intensity decreases (*e.g.*, in white pine and bean (Berry & Bjorkman, 1980), *Quercus petraea* (Jarvis, 1964), *Bischofolia javonica* (Kamaluddin & Grace, 1992) also occurred in western redcedar (Fig. 19). Thus, supporting the contention that shading increases the allocation of dry matter production to the shoot, an adaptive type of behaviour when light is limited (McLaren & Smith, 1978; Hoddinot & Hall, 1982; Givnish, 1988; Kozlowski *et al.* 1991). This contrasts with other conifers such as Loblolly and Ponderosa pine (Ledig *et al.* 1970), and western hemlock (Grossnickle, 1993), which show little phenotypic alteration of root/shoot balance.

In exposed full sun conditions which contribute to drought, more biomass may be allocated to roots than shoots in order to increase the ability of the plants to compensate for water loss. An increased root/shoot ratio in water

stress type environments was also found in western larch (Vance & Running, 1985), lodgepole pine (Comeau & Kimmins, 1989), Douglas fir (Keyes & Grier, 1981), red pine, white pine, jack pine and eastern larch (Logan, 1966). Grossnickle (1993) also found a larger root/shoot balance in western redcedar seedlings in low to moderate drought conditions.

Moderate shade treatment seems to be the best light conditions for overall growth of western redcedar as shown by the superior growth in almost all growth components (Fig. 18).

Effects of shade on the phenology of western redcedar

Although western redcedar does not have buds (Krasowski & Owens, 1991), new leaf growth in spring may be used to indicate start of the growing season (Parker & Johnson, 1987). New leaf growth in spring occurred first in the DS grown seedlings (27% light), and last in FS grown seedlings (100% light). The timing and duration of shoot growth are influenced by several environmental factors particularly temperature and photoperiod (Kozlowski *et al.* 1991). The decrease in these two factors in fall and their increase in spring may explain differences in phenology of shaded and unshaded grown seedlings in this research.

Because of the shade treatment, DS seedlings have lower PFD (Fig. 9) and temperature (Fig. 11) than both MS and FS seedlings. The combination of these two factors may be responsible for the earlier growth cessation in DS seedlings, probably due to the low activity of calvin cycle enzymes (Strand & Oquist, 1988), leading to a reduction of photosynthetic rates typically found in winter (*e.g.*, Bourdeau, 1959; Zelawski & Kucharska, 1967; Lundmark *et al.* 1988). Low rates of photosynthesis result in carbohydrate accumulation insufficient to maintain growth.

A shortening of day length causes cessation of: (1) shoot growth (*e.g.*, black locust, yellow poplar, weigela, and red maple, Kozlowski *et al.* 1991), (2) leaf growth (*e.g.*, smooth sumac and yellow poplar (after Kozlowski *et al.* 1991), and (3) indirectly, cambial activity, since it depends on photosynthate from leaves and hormones from active apical meristems (*e.g.* in red pine, Larson, 1962). In this research, the effect of the shade treatment itself combined with the greenhouse orientation and construction created a shorter photoperiod for DS seedlings than in MS and FS treatments (Fig. 10; Appendix I, Table 2). The FS seedlings, on the other hand, especially in the second year, experienced a longer growing period under favorable, moderate light and temperature conditions late fall. For example, there were significant increases in shoot and root

dry weight between October and November 1991 in FS seedlings (Appendix I, Table 4), which resulted in the continued growth during these months. Grossnickle (1993) found that under field conditions western redcedar continued to grow from July to November when western hemlock shoot growth had ceased. Parker & Johnson (1987) also noted that western redcedar trees growing in an open area often stop growth in late summer due to moisture stress and then start growth again after the first rain of autumn. The phenotypic character of full sun grown seedlings of western redcedar in this research shows a typical characteristic of the Cupressaceae family (*e.g., Chamaecyparis, Cupressus, Juniperus, Libocedrus*) which generally are slow to start growth in the spring, but grow steadily over a long growing season (Mitchell 1965; Parker & Johnson 1987).

In their first winter, however, FS seedlings experienced low temperature conditions that were exacerbated by high light. This condition may induce photoinhibition in FS seedlings perhaps as a protective mechanism for the photosynthetic apparatus against photodamage (Krause, 1988, 1994; Öquist *et al.* 1992), through the development of a carotenoid quenching mechanism. As was mentioned earlier, this type of protection may cost the FS seedlings a significant decrease in their photosynthetic rates. Since low photosynthesis also carries the consequences of low

carbohydrate production that is needed to start new growth, low carbohydrate production in FS seedlings may be responsible for the slow start of these seedlings in the spring. Higher respiration rates, in particular maintenance respiration in FS seedlings, may also be responsible for this late growth response of FS seedlings. On the other hand, at low temperatures, DS seedlings might also experience photoinhibition, but probably to a much lesser degree with the absence of high light, as indicated by their higher sF_p and sF_v/F_m compared to FS grown seedlings in December 1990 and February 1991 (Fig. 26, & 35B; Appendix II, Table 2) .

New leaf growth in FS seedlings which only occurred after the reddish color disappeared may indicate that it was necessary for FS seedlings to produce chlorophyll at the beginning of the growing season, therefore, FS new leaf growth was delayed relative to the DS seedlings. This could have been a result of lower efficiency in capturing light.

Under moderate shade conditions, western redcedar started new growth after DS seedlings but before the FS seedlings. Slightly bronzy leaf color of MS seedlings was also found in the winter. Thus, the same reason can probably be applied in explaining the slower start of growth of MS seedlings as compared to DS seedlings.

Effect of shade on pigment content

At the pigment level, shade grown leaves of western redcedar generally had more *chl-a,b* and total *chl* (*a+b*) content on a dry weight basis (Table 1). This is probably an acclimation of DS seedlings to maximize their light capturing ability in low light limited environment (Boardman, 1977; Givnish, 1988). A similar pattern of acclimation was found in Sitka spruce and European Beech (Lewandowska *et al.* 1976; Lichtenthaler *et al.* 1981). Increased chlorophyll content (dry weight basis) in shade plants has been shown to be largely due to the increase in *chl-b* (Armond *et al.* 1977; Boardman, 1977; Butler, 1978). Since *chl-b* is mainly associated with the PS II light harvesting complex (Butler, 1978), an increase in this component will also increase a plant's light harvesting ability (Goodchild *et al.* 1972; Björkman *et al.* 1972; Boardman, 1977). As a result, a lower *chl a/b* ratio can be expected in plants grown under low light conditions (Anderson *et al.* 1988) as compared to the higher *chl a/b* ratios commonly observed in sun grown leaves (*e.g.*, Boardman, 1977; Givnish, 1988). In this research, however, significantly higher *chl a/b* ratio in full sun grown seedlings was only found in April 1992. This may be due to

the higher carotenoid/chlorophyll (*car/chl*) ratio in FS leaves compare to DS seedlings.

Significantly higher *car/chl* ratio in FS than DS seedlings was found in March, June 1991, and April 1992 which may be responsible for the bronzy color changes in FS and some MS leaves, particularly in winter. Weger *et al.* (1993) suggest that rhodoxanthin was responsible for the color change in overwintering western redcedar leaves. Increased carotenoid content in Sitka spruce leaves was also found at low temperatures (Turner & Jarvis, 1975).

Carotenoids have two main functions in the photosynthetic system: (1) as an accessory light harvesting pigment which passes energy on to chlorophyll, and (2) as protection of the photosynthetic apparatus from light stress through carotenoid quenching (see *e.g.*, Siefermann-Harms, 1985, 1987; Codgell, 1988; Koyama, 1991; Huner *et al.* 1993; Owens, 1994). Recent research on the protective function of carotenoids involves the interconversion of three xanthophylls : Violaxanthin (V), Antheraxanthin (A) and Zeaxanthin (Z) (Demmig-Adams, 1990).

In winter, the protective action of carotenoids becomes particularly important especially under high light and low temperature conditions where the absorption of light may exceed the chloroplast's capacity for using products of the photochemical reactions (Powles, 1984). Without the

xanthophyll interconversion, the excess light energy may cause photodamage in the chloroplast (Björkman & Powles, 1984; Vidaver *et al.* 1991; Huner *et al.* 1993; Owens, 1994). To accommodate such environmental conditions, some conifers have the ability to dissipate the excess excitation light energy (Vidaver *et al.* 1991, Gillies, 1993; Osmond, 1994). The carotenoid zeaxanthin is believed to mediate this response in *Nerium oleander* (Demmig *et al.* 1988) and in western redcedar (Weger *et al.* 1993).

A similar bronzy color developed in FS seedlings in summer and may be caused by high light-water deficit stress.

Pigment changes which occur both in winter and summer demonstrate the ability of western redcedar to acclimate to (1) high light-low temperature, and (2) high light-water deficit stress, and in FS grown seedlings may serve as a protective mechanism against photoinhibition, *i.e.*, the light driven-dependent inhibition of the light dependent reactions of photosynthesis (Osmond, 1994). Western redcedar have been found to acclimate to high light environment by developing more wax on the adaxial leaf surface (Krasowski & Owens, 1991; Sasaerila, *et al.* 1991), which is commonly found in high light grown plant as a protection against photodamage. This protection also decreases photosynthetic rates (Stuhkfauth *et al.* 1990; Vidaver *et al.* 1991; Ögren, 1994), and as a consequence may

reduce the RGR of the FS seedlings despite higher available light energy.

Moderate shade treatment creates the most favorable growing conditions for western redcedar as shown by the superior growth of MS grown seedlings. The conclusion that western redcedar is a moderate shade tolerant tree species (Klinka *et al.* 1990; Minore, 1990; Kozlowski *et al.* 1991) seems to be supported by this research.

The effects of shade on seasonal patterns of CO_2 exchange and F_{var} transients

The photosynthetic characteristics of western redcedar seedlings appeared to be related to the light conditions under which they were grown as reported for other species (Björkman *et al.* 1972; Boardman, 1977; Givnish, 1988). High light grown seedlings (FS) showed higher light saturation rates and dark respiration rates (leaf area basis) than shaded seedlings (Fig. 36).

Deep shade grown seedlings exhibited higher photosynthetic rates (dry weight basis) compared to those of FS or MS seedlings (Fig. 29A). In this research, FS grown seedlings are more likely to experience higher temperatures in the summer, which could induce at least a moderate water deficit condition due to higher transpiration or low leaf

water potential. Low leaf water potential may cause increased resistance to CO_2 diffusion (Hodges & Scott, 1968), and hence a decrease in the CO_2 exchange rates of FS grown seedlings. Higher photosynthetic rates per dry weight in shade grown seedlings were also found in field experiments with Douglas-fir, grand fir, western hemlock, Sitka spruce, noble fir and scots pine (Hodges & Scott, 1968), and in beech (Lichtenthaler, 1981). Hodges & Scott (1968) found that higher photosynthetic rates in shade grown seedlings for all six species could still be obtained even 2-3 weeks after placing the shade plants in full sun conditions and on clear sunny days. However, other evidence has also shown that sun leaves have a greater mesophyll resistance (larger mesophyll area) than shade leaves (Nobel *et al.* 1975; Öquist *et al.* 1982; Prioul *et al.* 1975), and this resistance is the primary resistance for CO_2 transfer to the site of CO_2 fixation.

Another explanation for the low photosynthesis (dry weight basis) in FS seedlings, may be due to a repair process of the photosystem reaction center which reduced the efficiency and potential of photosynthesis (Long *et al.* 1992; Öquist *et al.* 1992; Huner *et al.* 1993; Ögren, 1994). The effect of high PFD on western redcedar grown under full sun, with or without the combination of low temperature in the winter or high temperature in the summer, had probably

induced photoinhibition in FS seedlings (*e.g.*, see review by Nishio *et al.* 1994). This process may be important as a mechanism to protect the photosynthetic apparatus from further damage. As noted by Öquist *et al.* 1992, photoinhibition is likely a long-term down-regulation of PS II photochemistry as a response to the demand for ATP and NADPH by the carbon reduction cycle under high light conditions, rather than merely damaging the photosynthetic apparatus. They reported that in sun plants there is an active repair cycle of PSII which substitutes photoinhibited reaction centers with photochemically active ones, thus conferring partial protection against photoinhibition.

Relatively higher dark respiration rates per unit leaf area and sF_o (Appendix II, Table 1) in FS seedlings supports the notion that higher respiration is needed by plants grown under harsh environments (Penning de Vries, 1975). Respiration is the sum of two functional components: growth respiration (*e.g.*, Lambers *et al.* 1983) and maintenance respiration (*e.g.*, Amthor, 1984). As defined by Penning de Vries (1975), maintenance respiration refers to the use of energy produced from CO_2 for (1) resynthesis of substances in the process of metabolism, *e.g.*, enzymatic protein, ribonucleic acid, and membrane lipids; (2) maintenance of required gradients of ions and metabolites, and (3) all processes involved in physiological acclimation and/or

adaptation to a changing or harsh environment. Thus, higher respiration rates in FS and also MS seedlings may be due to higher maintenance costs at the expense of growth of these two groups of seedlings. A question is why were the shoots of FS grown seedlings not as big as MS seedlings ? A possible explanation could be the higher maintenance respiration in the root than in the shoot (Hansen & Jensen, 1977; Hansen, 1978, 1979; Lambers et al. 1979, 1992). However, root respiration was not measured in this study. Slow growth in FS seedlings in the spring may also be the result of high maintenance respiration costs due to photoinhibition.

In February 1991, FS seedlings had the lowest photosynthetic rates (dry weight and leaf area basis), sF_o, sF_v/F_m, and $sF_{(p-t)}$, (Fig. 3A, 35A,B). In addition, consistently higher *car/chl* ratios in FS seedlings than the MS and DS grown seedlings may also contribute to the lower photosynthetic rates in FS seedlings perhaps due to their lower efficiency of "passing on" the excitation light energy as compared to chlorophyll (for review see Stuhlfauth *et al.* 1990).

1. Inactivation of photosynthesis

In late 1990 and early 1991, two main features of the F_{var} time course changed : (1) sF_p begins to decline in late fall and is accompanied by a decrease in CO_2 exchange rates, and (2) overall values of specific curve feature of the F_{var} transient (except sF_o) substantially decrease (Fig. 16).

Inactivation of photochemistry appears to account for the decline in sF_p, sF_t, sF_v/F_m of F_{var} transients and the photosynthetic rates from the three shade treatments to reach a winter minimum. Day length and temperature may be responsible for this inactivation as reported for norway spruce (Christersson, 1978) and white spruce seedlings (Vidaver *et al.* 1989). Consistent with the growth pattern previously discussed, the decline in photosynthetic activity toward winter also occurred first in DS seedlings, followed by MS and FS (note also the decreases of APS rates, sF_p and sF_t features of the F_{var} transient from October 1990 to February 1991 in Fig. 29). As mentioned earlier, due to the shade treatment applied to DS seedlings and features of the green house construction, much lower light intensity was received by DS seedlings as the plants entered the winter season. This low PFD and low temperature may have induced earlier inactivation of photosynthesis in DS seedlings due to the low available energy as compared to other treatments.

Excessive light absorption by photosynthetic antenna during low temperature periods, causes photoinhibition, which is the most common form of injury in the winter time (Öquist, 1983; Tao *et al.* 1988). In order to prevent or minimize the effects of photoinhibition, winter shading seems to be as essential as summer shading.

The decline in F_{var} signatures during the fall to winter transition period can be interpreted as inactivation of the oxygen evolving complex (OEC) as the high light-low temperature stress deepened, and is considered as a reversible inactivation of water splitting as well as a protective mechanism against photodamage (Vidaver *et al.* 1989). Similar results were found in a variety of stress resistant plants including evergreen conifers (Hawkins & Lister, 1985; Conroy *et al.* 1986; Dubé *et al.* 1986; Toivonen & Vidaver, 1988; Vidaver *et al.* 1989) and in *N. oleander* (Powles & Björkman, 1982). Inhibition of CO_2 assimilation by high light stress causes an increase in the production of superoxide due to the decreased demand for $NADPH^+$ (Furbank & Badger, 1983). If this production of superoxide exceeds the capacity of the scavenging system of the chloroplast, damage to membrane lipids and the thylakoid membrane would occur (Furbank & Badger, 1983). This explanation may apply to the steady decline in sF_p, sF_v/F_m and the photosynthetic rates in the winter as observed in this study. An alternative

explanation may involve changes in the chloroplast and thylakoid membrane, as have been reported for the fall-winter and winter-spring transition (Brugnoli & Björkman, 1992). Inactivation is thought to protect the chloroplast from photodamage during periods of stress such as chilling or water deficiency (Hawkins & Lister, 1985; Sibbald & Vidaver, 1987; Toivonen & Vidaver, 1988).

Evidence that only sF_v/F_m of MS and FS western redcedar seedlings significantly declined from November 1990 to February 1991 (Appendix II, Table 2) suggests the occurrence of a high light-low temperature stress in FS and MS seedlings which seems also indicated by the changes in their leaf color at this time.

2. The recovery of inactivated photosynthesis

The recovery from photosynthetic inactivation occurred earliest in DS, followed by MS and FS seedlings, which parallels the earlier new leaf growth found in DS seedlings. The changing environmental conditions in spring such as, increasing daylength and temperature, seems to provide more favorable growing conditions. For FS seedlings, however, the effect of high light-low temperature stress may have caused the degradation of the D1 protein (Kyle, 1987) as

seen from the lowest sF_v/F_m and/or sF_p and the changes in their leaf color. For FS seedlings, the recovery process of photosynthetic activity may involve some repair mechanism such as protein synthesis which may have not been necessary for the DS seedlings. An alternative explanation is that the high carotenoid content may also contribute to the slow response to the new growing season.

Overall, the recovery of photosynthetic activity was accompanied by an increase in all components of the F_{var} signature (Fig. 26A&B). This may indicate reactivation of the OEC as environmental conditions improve.

In 1991, new foliage developed from March to June and was associated with a pronounced sF_p spike in the F_{var} signature. However, a slightly different fluorescence signature (more rounded shape, with no sF_p spike) was detected at the end of 1991. As shown in Fig. 49, with new foliage present on the shoot (April 1992) there appears to be a different F_{var} pattern than when the shoot consists only of old leaves, as indicated by the decrease in sF_p, except for FS seedlings. A similar decrease in the F_{var} transient was also found by Hak *et al.* (1990) in ten tree species. For FS seedlings, however, it might be that FS seedlings had not yet developed as much new foliage as MS and DS seedlings.

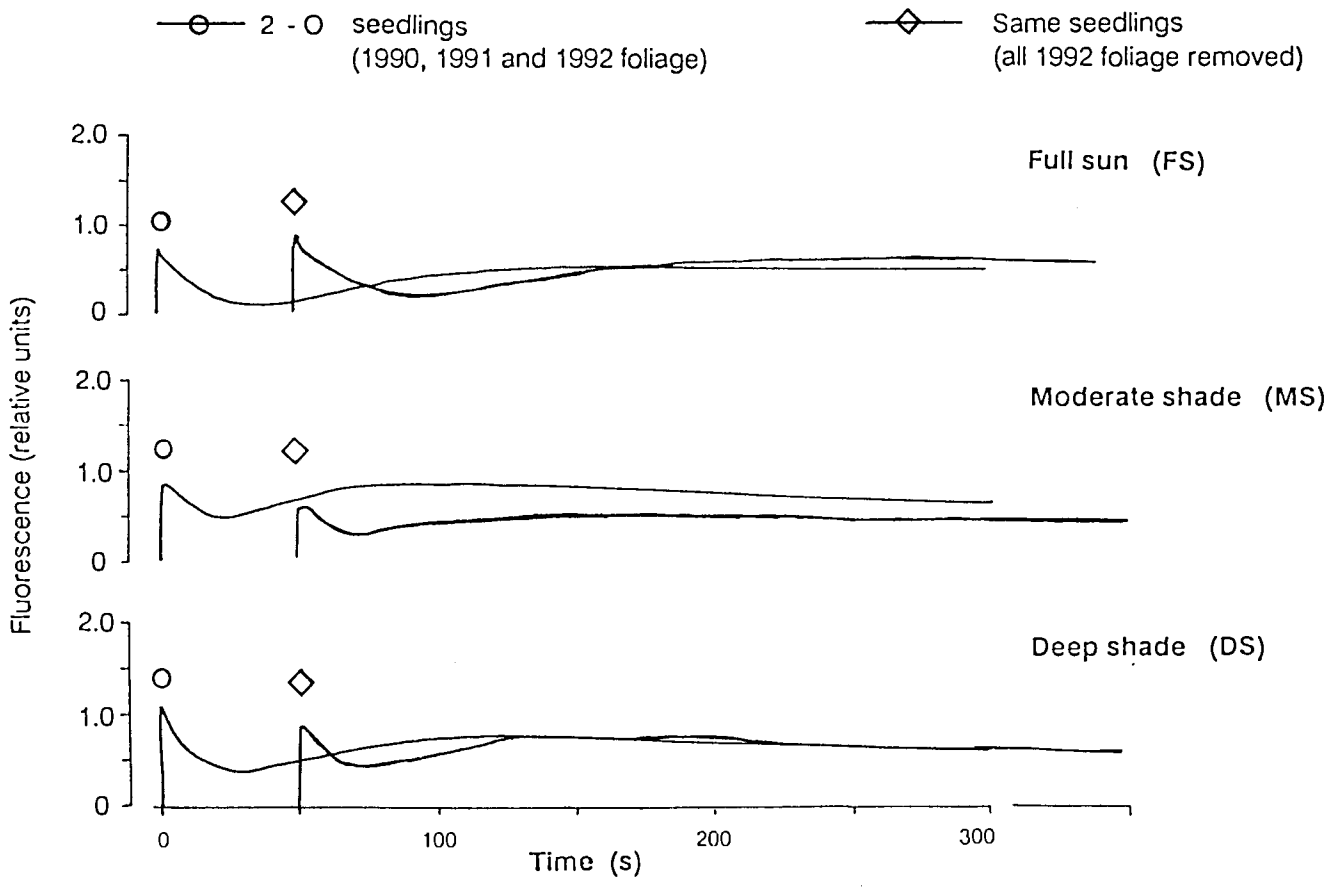


Figure 49. F_{var} fluorescence transient taken from 1990, 1991 and 1992 foliage, and without 1992 foliage of western redcedar seedlings grown under three shade treatments. (measurement was done in April 1992, n=5) (*cf.* Sasaerila & Brooke, 1992).

Effects of drought stress on photosynthesis and the F_{var} signature of second year western redcedar seedlings grown under three shade conditions

Regardless of the shade treatments given, photosynthesis and all features of the F_{var} transient (except sF_o) declined as the soil moisture content decreased (Fig. 48). Others have also found that a moderate leaf water deficit (decreased relative humidity) (Lange *et al.* 1971; Bunce, 1981), low soil water potential (Davies & Sharp, 1981; Gollan *et al.* 1986) caused a decline in the rate of leaf photosynthesis. Stomatal closure is recognized as the first line of defense against drought which prevents water loss (Brix, 1962). With closed stomata, the CO_2 exchange is also restricted. Thus zero net photosynthesis observed at the lowest soil moisture content (24% for FS and DS, 16% for MS) may be due to full stomatal closure (Jones, 1973; Levitt, 1980). In addition, water stress-related stomatal closure has been reported in many crops such as : cotton (Jordan & Ritchie, 1971), grape (Kriedelman & Smart, 1971); soybean (Boyer, 1970) and tomato (Duniway, 1971).

Much evidence has shown that drought also affects the non-stomatal components of the photosynthetic system (*e.g.*, Beadle & Jarvis, 1977; Bunce, 1977; Farquhar & Sharkey, 1982). One phenomenon that is consistently found in this

study, was that all components (except sF_O) of the F_{var} transient declined as drought stress increased. A similar drought response was found by Govindjee *et al.* 1980; Toivonen & Vidaver, 1988; Massaccii & Jones, 1990; Ögren, 1990.

Dry environments in nature are commonly accompanied with high PFD and temperatures. In such cases, light absorption can easily exceed the capacity of the chloroplast in using products of the photochemical reactions (Powles, 1984). When the photochemical capacity is exceeded, it may cause inactivation of the reaction centres or may cause photodamage to the chloroplast (Björkman & Powles, 1984; Gillies & Vidaver, 1990; Vidaver *et al.* 1991).

The bronzy color (increased carotenoid) developed by FS leaves under drought stress may support the hypothesis that a photoinhibitory stress under drought condition may exist in combination with high light (Björkman, 1987). This increase may be a mechanism to protect the photosynthetic apparatus from injury through dissipation of excess energy (Demmig-Adams, 1990). The absence of a bronzy color in leaves of shade seedlings may indicate the absence of photoinhibition (*e.g.*, Foyer *et al.* 1989; Björkman & Powles, 1984), or presence but only at a lesser degree (Krause, 1994).

There were no significant changes in sF_v/F_m ratio of water stressed western redcedar, a well known indicator of the presence of photoinhibition stress (Öquist *et al.* 1992).

The mechanism of photoinhibition is still not fully understood (Critchley, 1988; Krause, 1988; Öquist *et al.* 1992), nor is the recovery mechanism. Based on the type of photoinhibition, fast and slow recovery processes have been suggested (Öquist *et al.* 1992). Fast recovery occurs when photoinhibition is caused by the formation of a quencher in the antennae of PS II (Demmig & Björkman, 1987). This quencher has been reported by Demmig-Adams (1990) and supported by Weger *et al.* (1993) in western redcedar, to be a carotenoid (zeaxanthin) which causes a decrease in yield of photochemistry by competing with the PSII reaction centre. Recovery of this type is relatively fast because no protein synthesis is needed. Slow recovery occurs when photoinhibition has caused damage to the components of the reaction centre (photodamage), especially the D1 protein (Kyle, 1987). Protein synthesis is needed for this type of recovery to replace the damaged protein, and therefore will be slower.

In the drought experiment with western redcedar, more carotenoid and a relatively constant sF_v/F_m ratio (stable PS II) found in FS seedlings may indicate the occurrence of the first type of photoinhibition (and recovery). On the other

hand, the second type of recovery probably is responsible for the slow recovery of photosynthesis, hence spring growth in FS seedlings.

Chlorophyll-a fluorescence characteristics of sun and shade grown western redcedar

Unlike other characteristics of sun and shade grown plants, there is little information on differences in variable fluorescence of these plants. This may be caused by differences in instruments particularly as related to the excitation PFD being used in the measurements. Differences in seedling treatment just before measurement (preconditioning) may also contribute to these differences (Mohammed *et al. in press*). In this study, efforts to develop specific characteristics of F_{var} for sun and shade grown seedlings is difficult because fluorescence induction was measured at an excitation PFD of 100 $\mu mol.m^{-2}.s^{-1}$ which was below PFD required for light saturated photosynthetic rates. This is one of the weaknesses of the present integrating chlorophyll fluorescence instrument, in spite of its excellent solution for the sampling problem (Mohammed *et al. in press*). However, although the differences in F_{var} fluorescence components are not always statistically significant between sun and shade grown

western redcedar seedlings, they were consistently observed in this research. This difference is not only as a response to the given shade treatment but also to seasonal changes. These differences include : (1) sF_o, generally MS > DS > FS (Fig. 33A; Appendix II, Table 2), (2) sF_t, except for September to November 1992, generally in order of MS > DS > FS (Fig. 33B; Table 2), and (3) sF_v/F_m overall DS > MS > FS (Fig. 35A; Appendix II, Table 2).

Differences in anatomical structure, metabolic and physiological activity documented for sun and shade plants (*e.g.*, Schulze, 1972; Lichtenthaler *et al.* 1981), may cause differences in the variable fluorescence signal measured with an equal light intensity for all shade treatments in this research, for example, higher efficiency of light capturing systems in deep shade grown seedlings. Light intensity which may be too high for shade grown plants, may not be high enough for FS grown plants. Results for F_{var} fluorescence of western redcedar measured at different excitation PFD showed that sF_o, sF_p, sF_v/F_m components (except sF_t) all decreased with decreasing PFD (Appendix III, Table 1,2).

It is important to keep in mind that this discussion mainly concerns results found in the first and second year (1990 and 1991), because a different software program and instrument were used for 1992 data. Moreover, limitation in

growing space for roots, drought stress (water deficits, nutritional), and self-shading factors may have influenced characteristics of the chlorophyll fluorescence transients in 1992.

The absolute height (sF_p) of the F_{var} signature was generally higher in DS seedling than in FS seedlings (Fig. 26). The greater light absorption and reabsorption in sun leaves than shade leaves, which reduces the amount of light emitted to the fluorescence detector (Stein *et al.* 1990) might explain this difference. Sun grown conifers often have a double layer of palisade mesophyll as opposed to a single layer in leaves of shade grown plants (Vidaver *et al.* 1991). Near the end of 1991, sF_p of FS seedlings had increased relative to MS and DS seedlings (Fig. 26). This could be due to the effect of self-shading and the acclimation of old and new leaves to the light environment after the first year growth.

Steady state fluorescence, sF_t, of all seedlings of western redcedar showed high response to seasonal environmental changes, and thus, can be used as a good indicator for a stress environment. For example, a significantly low sF_t of FS seedlings coincided with the high light and low temperature stress between November 1990 and February 1991, and the high light and temperature conditions that may have contributed to water stress between

June and August 1991. Under more favorable growing conditions such as between August and November 1991, sF_t of FS seedlings began to increase (Fig. 33B). sF_t had a strong relationship with photosynthetic rate (sF_o basis) (Fig. 34) and thus shows a close relationship with CO_2 fixation as already established by others (Hipkins & Baker, 1986).

Effects of different intensity of light acclimation and light excitation on F_{var} fluorescence transients

The amount of fluorescence emission is determined by the duration and number of photons reaching the absorption pigments in the leaf from which fluorescence is detected, and also by the efficiency of photosynthetic quantum conversion (Lichtenthaler *et al.* 1981; Lichtenthaler *et al.* 1986; Murphy, 1990).

In this research, regardless of the shade treatments, the sF_o, sF_p, sF_v/F_m (calculated based on the sF_p) of western redcedar seedlings declined with decreasing excitation PFD (Fig. 35, 40; Appendix III, Table 1,2) probably due to the diminished amount of de-excitation processes such as chlorophyll fluorescence at lower PFD. This result supports the contention that the higher the light intensity, the more chlorophyll will be reached and

activated, and consequently, the more fluorescence emission will be detected resulting in higher sF_p components.

An interesting result from the experiments with light intensity, is that the highest sF_v/F_m ratio occurred at the highest excitation PFD (400 $\mu mol.m^{-2}.s^{-1}$). The lower sF_v/F_m (0.39 - 0.49) than commonly reported (0.6 - 0.8) (*e.g.*, Björkman & Demmig, 1987) was probably due to the lower excitation PFD (100 $\mu mol.m^{-2}.s^{-1}$) that was being used in the chlorophyll fluorescence measurement, as compared to the excitation PFD used with other instruments (Table 6). However, the fundamental difference between the integrated fluorometer and other fluorometers may be due to differences in determining the initial fluorescence (F_o or sF_o in this research). For western redcedar, the initial fluorescence (sF_o) was determined with an excitation PFD of 100 $\mu mol.m^{-2}.s^{-1}$, whereas 0.6 $\mu mol.m^{-2}.s^{-1}$ was used by Björkman & Demmig (1987). Increase in excitation PFD has been shown to increase sF_o in this research (Appendix III, Table 1&2). This increase affects the sF_v/F_m, *i.e.*, by increasing the denominator of the formula $sF_v/F_m = sF_p / (sF_p + sF_o)$, thus lowering sF_v/F_m.

Although sF_v/F_m found in this research is slightly lower than generally reported in the literatures, the seasonal fluctuation and variation of F_{var} components demonstrates the sensitivity and capability of the

integrating sphere fluorometer as a reliable physiological detector. However, an improvement in the instrument would be to provide different excitation PFD's for the determination of sF_o.

Table 6. Specification of chlorophyll fluorometer

PFD ($\mu mol.m^{-2}.s^{-1}$)	PSM Bio-Monitor	MFMS Hasan-. Tech Ltd.	PAM 101 Heinz Walz	Integrated Fluorometer
Actinic Beam	0 - 600	n/a	0 - 1000	100
Saturated beam	n/a	±5000	up to 10,000	100

Source : Bolhar-Nordenkampf *et al.* (1989); Mohammed, *et al.* (*in press*).

Conclusions: Application of Results to Forestry

There is an increasing need for forest planting stock to meet critical specifications, such as the ratio between above and below ground biomass, which determines the survival ability of seedlings. The stock must also be grown as inexpensively as possible.

This study demonstrates that providing shade growing conditions may be an inexpensive way to achieve a desired balance between root and shoot biomass. This study also provides growth and physiological data which demonstrates how variation in the light growing conditions can markedly alter the growth rate and form of western redcedar.

The implications of this study are also relevant to forest management. There is an obvious requirement to take into account, the quality and quantity of radiation reaching the planting sites (Messier & Bellefleur, 1988) and the significance of competing vegetation in altering the light environment of seedlings. For instance, moderately shaded western redcedar seedlings show a significant response to shoot elongation compared to those grown under deeply shaded or high light environments. Thus, moderate shade grown seedlings may be better competitors in the field. Other studies have shown that a reduction in light level to about 75% of full sunlight provides enough light for the survival

of most coastal conifers under a range of environmental conditions (Strothman, 1972; Emmingham & Waring, 1973). However, when the planting sites are likely to experience drought conditions, higher light growing conditions may be a better choice due to the better root formation which results in a higher competitive ability as compared to shaded seedlings.

Visual changes in the leaf color of western redcedar can be used as an indicator of the presence of a stress environment. It could be used as a warning sign of both stress conditions or the success in inducing stress-growth to western redcedar (for example, in order to promote more root than shoot growth).

The use of an integrating fluorometer as a rapid, non-destructive instrument for monitoring tree seedling physiology has had several reviews (*e.g.*, Öquist *et al.* 1992; Walker, 1992). F_{var} data for western redcedar seedlings show responses which correspond to seasonal environmental changes, drought and the light environment in which seedling growth occurs. However, the use of different measurement protocols between researchers raises questions about direct comparisons of F_{var} data obtained with different instruments. Therefore, searching for comparable F_{var} data by improving the assessment technique should be emphasized.

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Appendix I

Table 1. Greenhouse photon flux density ($\mu mol.m^{-2}.s^{-1}$) measured under both clear sunny and cloudy overcast skies at different times of the year (mean ± SE, n=5, except for * = single measurement).

Date	Time	Treatment	Light intensity: Above screen	Below screen	Under canopy	Percent below/above Screen	Canopy**
21-Jun-90 (Sunny)*	12:00	FS	1600	1600	-	100	
		MS	1500	700	-	47	
		DS	1450	320	-	22	
29-Sep-90 (Sunny)*	12:00	FS	1000	1000	-	100	
		MS	1065	700	-	66	
		DS	125	25	-	20	
3-Jul-91 (Sunny)*	12:00	FS	1500	1500	-	100	
		MS	1290	570	-	44	
		DS	1200	270	-	22	
11-Jul-91 (Cloudy)	12:00	FS	440	440	-	100	
		MS	386	178	-	46	
		DS	451	125	-	28	
5-Sep-91 (Sunny)	12:00	FS	1000	1000	-	100	
		MS	1000	450	-	45	
		DS	150	40	-	27	
25-May-92 (Sunny)	12:00	FS	1500	1500	-	100	
		MS	402	179	-	44	
		DS	425	110	-	26	
3-Aug-92 (Sunny)	12:00	FS	1500	1500	30	100	2.0
		MS	720	380	12.9	53	1.8
		DS	386	118	9	30	2.3
	17:00	FS	602	602	18	100	3.0
		MS	158	78	4	49	2.5
		DS	155	46	9	30	5.8
4-Aug-92 (Cloudy)	12:00	FS	296	296	14	100	4.7
		MS	246	128	3.8	52	1.5
		DS	234	72	7.4	31	3.2

Appendix I
Table 1. Continued.

20-Aug-92 (Sunny)	10:00	FS	1120	1120	21.2	100	2.0
		MS	658	362	4.4	55	0.7
		DS	174	37.4	6.6	21.5	3.8
	12:00	FS	1320	1320	31.2	100	2.4
		MS	578	309	2.4	53	0.4
		DS	562	119	4.3	21	0.8
	14:00	FS	1400	1400	28	100	2.0
		MS	807	400	4.8	50	1.2
		DS	178	57	4.2	32	2.4
	16:00	FS	914	914	23	100	2.5
		MS	414	200	3.2	48	0.8
		DS	156	44	1.8	28	1.1
22-Sep-92 (Sunny)	10:00	FS	1000	1000	17.2	100	1.7
		MS	484	268	5.4	55	1.1
		DS	370	79.2	6.2	21	1.7
	12:00	FS	1100	1100	21.6	100	2.0
		MS	676	346	3	51	0.4
		DS	150	40	2.6	27	1.7
	14:00	FS	1060	1060	20.2	100	1.9
		MS	1040	498	4	48	0.4
		DS	217	60	2.2	28	1.0
	16:00	FS	920	920	24	100	2.6
		MS	788	380	2.4	48	0.3
		DS	156	46	2	29	1.3
	18:00	FS	20	20	2	100	10.0
		MS	16	8	1.4	50	8.7
		DS	15	5	1.4	33	9.3

Appendix I
Table 1. Continued.

24-Sep-92	10:00	FS	50	50	2.8	100	5.6
(Cloudy)		MS	30	15.8	2	55	6.7
		DS	30	10.8	1.8	36	6.0
	12:00	FS	30	30	2	100	6.7
		MS	30	16.2	2	54	6.7
		DS	30	10	2	33	6.7
	14:00	FS	20	20	2	100	10.0
		MS	16	8	2	50	12.5
		DS	15	5	1.6	33	10.7
	16:00	FS	20	20	1.6	100	8.0
		MS	16	8	1.4	50	9.0
		DS	15	4.2	1.6	28	11.0
29-Oct-92	12:00	FS	400	400	7.6	100	1.9
(Sunny)		MS	380	178	2	47	0.5
		DS	150	40	2.2	27	1.5
28-Nov-92	12:00	FS	380	380	5.4	100	1.4
(Sunny)		MS	342	157	2	46	0.6
		DS	100	28	2.2	28	2.2
14-Dec-92	12:00	FS	320	320	6	100	1.9
(Sunny)		MS	280	142	2	51	0.7
		DS	100	26	2.4	26	2.4

Note : ** = Percentage of light below the tree canopy to that above the shade screen.

Appendix I

Table 2. Greenhouse photon flux density ($\mu mol.m^{-2}.s^{-1}$) measured above the screen under clear sunny and overcast cloudy days from mid June to December 1993 (mean ± SE, n=5).

Date/Time		Full sun	Moderate shade	Deep shade
12-Jun-93				
Sunny	10:00	1100 ± 0	1080 ± 20	1080 ± 20
	12:00	1500 ± 0	1300 ± 122	1200 ± 122
	14:00	1500 ± 0	796 ± 247	598 ± 246
	16:00	1040 ± 24	586 ± 169	290 ± 3
21-Jun-93				
Cloudy	12:00	138 ± 6	110 ± 11	108 ± 11
7-Jul-93				
Sunny	10:00	1100 ± 0	1060 ± 24	1060 ± 24
	12:00	1500 ± 0	1228 ± 248	1184 ± 244
	14:00	1500 ± 0	1260 ± 112	700 ± 307
	16:00	1200 ± 0	960 ± 103	354 ± 22
	18:00	1000 ± 0	360 ± 19	150 ± 0
22-Jul-93				
Cloudy	12:00	144 ± 2	106 ± 11	100 ± 4
15-Aug-93				
Sunny	10:00	882 ± 5	878 ± 7	866 ± 2
	12:00	906 ± 2	708 ± 5	380 ± 12
	14:00	1100 ± 0	780 ± 132	200 ± 0
	16:00	724 ± 51	556 ± 100	148 ± 21
21-Aug-93				
Cloudy	12:00	286 ± 2	236 ± 2	238 ± 2

Appendix I
Table 2. Continued.

Date		Full sun	Moderate shade	Deep shade
9-Sep-93				
Sunny	10:00	900 ± 3	804 ± 2	804 ± 2
	12:00	1100 ± 0	1060 ± 24	644 ± 114
	14:00	1020 ± 20	920 ± 49	368 ± 158
	16:00	612 ± 4	564 ± 41	94 ± 2
	18:00	19.6 ± 0	16 ± 0	16 ± 0
19-Sep-93				
Cloudy	10:00	50.2 ± 0	49.2 ± 0	49.2 ± 0
	12:00	30 ± 0	29.2 ± 0	29 ± 0
	14:00	20 ± 0	19.2 ± 0.4	19.2 ± 0.5
	16:00	19.4 ± 0.2	18.8 ± 0.5	19.6 ± 0.2
20-Oct-93				
Sunny	10:00	300 ± 0	264 ± 22	264 ± 22
	12:00	346 ± 2	314 ± 15	162 ± 5
	14:00	546 ± 2	480 ± 34	104 ± 2
21-Oct-93	16:00	402 ± 4	260 ± 39	55.4 ± 0
Sunny				
14-Oct-93				
Cloudy	12:00	20 ± 0	19 ± 0.4	19 ± 0.4
12-Nov-93				
Sunny	10:00	50.6 ± 0.4	50.4 ± 0.2	50.6 ± 0.2
	12:00	384 ± 2	330 ± 20	194 ± 2
	14:00	206 ± 2	192 ± 5	102 ± 4
	16:00	20 ± 0	16.8 ± 0.8	15.8 ± 0.2
13-Nov-93				
Cloudy	12:00	20 ± 0	18.8 ± 0.5	18.8 ± 0.5
Dec-93				
Sunny	12:00	292 ± 4.9	278 ± 2	97 ± 3.7
Dec-93				
Cloudy	12:00	20 ± 0	18.4 ± 0.4	18.4 ± 0.4

Appendix I
Table 3. Leaf area (mm^2) of western redcedar seedlings grown under three different shade conditions (mean ± SE, n=5).

HARVEST DATE		Shade Treatment		
		Full sun	Moderate Shade	Deep Shade
		Leaf Area		
1990	13-Nov	348 ± 32 *a*	412 ± 29 *a*	225 ± 14 *b*
1991	2-Feb	461 ± 22 *b*	660 ± 47 *a*	402 ± 31 *b*
	23-Mar	466 ± 19 *b*	850 ± 112 *a*	442 ± 70 *b*
	18-Apr	662 ± 39 *b*	1064 ± 141 *a*	784 ± 82 *ab*
	20-May	922 ± 86 *b*	1837 ± 167 *a*	1086 ± 173 *b*
	1-Jul	1176 ± 111 *b*	2203 ± 390 *a*	1699 ± 141 *ab*
	9-Aug	2770 ± 66 *b*	6532 ± 725 *a*	3684 ± 512 *b*
	8-Sep	3217 ± 333 *b*	6039 ± 387 *a*	3582 ± 461 *b*
	2-Oct	3397 ± 312 *c*	6646 ± 252 *a*	4558 ± 321 *b*
	9-Nov	*5037 ± 601 *b*	7013 ± 326 *a*	4064 ± 248 *b*
1992	14-Apr	5558 ± 501 *ab*	6770 ± 760 *a*	4239 ± 276 *b*
	18-May	5400 ± 326 *b*	8429 ± 215 *a*	4965 ± 205 *b*
	22-Nov	7020 ± 903 *b*	15326 ± 516 *a*	9310 ± 224 *b*

Notes:
Means with the same letter are not significantly different between treatments for a particular harvest date ($\alpha<0.05$, Student-Newman-Keuls test).

* n=4.

Appendix I

Table 4. Leaf, stem, shoot, root and total dry weights (mg) of western redcedar seedlings grown under three shade conditions (mean ± SE, n=5, except * n=4).

HARVEST DATE		Shade Treatment: Full sun	Moderate Shade	Deep Shade
			Leaf	
1990	31-Jul	5 ± 0.6 *a*	5 ± 0.4 *a*	3 ± 0.5 *b*
	21-Aug	15 ± 2 *a*	11 ± 1 *b*	7 ± 0.4 *c*
	11-Sep	43 ± 5 *a*	33 ± 3 *a*	18 ± 0.7 *b*
	2-Oct	76 ± 17 *a*	68 ± 7 *a*	28 ± 2 *b*
	13-Nov	69 ± 8 *a*	91 ± 7 *a*	34 ± 4 *b*
1991	2-Feb	117 ± 7 *a*	106 ± 6 *a*	47 ± 3 *b*
	23-Mar	123 ± 21 *a*	135 ± 13 *a*	49 ± 4 *b*
	18-Apr	157 ± 12 *a*	182 ± 17 *a*	60 ± 4 *b*
	20-May	191 ± 23 *a*	239 ± 25 *a*	111 ± 14 *b*
	1-Jul	224 ± 15 *b*	394 ± 52 *a*	185 ± 13 *b*
	9-Aug	433 ± 13 *a*	598 ± 70 *a*	300 ± 29 *b*
	8-Sep	586 ± 50 *a*	748 ± 33 *a*	399 ± 42 *b*
	2-Oct	610 ± 79 *a*	1029 ± 88 *a*	546 ± 106 *b*
	9-Nov	*970 ± 91 *a*	1105 ± 111 *a*	478 ± 55 *b*
1992	14-Apr	1461 ± 116 *a*	1309 ± 112 *a*	663 ± 55 *b*
	18-May	1303 ± 148 *a*	1558 ± 140 *a*	711 ± 63 *b*
	22-Nov	1554 ± 25 *b*	3005 ± 186 *a*	980 ± 211 *c*

Appendix I
Table 4. Continued.

	Date	Full sun		Moderate shade		Deep shade	
				Stem			
1990	31-Jul	1 ± 0.2	*a*	2 ± 0.2	*a*	2 ± 0.8	*a*
	21-Aug	5 ± 1	*a*	3 ± 1	*b*	2 ± 0.2	*b*
	11-Sep	14 ± 2	*a*	12 ± 1	*a*	6 ± 0.4	*b*
	2-Oct	33 ± 9	*a*	19 ± 1	*a*	8 ± 1	*b*
	13-Nov	18 ± 2	*b*	25 ± 2	*a*	10 ± 1	*c*
1991	2-Feb	33 ± 2	*a*	34 ± 4	*a*	16 ± 4	*b*
	23-Mar	33 ± 2	*a*	32 ± 5	*a*	17 ± 2	*b*
	18-Apr	33 ± 5	*a*	33 ± 4	*a*	16 ± 1	*b*
	20-May	40 ± 5	*a*	56 ± 9	*a*	24 ± 2	*b*
	1-Jul	52 ± 3	*b*	104 ± 11	*a*	48 ± 2	*b*
	9-Aug	108 ± 19	*b*	195 ± 19	*a*	75 ± 8	*b*
	8-Sep	173 ± 16	*b*	276 ± 7	*a*	128 ± 12	*c*
	2-Oct	216 ± 31	*b*	412 ± 34	*a*	173 ± 34	*b*
	9-Nov	*325 ± 35	*b*	423 ± 29	*a*	178 ± 14	*c*
1992	14-Apr	454 ± 40	*a*	537 ± 26	*a*	239 ± 29	*b*
	18-May	541 ± 81	*a*	682 ± 65	*a*	282 ± 30	*b*
	22-Nov	885 ± 112	*b*	1591 ± 65	*a*	498 ± 55	*c*

Appendix I
Table 4. Continued.

	Date	Full sun		Moderate shade		Deep shade	
				Shoot			
1990	31-Jul	6 ± 1	*a*	7 ± 1	*a*	4 ± 0.8	*a*
	21-Aug	21 ± 2	*a*	14 ± 2	*b*	9 ± 0.6	*c*
	11-Sep	57 ± 7	*a*	46 ± 4	*a*	24 ± 1	*b*
	2-Oct	109 ± 12	*a*	87 ± 8	*a*	36 ± 3	*b*
	13-Nov	86 ± 10	*a*	116 ± 8	*a*	45 ± 5	*b*
1991	2-Feb	149 ± 8	*a*	140 ± 8	*a*	63 ± 3	*b*
	23-Mar	156 ± 22	*a*	167 ± 16	*a*	66 ± 2	*b*
	18-Apr	189 ± 16	*a*	215 ± 20	*a*	75 ± 5	*b*
	20-May	231 ± 28	*a*	294 ± 33	*a*	135 ± 16	*b*
	1-Jul	276 ± 14	*b*	496 ± 53	*a*	232 ± 12	*b*
	9-Aug	541 ± 27	*b*	792 ± 84	*a*	375 ± 35	*c*
	8-Sep	759 ± 62	*b*	1024 ± 38	*a*	527 ± 51	*c*
	2-Oct	826 ± 108	*b*	1441 ± 120	*a*	719 ± 139	*b*
	9-Nov	*1296 ± 123	*a*	1528 ± 138	*a*	656 ± 67	*b*
1992	14-Apr	1914 ± 148	*a*	1846 ± 127	*a*	902 ± 78	*b*
	18-May	1844 ± 219	*a*	2239 ± 204	*a*	992 ± 89	*b*
	22-Nov	2439 ± 340	*b*	4596 ± 240	*a*	1477 ± 189	*c*

Appendix I
Table 4. Continued.

	Date	Full sun	Moderate shade	Deep shade
			Root	
1990	31-Jul	2 ± 0.3 *a*	2 ± 0.3 *a*	1 ± 0.2 *a*
	21-Aug	8 ± 0.8 *a*	5 ± 0.8 *b*	2 ± 0.3 *c*
	11-Sep	26 ± 3 *a*	12 ± 1.2 *b*	5 ± 0.3 *c*
	2-Oct	37 ± 8 *a*	24 ± 1.1 *a*	7 ± 0.5 *b*
	13-Nov	60 ± 6 *a*	43 ± 3 *b*	10 ± 0.8 *c*
1991	2-Feb	87 ± 10 *a*	53 ± 5 *b*	19 ± 1.1 *c*
	23-Mar	99 ± 15 *a*	57 ± 7 *b*	21 ± 2 *c*
	18-Apr	153 ± 12 *a*	88 ± 6 *b*	26 ± 3 *c*
	20-May	150 ± 24 *a*	111 ± 15 *a*	34 ± 3 *b*
	1-Jul	200 ± 30 *a*	196 ± 17 *a*	58 ± 6 *b*
	9-Aug	349 ± 26 *a*	214 ± 23 *b*	96 ± 11 *c*
	8-Sep	410 ± 31 *a*	264 ± 14 *b*	116 ± 9 *c*
	2-Oct	419 ± 22 *a*	293 ± 16 *a*	129 ± 30 *b*
	9-Nov	*551 ± 40 *a*	365 ± 41 *a*	169 ± 36 *b*
1992	14-Apr	953 ± 100 *a*	472 ± 51 *b*	186 ± 11 *c*
	18-May	894 ± 76 *a*	494 ± 49 *b*	212 ± 15 *c*
	22-Nov	1502 ± 232 *a*	1662 ± 286 *a*	556 ± 108 *b*

Appendix I.
Table 4. Continued.

	Date	Full sun		Moderate shade		Deep shade	
				Total			
1990	31-Jul	8 ± 1	*a*	9 ± 0.5	*a*	6 ± 0.9	*a*
	21-Aug	28 ± 3	*a*	19 ± 3	*b*	12 ± 0.5	*c*
	11-Sep	84 ± 10	*a*	58 ± 5	*b*	29 ± 1.1	*c*
	2-Oct	146 ± 12	*a*	111 ± 8	*b*	44 ± 3	*c*
	13-Nov	146 ± 16	*a*	159 ± 10	*a*	55 ± 6	*b*
1991	2-Feb	236 ± 15	*a*	193 ± 12	*b*	83 ± 4	*c*
	23-Mar	255 ± 35	*a*	224 ± 22	*a*	87 ± 5	*b*
	18-Apr	342 ± 26	*a*	303 ± 25	*a*	101 ± 7	*b*
	20-May	381 ± 47	*a*	405 ± 46	*a*	170 ± 18	*b*
	1-Jul	476 ± 36	*b*	693 ± 64	*a*	290 ± 15	*c*
	9-Aug	891 ± 47	*a*	1006 ± 101	*a*	472 ± 45	*b*
	8-Sep	1169 ± 73	*a*	1288 ± 48	*a*	643 ± 60	*b*
	2-Oct	1245 ± 117	*a*	1734 ± 136	*a*	848 ± 169	*b*
	9-Nov	*1847 ± 143	*a*	1893 ± 171	*a*	825 ± 98	*b*
1992	14-Apr	2867 ± 183	*a*	2318 ± 171	*a*	1088 ± 88	*b*
	18-May	2738 ± 282	*a*	2734 ± 247	*a*	1204 ± 87	*b*
	22-Nov	3941 ± 552	*b*	6258 ± 457	*a*	2034 ± 209	*c*

Notes:
Means with the same letter are not significantly different between treatments for a particular harvest date ($\alpha<0.05$, Student-Newman-Keuls test).
Within a treatment, means connected with the same vertical line are not significantly different ($\alpha<0.05$, Student-Newman-Keuls test).

Appendix I

Table 5. Shoot length (cm) of western redcedar seedlings grown under three shade treatments (mean ± SE, n=5).

DATE		Shade Treatment		
		Full sun	Moderate Shade	Deep Shade
1990	3-Jun	1.12 ± 0.08 *a*	1.25 ± 0.11 *a*	1.27 ± 0.07 *a*
	17-Jun	2.14 ± 0.16 *a*	2.22 ± 0.06 *a*	2.50 ± 0.14 *a*
	31-Jul	2.41 ± 0.15 *a*	2.92 ± 0.34 *a*	3.14 ± 0.33 *a*
	21-Aug	3.86 ± 0.20 *a*	3.75 ± 0.37 *a*	3.64 ± 0.24 *a*
	11-Sep	5.52 ± 0.33 *a*	6.66 ± 0.23 *a*	5.84 ± 0.37 *a*
	2-Oct	6.20 ± 0.46 *b*	8.14 ± 0.47 *a*	5.88 ± 0.26 *b*
	13-Nov	6.32 ± 0.48 *b*	8.20 ± 0.53 *a*	6.24 ± 0.30 *b*
1991	2-Feb	6.28 ± 0.27 *b*	8.18 ± 0.27 *a*	6.36 ± 0.20 *b*
	23-Mar	6.52 ± 0.26 *b*	8.12 ± 0.19 *a*	6.48 ± 0.30 *b*
	18-Apr	6.48 ± 0.40 *a*	8.58 ± 0.79 *a*	7.32 ± 0.39 *a*
	20-May	7.40 ± 0.35 *b*	10.12 ± 1.08 *a*	8.88 ± 0.34 *ab*
	1-Jul	8.18 ± 0.73 *c*	15.52 ± 1.03 *a*	11.94 ± 0.57 *b*
	9-Aug	12.68 ± 1.27 *b*	21.90 ± 0.80 *a*	14.54 ± 1.02 *b*
	8-Sep	16.90 ± 1.61 *b*	28.02 ± 1.07 *a*	18.26 ± 0.79 *b*
	2-Oct	19.46 ± 1.31 *b*	29.94 ± 0.82 *a*	18.20 ± 0.25 *b*
	9-Nov	23.42 ± 1.67 *b*	31.90 ± 0.89 *a*	21.74 ± 1.99 *b*
1992	14-Apr	25.00 ± 1.27 *b*	29.40 ± 0.66 *a*	22.18 ± 1.30 *b*
	18-May	29.30 ± 1.54 *b*	38.20 ± 0.78 *a*	24.80 ± 1.31 *c*
	22-Nov	32.47 ± 1.45 *b*	40.12 ± 1.52 *a*	28.23 ± 1.55 *b*

Notes:

Means with the same letter were not significantly different between treatments for a particular harvest date ($\alpha<0.05$, Student-Newman-Keuls test).

Within a treatment, means connected with the same vertical line are not significantly different ($\alpha<0.05$, Student-Newman-Keuls test).

Appendix I

Table 6. Root/shoot ratio, root weight ratio, leaf weight ratio, specific leaf area, leaf area ratio of western redcedar seedlings grown under three shade conditions (mean ± SE, n=5).

HARVEST DATE		Shade Treatment		
		Full sun	Moderate Shade	Deep Shade
			Root-shoot ratio	
1990	31-Jul	0.41 ± 0.03 *a*	0.31 ± 0.08 *a*	0.32 ± 0.04 *a*
	21-Aug	0.37 ± 0.02 *a*	0.33 ± 0.04 *a*	0.27 ± 0.04 *a*
	11-Sep	0.47 ± 0.03 *a*	0.26 ± 0.02 *b*	0.21 ± 0.01 *b*
	2-Oct	0.36 ± 0.08 *a*	0.28 ± 0.02 *a*	0.20 ± 0.01 *a*
	13-Nov	0.71 ± 0.06 *a*	0.37 ± 0.02 *b*	0.23 ± 0.01 *c*
1991	2-Feb	0.58 ± 0.06 *a*	0.38 ± 0.03 *b*	0.31 ± 0.02 *b*
	23-Mar	0.63 ± 0.06 *a*	0.34 ± 0.01 *b*	0.32 ± 0.04 *b*
	18-Apr	0.81 ± 0.04 *a*	0.41 ± 0.02 *b*	0.34 ± 0.02 *c*
	20-May	0.66 ± 0.07 *a*	0.38 ± 0.04 *b*	0.26 ± 0.03 *b*
	1-Jul	0.73 ± 0.11 *a*	0.40 ± 0.08 *b*	0.25 ± 0.03 *b*
	9-Aug	0.65 ± 0.04 *a*	0.28 ± 0.02 *b*	0.26 ± 0.01 *b*
	8-Sep	0.55 ± 0.06 *a*	0.26 ± 0.01 *b*	0.22 ± 0.01 *b*
	2-Oct	0.53 ± 0.06 *a*	0.20 ± 0.01 *b*	0.18 ± 0.01 *b*
	9-Nov	*0.43 ± 0.04 *a*	0.24 ± 0.02 *b*	0.25 ± 0.03 *b*
1992	14-Apr	0.51 ± 0.08 *a*	0.25 ± 0.02 *b*	0.21 ± 0.01 *b*
	18-May	0.49 ± 0.03 *a*	0.22 ± 0.01 *b*	0.22 ± 0.03 *b*
	22-Nov	0.62 ± 0.05 *a*	0.36 ± 0.05 *b*	0.40 ± 0.09 *b*

Appendix I
Table 6. Continued.

	DATE	Full sun	Moderate shade	Deep shade
		Root Weight Ratio		
1990	31-Jul	0.29 ± 0.01 *a*	0.23 ± 0.04 *a*	0.24 ± 0.02 *a*
	21-Aug	0.27 ± 0.02 *a*	0.24 ± 0.02 *a*	0.21 ± 0.02 *a*
	11-Sep	0.32 ± 0.01 *a*	0.21 ± 0.01 *b*	0.18 ± 0.01 *b*
	2-Oct	0.26 ± 0.04 *a*	0.22 ± 0.01 *a*	0.17 ± 0.01 *a*
	13-Nov	0.41 ± 0.02 *a*	0.27 ± 0.01 *b*	0.19 ± 0.01 *c*
1991	2-Feb	0.36 ± 0.03 *a*	0.28 ± 0.01 *b*	0.23 ± 0.01 *b*
	23-Mar	0.38 ± 0.02 *a*	0.25 ± 0.01 *b*	0.23 ± 0.02 *b*
	18-Apr	0.45 ± 0.01 *a*	0.29 ± 0.01 *b*	0.25 ± 0.01 *c*
	20-May	0.39 ± 0.03 *a*	0.27 ± 0.02 *b*	0.20 ± 0.01 *c*
	1-Jul	0.41 ± 0.04 *a*	0.29 ± 0.02 *b*	0.20 ± 0.02 *c*
	9-Aug	0.39 ± 0.01 *a*	0.22 ± 0.01 *b*	0.20 ± 0.01 *b*
	8-Sep	0.35 ± 0.02 *a*	0.20 ± 0.05 *b*	0.18 ± 0.01 *b*
	2-Oct	0.35 ± 0.03 *a*	0.17 ± 0.01 *b*	0.15 ± 0.01 *b*
	9-Nov	*0.30 ± 0.02 *a*	0.19 ± 0.01 *b*	0.20 ± 0.02 *b*
1992	14-Apr	0.33 ± 0.03 *a*	0.20 ± 0.01 *b*	0.17 ± 0.01 *b*
	18-May	0.33 ± 0.01 *a*	0.18 ± 0.01 *b*	0.18 ± 0.02 *b*
	22-Nov	0.38 ± 0.02 *a*	0.26 ± 0.03 *a*	0.29 ± 0.04 *a*

Appendix I
Table 6. Continued.

	DATE	Full sun	Moderate shade	Deep shade
		Leaf Weight Ratio		
1990	31-Jul	0.54 ± 0.01 *a*	0.60 ± 0.02 *a*	0.46 ± 0.08 *a*
	21-Aug	0.54 ± 0.01 *a*	0.60 ± 0.03 *a*	0.58 ± 0.02 *a*
	11-Sep	0.52 ± 0.01 *b*	0.57 ± 0.03 *a*	0.62 ± 0.01 *a*
	2-Oct	0.50 ± 0.09 *a*	0.61 ± 0.02 *a*	0.64 ± 0.01 *a*
	13-Nov	0.46 ± 0.01 *c*	0.57 ± 0.02 *a*	0.62 ± 0.01 *a*
1991	2-Feb	0.50 ± 0.03 *a*	0.55 ± 0.02 *a*	0.58 ± 0.04 *a*
	23-Mar	0.48 ± 0.02 *b*	0.61 ± 0.01 *a*	0.57 ± 0.04 *ab*
	18-Apr	0.46 ± 0.02 *b*	0.60 ± 0.01 *a*	0.60 ± 0.01 *a*
	20-May	0.50 ± 0.03 *b*	0.59 ± 0.01 *a*	0.65 ± 0.02 *a*
	1-Jul	0.48 ± 0.03 *b*	0.56 ± 0.03 *a*	0.64 ± 0.02 *a*
	9-Aug	0.49 ± 0.02 *b*	0.59 ± 0.02 *a*	0.64 ± 0.01 *a*
	8-Sep	0.50 ± 0.01 *b*	0.58 ± 0.01 *a*	0.62 ± 0.01 *a*
	2-Oct	0.48 ± 0.02 *b*	0.59 ± 0.01 *a*	0.64 ± 0.01 *a*
	9-Nov	*0.52 ± 0.02 *b*	0.58 ± 0.01 *a*	0.58 ± 0.01 *a*
1992	14-Apr	0.51 ± 0.02 *b*	0.56 ± 0.01 *ab*	0.61 ± 0.01 *a*
	18-May	0.47 ± 0.01 *b*	0.57 ± 0.02 *a*	0.59 ± 0.02 *a*
	22-Nov	0.39 ± 0.01 *a*	0.48 ± 0.02 *a*	0.41 ± 0.04 *a*

Appendix I
Table 6. Continued.

DATE		Full sun	Moderate shade	Deep shade
			Specific Leaf Area	
1990	13-Nov	5.19 ± 0.34 *b*	4.56 ± 0.14 *b*	6.65 ± 0.30 *a*
1991	2-Feb	3.95 ± 0.13 *c*	6.28 ± 0.50 *b*	8.59 ± 0.70 *a*
	23-Mar	4.31 ± 0.83 *b*	6.26 ± 0.54 *ab*	8.86 ± 1.04 *a*
	18-Apr	4.29 ± 0.32 *b*	5.99 ± 0.97 *b*	13.14 ± 1.19 *a*
	20-May	5.20 ± 1.03 *b*	7.77 ± 0.39 *a*	9.83 ± 0.93 *a*
	1-Jul	5.27 ± 0.47 *b*	5.49 ± 0.27 *b*	9.28 ± 0.83 *a*
	9-Aug	6.41 ± 0.22 *b*	11.03 ± 0.49 *a*	12.07 ± 0.60 *a*
	8-Sep	5.48 ± 0.25 *b*	8.15 ± 0.67 *a*	8.95 ± 0.50 *a*
	2-Oct	5.71 ± 0.38 *b*	6.58 ± 0.35 *b*	9.03 ± 0.88 *a*
	9-Nov	*5.20 ± 0.39 *b*	6.48 ± 0.35 *b*	8.89 ± 1.01 *a*
1992	14-Apr	3.83 ± 0.22 c	5.16 ± 0.25 b	6.48 ± 0.43 a
	18-May	4.38 ± 0.61 *b*	5.59 ± 0.51 *ab*	7.18 ± 0.58 *a*
	22-Nov	4.63 ± 0.28 *b*	5.14 ± 0.16 *b*	11.62 ± 2.19 *a*

Appendix I
Table 6. Continued.

DATE		Full sun	Moderate shade	Deep shade
			Leaf Area Ratio	
1990	13-Nov	2.42 ± 0.14 *b*	2.59 ± 0.11 *b*	4.16 ± 0.17 *a*
1991	2-Feb	1.98 ± 0.13 *c*	3.44 ± 0.24 *b*	4.94 ± 0.51 *a*
	23-Mar	2.01 ± 0.35 *b*	3.78 ± 0.30 *a*	5.06 ± 0.73 *a*
	18-Apr	1.96 ± 0.13 *c*	3.57 ± 0.53 *b*	7.74 ± 0.52 *a*
	20-May	2.57 ± 0.44 *c*	4.60 ± 0.25 *b*	6.31 ± 0.52 *a*
	1-Jul	2.56 ± 0.41 *b*	3.11 ± 0.29 *b*	5.88 ± 0.45 *a*
	9-Aug	3.14 ± 0.18 *c*	6.47 ± 0.25 *b*	7.68 ± 0.45 *a*
	8-Sep	2.74 ± 0.18 *b*	4.73 ± 0.39 *a*	5.51 ± 0.27 *a*
	2-Oct	2.74 ± 0.14 *c*	3.89 ± 0.18 *b*	5.83 ± 0.59 *a*
	9-Nov	*2.71 ± 0.15 *c*	3.76 ± 0.18 *b*	5.14 ± 0.56 *a*
1992	14-Apr	1.94 ± 0.14 *c*	2.90 ± 0.13 *b*	3.94 ± 0.23 *a*
	18-May	2.05 ± 0.24 *c*	3.19 ± 0.30 *b*	4.19 ± 0.28 *a*
	22-Nov	1.80 ± 0.09 *b*	2.48 ± 0.13 *b*	4.92 ± 1.12 *a*

Notes:
Means with the same letter are not significantly different between treatments for a particular harvest date ($\alpha<0.05$, Student-Newman-Keuls test).

* n=4.

Appendix I
Table 7. Mean RGR of root, shoot and total biomass ($mg.g^{-1}.day^{-1}$) of western redcedar seedlings grown under three shade conditions. Calculation based on the mean data from 02 June 1990, 13 November 1991 and 14 April 1992 for the 1990, 1991, and 1992 data respectively.

RGR-Root

HARVEST DATE		Shade Treatment		
		Full sun	Moderate Shade	Deep Shade
1990	2-Jun	0	0	0
	31-Jul	0.072	0.068	0.057
	21-Aug	0.067	0.059	0.048
	11-Sep	0.065	0.055	0.045
	2-Oct	0.055	0.051	0.039
	13-Nov	0.042	0.040	0.030
1991	2-Feb	0	0	0
	23-Mar	0.003	0.001	0.002
	18-Apr	0.008	0.007	0.004
	20-May	0.005	0.007	0.005
	1-Jul	0.006	0.009	0.007
	9-Aug	0.007	0.007	0.009
	8-Sep	0.007	0.007	0.008
	2-Oct	0.007	0.007	0.008
	9-Nov	0.007	0.007	0.008
1992	14-Apr	0	0	0
	18-May	-0.002	0.001	0.004
	22-Nov	0.002	0.006	0.005

ANOVA table of root relative growth rate based on RGR comparison method by Cain and Ormrod (1984). Comparison was only between RGR of November each year.

Source of Variance	DF	MS	Fvalue	P
Treatment	2	7.710	87.770	0.0001
Day	2	49.630	565.080	0.0001
Day*treatment	4	0.258	2.940	0.0335
Error	36	0.088		

Appendix I
Table 7. Continued.

RGR-Shoot

HARVEST DATE		Shade Treatment		
		Full sun	Moderate Shade	Deep Shade
1990	2-Jun	0	0	0
	31-Jul	0.067	0.070	0.059
	21-Aug	0.064	0.058	0.051
	11-Sep	0.060	0.058	0.049
	2-Oct	0.054	0.052	0.044
	13-Nov	0.037	0.039	0.032
1991	2-Feb	0	0	0
	23-Mar	0.001	0.004	0.001
	18-Apr	0.003	0.006	0.002
	20-May	0.004	0.007	0.007
	1-Jul	0.007	0.009	0.009
	9-Aug	0.007	0.009	0.009
	8-Sep	0.007	0.009	0.010
	2-Oct	0.007	0.010	0.010
	9-Nov	0.008	0.009	0.008
1992	14-Apr	0	0	0
	18-May	-0.001	0.006	0.003
	22-Nov	0.001	0.004	0.002

ANOVA table of shoot relative growth rate based on RGR comparison method by Cain and Ormrod (1984). Comparison was only between RGR of November each year.

Source of Variance	DF	MS	Fvalue	P
Treatment	2	3.774	69.830	0.0001
Day	2	50.153	928.030	0.0001
Day*treatment	4	0.085	1.580	0.0217
Error	36	0.054		

Appendix I
Table 7. Continued.

RGR-Total plant

HARVEST DATE		Shade Treatment		
		Full sun	Moderate Shade	Deep Shade
1990	2-Jun	0	0	0
	31-Jul	0.068	0.069	0.058
	21-Aug	0.065	0.058	0.050
	11-Sep	0.061	0.057	0.048
	2-Oct	0.054	0.052	0.043
	13-Nov	0.039	0.039	0.032
1991	2-Feb	0	0	0
	23-Mar	0.002	0.003	0.001
	18-Apr	0.005	0.006	0.003
	20-May	0.004	0.007	0.007
	1-Jul	0.005	0.009	0.008
	9-Aug	0.007	0.009	0.009
	8-Sep	0.007	0.009	0.009
	2-Oct	0.007	0.009	0.010
	9-Nov	0.007	0.008	0.008
1992	14-Apr	0	0	0
	18-May	-0.001	0.005	0.003
	22-Nov	0.001	0.004	0.003

ANOVA table of total relative growth rate based on RGR comparison method by Cain and Ormrod (1984). Comparison was only between RGR of November each year.

Source of Variance	DF	MS	Fvalue	P
Treatment	2	4.346	88.550	0.0001
Day	2	49.766	1013.000	0.0001
Day*treatment	4	0.095	1.950	0.1239
Error	36	0.049		

Appendix I

Table 8. Mean RGR of root, shoot and total biomass ($mg.g^{-1}.day^{-1}$) of western redcedar seedlings grown under three shade conditions. Calculation based on the mean data from 02 June 1990 harvest.

RGR-Root

HARVEST DATE		Shade Treatment		
		Full sun	Moderate Shade	Deep Shade
1990	2-Jun	0	0	0
	31-Jul	0.072	0.068	0.057
	21-Aug	0.067	0.059	0.048
	11-Sep	0.065	0.055	0.045
	2-Oct	0.055	0.051	0.039
	13-Nov	0.042	0.040	0.030
1991	2-Feb	0.029	0.027	0.022
	23-Mar	0.024	0.022	0.018
	18-Apr	0.023	0.022	0.018
	20-May	0.021	0.020	0.017
	1-Jul	0.020	0.020	0.016
	9-Aug	0.019	0.018	0.016
	8-Sep	0.018	0.017	0.015
	2-Oct	0.017	0.016	0.015
	9-Nov	0.017	0.016	0.014
1992	14-Apr	0.013	0.012	0.011
	18-May	0.013	0.012	0.011
	22-Nov	0.011	0.011	0.009

Appendix I
Table 8. Continued.

RGR-Shoot

HARVEST DATE		Shade Treatment		
		Full sun	Moderate Shade	Deep Shade
1990	2-Jun	0	0	0
	31-Jul	0.067	0.070	0.059
	21-Aug	0.064	0.058	0.051
	11-Sep	0.060	0.058	0.049
	2-Oct	0.054	0.052	0.044
	13-Nov	0.037	0.039	0.032
1991	2-Feb	0.026	0.026	0.022
	23-Mar	0.022	0.022	0.018
	18-Apr	0.020	0.021	0.017
	20-May	0.019	0.020	0.017
	1-Jul	0.017	0.019	0.017
	9-Aug	0.017	0.018	0.016
	8-Sep	0.017	0.018	0.016
	2-Oct	0.016	0.017	0.016
	9-Nov	0.016	0.016	0.015
1992	14-Apr	0.013	0.013	0.012
	18-May	0.012	0.012	0.011
	22-Nov	0.010	0.011	0.009

Appendix I

Table 8. Continued.

RGR-Total

HARVEST DATE		Shade Treatment		
		Full sun	Moderate Shade	Deep Shade
1990	2-Jun	0	0	0
	31-Jul	0.068	0.069	0.058
	21-Aug	0.065	0.058	0.050
	11-Sep	0.061	0.057	0.048
	2-Oct	0.054	0.052	0.043
	13-Nov	0.039	0.039	0.032
1991	2-Feb	0.027	0.026	0.022
	23-Mar	0.022	0.022	0.018
	18-Apr	0.021	0.021	0.017
	20-May	0.020	0.020	0.017
	1-Jul	0.018	0.019	0.017
	9-Aug	0.018	0.018	0.016
	8-Sep	0.017	0.018	0.016
	2-Oct	0.017	0.017	0.016
	9-Nov	0.016	0.016	0.014
1992	14-Apr	0.013	0.013	0.011
	18-May	0.012	0.012	0.011
	22-Nov	0.010	0.011	0.009

Appendix I

Table 9. NAR ($mg.dm^{-2}.day^{-1}$) of western redcedar seedlings grown under three shade conditions. Calculation based on the mean data from 02 June 1990 harvest.

HARVEST DATE		Shade Treatment		
		Full sun	Moderate Shade	Deep Shade
	13-Nov	0.0000	0.0000	0.0000
1991	2-Feb	0.0028	0.0008	0.0011
	23-Mar	0.0021	0.0008	0.0008
	18-Apr	0.0026	0.0013	0.0007
	20-May	0.0021	0.0014	0.0011
	1-Jul	0.0021	0.0022	0.0014
	9-Aug	0.0024	0.0014	0.0013
	8-Sep	0.0027	0.0018	0.0016
	2-Oct	0.0025	0.0022	0.0017
	9-Nov	0.0027	0.0021	0.0016
1992	14-Apr	0.0028	0.0018	0.0015
	18-May	0.0026	0.0018	0.0014
	22-Nov	0.0023	0.0020	0.0010

Appendix II

Table 1. CO_2 exchange rates of westren redcedar seedlings under three shade treatments. Rates expressed on the basis of : foliage oven dry weight (mg $CO_2.h^{-1}.g\ odw^{-1}$), leaf area (mg $CO_2.h^{-1}.dm^{-2}$), and sF_o (mg $CO_2.h^{-1}.0.01sF_o^{-1}$). (mean ± SE, n=5, unless indicated by * = 3, and ** = 4).

HARVEST DATE	Shade Treatment: Full sun [100%]	Moderate shade [49%]	Deep shade [27%]
	Photosynthetic rates (dry weight basis)		
1990 23-Oct	5.92 ± 0.47 *c*	10.93 ± 1.21 *b*	14.63 ± 0.62 *a*
13-Nov	5.32 ± 0.47 *b*	7.87 ± 1.11 *ab*	10.47 ± 1.56 *a*
1991 2-Feb	*2.45 ± 0.23 *b*	*4.32 ± 0.51 *a*	*5.08 ± 0.44 *a*
23-Mar	3.61 ± 0.91 *b*	5.43 ± 0.35 *ab*	8.06 ± 0.92 *a*
18-Apr	3.64 ± 0.40 *c*	6.79 ± 0.92 *b*	11.44 ± 0.91 *a*
1-Jul	9.69 ± 0.99 *b*	13.02 ± 0.43 *a*	15.75 ± 1.01 *a*
8-Aug	6.98 ± 0.58 *b*	8.39 ± 1.14 *ab*	11.55 ± 1.35 *a*
8-Sep	6.45 ± 0.54 *a*	10.45 ± 2.37 *a*	10.21 ± 0.42 *a*
2-Oct	7.23 ± 1.10 *a*	7.47 ± 0.49 *a*	9.41 ± 1.42 *a*
9-Nov	**7.20 ± 1.32 *a*	6.47 ± 0.31 *a*	7.75 ± 0.62 *a*
1992 14-Apr	4.52 ± 0.41 *b*	5.46 ± 0.48 *ab*	6.83 ± 0.75 *a*
18-May	5.22 ± 0.67 *b*	4.28 ± 0.43 *b*	7.41 ± 0.72 *a*
22-Nov	3.04 ± 0.42 *a*	2.89 ± 0.37 *a*	4.28 ± 1.26 *a*

Appendix II
Table 1. Continued.

	Date	Full sun	Moderate shade	Deep shade
		Dark respiration rates (dry weight basis)		
1990	23-Oct	1.67 ± 0.27 *b*	1.14 ± 0.19 *b*	2.92 ± 0.14 *a*
	13-Nov	1.43 ± 0.45 *ab*	0.84 ± 0.18 *a*	2.38 ± 0.39 *b*
1991	2-Feb	*0.44 ± 0.12 *a*	*0.63 ± 0.04 *a*	*0.66 ± 0.18 *a*
	23-Mar	1.00 ± 0.36 *a*	1.08 ± 0.03 *a*	1.10 ± 0.06 *a*
	18-Apr	1.68 ± 0.20 *a*	2.50 ± 0.52 *a*	2.94 ± 0.57 *a*
	1-Jul	1.57 ± 0.29 *a*	1.94 ± 0.12 *a*	2.08 ± 0.26 *a*
	8-Aug	1.50 ± 0.09 *b*	2.74 ± 0.19 *a*	1.45 ± 0.12 *b*
	8-Sep	2.36 ± 0.08 *a*	1.95 ± 0.18 *a*	1.90 ± 0.10 *a*
	2-Oct	3.21 ± 0.23 *a*	2.25 ± 0.35 *a*	2.88 ± 0.63 *a*
	9-Nov	**1.54 ± 0.37 *a*	1.12 ± 0.09 *a*	1.31 ± 0.29 *a*
1992	14-Apr	1.36 ± 0.07 *a*	1.29 ± 0.09 *a*	1.47 ± 0.05 *a*
	18-May	1.25 ± 0.12 *a*	1.84 ± 0.24 *a*	1.81 ± 0.14 *a*
	22-Nov	0.52 ± 0.06 *a*	0.44 ± 0.07 *a*	0.74 ± 0.12 *a*

Appendix II
Table 1. Continued.

Date	Full sun	Moderate shade	Deep shade
	Photosynthetic rates (leaf area basis)		
1990 13-Nov	9.31 ± 0.90 *b*	15.84 ± 2.50 *a*	12.94 ± 1.22 *ab*
1991 2-Feb	*5.38 ± 0.31 *a*	*5.90 ± 0.71 *a*	*5.88 ± 0.35 *a*
23-Mar	8.15 ± 1.09 *a*	8.80 ± 0.52 *a*	10.00 ± 2.16 *a*
18-Apr	8.08 ± 0.99 *a*	11.17 ± 1.54 *a*	7.92 ± 0.86 *a*
1-Jul	18.83 ± 2.33 *b*	24.05 ± 1.80 *a*	17.30 ± 1.32 *b*
8-Aug	10.87 ± 0.79 *a*	7.57 ± 0.94 *a*	9.80 ± 1.40 *a*
8-Sep	12.03 ± 1.47 *a*	12.89 ± 2.62 *a*	11.46 ± 0.38 *a*
2-Oct	12.75 ± 1.99 *a*	11.44 ± 0.79 *a*	10.15 ± 0.74 *a*
9-Nov	**13.5 ± 1.44 *a*	10.03 ± 0.34 *b*	9.10 ± 1.25 *b*
1992 14-Apr	12.22 ± 1.79 *a*	10.56 ± 0.67 *a*	10.50 ± 0.85 *a*
18-May	12.17 ± 1.07 *a*	7.66 ± 0.36 *b*	10.47 ± 0.92 *a*
22-Nov	10.88 ± 1.19 *a*	8.70 ± 1.36 *a*	8.71 ± 2.47 *a*

Appendix II
Table 1. Continued.

Date	Full sun	Moderate shade	Deep shade
	Dark respiration rates (leaf area basis)		
1990 13-Nov	2.30 ± 0.54 *a*	1.63 ± 0.30 *a*	3.03 ± 0.47 *a*
1991 2-Feb	*0.94 ± 0.21 *a*	*0.88 ± 0.13 *a*	*0.77 ± 0.22 *a*
23-Mar	2.06 ± 0.32 *a*	1.80 ± 0.21 *a*	1.35 ± 0.24 *a*
18-Apr	3.72 ± 0.40 *a*	3.87 ± 0.39 *a*	1.94 ± 0.25 *b*
1-Jul	3.12 ± 0.70 *a*	3.61 ± 0.40 *a*	2.24 ± 0.22 *a*
8-Aug	2.35 ± 0.18 *a*	2.49 ± 0.16 *a*	1.22 ± 0.13 *b*
8-Sep	4.35 ± 0.30 *a*	2.44 ± 0.26 *b*	2.13 ± 0.10 *b*
2-Oct	5.77 ± 0.62 *a*	3.44 ± 0.55 *b*	3.06 ± 0.47 *b*
9-Nov	**2.99 ± 0.74 *a*	1.74 ± 0.11 *a*	1.46 ± 0.30 *a*
1992 14-Apr	3.64 ± 0.39 *a*	2.52 ± 0.22 *b*	2.31 ± 0.12 *b*
18-May	2.99 ± 0.36 *a*	3.32 ± 0.39 *a*	2.54 ± 0.13 *a*
22-Nov	1.92 ± 0.25 *a*	1.30 ± 0.20 *a*	1.49 ± 0.22 *a*

Appendix II
Table 1. Continued.

	Date	Full sun	Moderate shade	Deep shade
		Photosynthetic rate (sFo basis)		
1990	23-Oct	0.39 ± 0.02 *b*	0.59 ± 0.04 *a*	0.35 ± 0.03 *b*
	13-Nov	0.30 ± 0.06 *b*	0.55 ± 0.06 *a*	0.37 ± 0.03 *ab*
1991	2-Feb	*0.31 ± 0.03 *a*	*0.13 ± 0.09 *a*	*0.25 ± 0.03 *a*
	23-Mar	0.44 ± 0.05 *a*	0.59 ± 0.07 *a*	0.47 ± 0.06 *a*
	18-Apr	0.66 ± 0.15 *a*	0.69 ± 0.04 *a*	0.56 ± 0.05 *a*
	1-Jul	1.52 ± 0.12 *a*	1.72 ± 0.43 *a*	1.32 ± 0.04 *a*
	8-Aug	1.36 ± 0.03 *a*	1.37 ± 0.24 *a*	1.14 ± 0.08 *a*
	8-Sep	1.42 ± 0.16 *b*	2.05 ± 0.47 *a*	1.43 ± 0.11 *b*
	2-Oct	1.86 ± 0.20 *b*	2.79 ± 0.25 *a*	1.93 ± 0.12 *b*
	9-Nov	**2.31 ± 0.59 *a*	2.02 ± 0.20 *a*	1.29 ± 0.10 *b*
1992	14-Apr	4.87 ± 0.53 *a*	4.50 ± 0.48 *a*	2.91 ± 0.16 *b*
	18-May	4.63 ± 0.42 *a*	4.09 ± 0.21 *ab*	3.27 ± 0.20 *b*
	22-Nov	4.17 ± 0.78 *a*	4.20 ± 0.53 *a*	4.04 ± 0.67 *a*

Appendix II

Table 1. Continued.

Date		Full sun	Moderate shade	Deep shade
		Dark respiration rates (sFo basis)		
1990	23-Oct	0.11 ± 0.02 *a*	0.06 ± 0.01 *b*	0.07 ± 0.01 *b*
	13-Nov	0.07 ± 0.01 *a*	0.06 ± 0.01 *a*	0.09 ± 0.01 *a*
1991	2-Feb	*0.05 ± 0.01 *a*	*0.02 ± 0.02 *a*	*0.03 ± 0.01 *a*
	23-Mar	0.11 ± 0.02 *a*	0.11 ± 0.01 *a*	0.06 ± 0.01 *b*
	18-Apr	0.30 ± 0.05 *a*	0.25 ± 0.03 *ab*	0.14 ± 0.03 *b*
	1-Jul	0.24 ± 0.04 *a*	0.25 ± 0.02 *a*	0.17 ± 0.01 *a*
	8-Aug	0.29 ± 0.03 *b*	0.45 ± 0.05 *a*	0.15 ± 0.02 *c*
	8-Sep	0.52 ± 0.04 *a*	0.38 ± 0.02 *b*	0.26 ± 0.01 *c*
	2-Oct	0.86 ± 0.07 *a*	0.85 ± 0.15 *a*	0.57 ± 0.06 *b*
	9-Nov	**0.45 ± 0.08 *a*	0.35 ± 0.04 *ab*	0.21 ± 0.05 *c*
1992	14-Apr	1.46 ± 0.10 *a*	1.05 ± 0.05 *ab*	0.64 ± 0.03 *b*
	18-May	1.13 ± 0.10 *b*	1.78 ± 0.22 *a*	0.80 ± 0.03 *c*
	22-Nov	0.70 ± 0.08 *a*	0.66 ± 0.12 *a*	0.74 ± 0.11 *a*

Notes:

Means with the same letter are not significantly different between treatments for a particular harvest date ($\alpha<0.05$, Student-Newman-Keuls test).
Within a treatment, means connected with the same vertical line are not significantly different ($\alpha<0.05$, Student-Newman-Keuls test).
Only about 2/3 of the seedling's shoot fit into the cuvette during the 1992 measurement.

Appendix II

Table 2. Variable chlorophyll fluorescence transient features of western redcedar grown under three shade treatments (mean ± SE, n=5, unless indicated by * n=3, and ** n=4).

HARVEST DATE		Shade Treatment: Full sun [100%]		Moderate shade [49%]		Deep shade [27%]	
		sFo (relative units)					
1990	23-Oct	71 ± 6	b	116 ± 4	a	71 ± 3	b
	13-Nov	114 ± 8	a	117 ± 4	a	78 ± 3	b
	14-Dec	70 ± 2	b	126 ± 9	a	83 ± 4	b
1991	2-Feb	*76 ± 2	b	*104 ± 2	a	*85 ± 8	b
	23-Mar	85 ± 3	b	126 ± 10	a	83 ± 3	b
	18-Apr	87 ± 10	b	163 ± 9	a	108 ± 5	b
	1-Jul	140 ± 5	c	297 ± 12	a	218 ± 7	b
	8-Aug	231 ± 17	b	360 ± 19	a	297 ± 30	ab
	8-Sep	266 ± 16	b	380 ± 4	a	282 ± 19	b
	2-Oct	223 ± 12	b	273 ± 2	a	237 ± 10	b
	9-Nov	**310 ± 13	b	353 ± 11	a	280 ± 9	b
1992	14-Apr	135 ± 4	b	158 ± 6	a	151 ± 4	a
	18-May	141 ± 2	b	158 ± 5	a	157 ± 3	a
	22-Nov	90 ± 4	a	104 ± 3	a	100 ± 5	a

Appendix II
Table 2. Continued.

DATE		Full sun	Moderate shade	Deep shade
		sFt (relative units)		
1990	23-Oct	0.20 ± 0.06 *b*	0.35 ± 0.04 *ab*	0.40 ± 0.09 *a*
	13-Nov	0.13 ± 0.02 *c*	0.50 ± 0.03 *a*	0.34 ± 0.05 *b*
	14-Dec	-0.23 ± 0.02 *b*	-0.03 ± 0.05 *a*	-0.11 ± 0.04 *a*
1991	2-Feb	*-0.12 ± 0.01 *a*	*-0.22 ± 0.06 *a*	*-0.16± 0.02 *a*
	23-Mar	0.13 ± 0.03 *a*	0.23 ± 0.07 *a*	0.19 ± 0.03 *a*
	18-Apr	0.07 ± 0.01 *a*	0.16 ± 0.03 *a*	0.09 ± 0.05 *a*
	1-Jul	0.30 ± 0.06 *b*	0.54 ± 0.04 *a*	0.43 ± 0.07 *ab*
	8-Aug	0.32 ± 0.08 *b*	0.70 ± 0.09 *a*	0.39 ± 0.07 *b*
	8-Sep	0.40 ± 0.09 *a*	0.54 ± 0.09 *a*	0.32 ± 0.04 *a*
	2-Oct	0.88 ± 0.08 *ab*	0.98 ± 0.04 *a*	0.69 ± 0.04 *b*
	9-Nov	**0.74 ± 0.04 *a*	0.80 ± 0.05 *a*	0.51 ± 0.1 *b*
1992	14-Apr	0.65 ± 0.08 *a*	0.74 ± 0.07 *a*	0.67 ± 0.04 *a*
	18-May	0.20 ± 0.05 *b*	0.29 ± 0.02 *b*	0.44 ± 0.03 *a*
	22-Nov	0.13 ± 0.04 *b*	0.10 ± 0.06 *b*	0.35 ± 0.07 *a*

Appendix II
Table 2. Continued.

DATE		Full sun	Moderate shade	Deep shade
		sFv/Fm (relative units)		
1990	23-Oct	0.61 ± 0.05 *b*	0.62 ± 0.01 *b*	0.70 ± 0.01 *a*
	13-Nov	0.70 ± 0.23 *a*	0.69 ± 0.02 *a*	0.68 ± 0.02 *a*
	14-Dec	0.55 ± 0.10 *b*	0.60 ± 0.01 *a*	0.65 ± 0.02 *a*
1991	2-Feb	*0.45 ± 0.12 *a*	*0.53 ± 0.03 *a*	*0.61 ± 0.05 *a*
	23-Mar	0.56 ± 0.11 *a*	0.65 ± 0.01 *a*	0.61 ± 0.03 *a*
	18-Apr	0.59 ± 0.08 *b*	0.70 ± 0.01 *a*	0.67 ± 0.02 *a*
	1-Jul	0.64 ± 0.07 *a*	0.62 ± 0.01 *a*	0.68 ± 0.01 *a*
	8-Aug	0.56 ± 0.19 *a*	0.49 ± 0.05 *a*	0.57 ± 0.02 *a*
	8-Sep	0.58 ± 0.05 *a*	0.50 ± 0.01 *b*	0.54 ± 0.02 *ab*
	2-Oct	0.44 ± 0.04 *a*	0.39 ± 0.01 *a*	0.39 ± 0.02 *a*
	9-Nov	**0.38 ± 0.05 *a*	0.41 ± 0.02 *a*	0.48 ± 0.05 *a*
1992	14-Apr	0.47 ± 0.04 *a*	0.51 ± 0.01 *a*	0.51 ± 0.04 *a*
	18-May	0.34 ± 0.02 *a*	0.33 ± 0.01 *a*	0.39 ± 0.01 *a*
	22-Nov	0.62 ± 0.12 *a*	0.53 ± 0.03 *a*	0.54 ± 0.06 *a*

Appendix II
Table 2. Continued.

DATE		Full sun	Moderate shade	Deep shade
		sF(p-t) (relative units)		
1990	23-Oct	1.40 ± 0.19 *b*	1.31 ± 0.04 *b*	1.96 ± 0.15 *a*
	13-Nov	2.23 ± 0.08 *a*	1.78 ± 0.22 *a*	1.80 ± 0.14 *a*
	14-Dec	1.47 ± 0.04 *b*	1.59 ± 0.09 *b*	1.99 ± 0.15 *a*
1991	2-Feb	*0.96 ± 0.18 *a*	*1.36 ± 0.05 *a*	*1.76 ± 0.33 *a*
	23-Mar	1.13 ± 0.11 *a*	1.59 ± 0.11 *a*	1.45 ± 0.26 *a*
	18-Apr	1.39 ± 0.08 *b*	2.12 ± 0.07 *a*	1.95 ± 0.17 *a*
	1-Jul	1.52 ± 0.19 *a*	1.10 ± 0.06 *b*	1.66 ± 0.08 *a*
	8-Aug	0.93 ± 0.11 *a*	0.31 ± 0.27 *a*	0.95 ± 0.10 *a*
	8-Sep	1.00 ± 0.24 *a*	0.46 ± 0.09 *a*	0.88 ± 0.11 *a*
	2-Oct	-0.05 ± 0.15 *a*	-0.34 ± 0.07 *a*	-0.06 ± 0.06 *a*
	9-Nov	**-0.14 ± 0.06 *a*	-0.11 ± 0.06 *a*	0.46 ± 0.25 *a*
1992	14-Apr	0.25 ± 0.02 *a*	0.33 ± 0.03 *a*	0.42 ± 0.18 *a*
	18-May	0.31 ± 0.07 *a*	0.21 ± 0.02 *a*	0.19 ± 0.01 *a*
	22-Nov	1.56 ± 0.19 *a*	1.05 ± 0.15 *a*	1.00 ± 0.33 *a*

Notes :

Means with the same letter are not significantly different between treatments for a particular harvest date ($\alpha<0.05$, Student-Newman-Keuls test).
Within a treatment, means connected with the same vertical line are not significantly different ($\alpha<0.05$, Student-Newman-Keuls test).
A different fluorometer and software were used for the 1992 measurements. In addition, only about 2/3 of the seedling's shoot was enclosed in the fluorometer sphere due to the seedlings size.

Appendix II

Table 3. Changes in photosynthetic rates (mg $CO_2.h^{-1}.plant^{-1}$) of 1-year-old (May 1991) western redcedar grown under three shade treatments as the response to changes in PFD ($\mu mol.m^{-2}.s^{-1}$). (Mean, n=2).

Light intensity ($\mu mol.m^{-2}.s^{-1}$)	Shade Treatment		
	Full sun	Moderate shade	Deep shade
1500	2.96	2.50	2.15
1250	2.96	2.50	2.15
1000	2.50	2.22	2.09
750	2.16	2.00	1.85
500	1.85	1.66	1.63
250	1.66	1.56	1.40
200	1.31	1.23	1.11
100	0.61	0.70	0.59

Appendix II

Table 4. Changes in photosynthetic rates (mg $CO_2.h^{-1}.plant^{-1}$) of 14-month-old (July 1991) western redcedar grown under three shade treatments as the response to changes in PFD ($\mu mol.m^{-2}.s^{-1}$). Based on a single measurement.

Light intensity ($\mu mol.m^{-2}.s^{-1}$)	Shade Treatment		
	Full sun	Moderate shade	Deep shade
1200	3.33	7.99	2.86
1000	3.33	7.99	2.86
800	3.00	7.99	2.86
600	2.66	6.95	2.58
400	1.95	6.66	2.50
200	1.67	5.00	1.95
100	0.73	2.66	0.89
Dark Resp.	0.50	0.64	0.34

Appendix II

Table 5. Changes in photosynthetic rates (mg $CO_2.h^{-1}.dm^{-2}$) of 2-year-old (August 1992) western redcedar grown under three shade treatments as the response to changes in PFD ($\mu mol.m^{-2}.s^{-1}$). (Mean ± SE, n=3).

Light Intensity (μmol.m-2.s-1)	Shade Treatment		
	Full sun [100%]	Moderate shade [49%]	Deep shade [27%]
1500	16.71 ± 2.4	13.57 ± 2.2	11.95 ± 0.8
1250	15.75 ± 2.4	13.57 ± 2.2	11.95 ± 0.8
1000	14.63 ± 2.2	12.27 ± 1.8	11.95 ± 0.8
750	13.70 ± 1.9	11.05 ± 1.6	11.41 ± 0.8
500	12.73 ± 1.8	10.05 ± 1.4	10.71 ± 0.8
250	8.96 ± 1.2	6.78 ± 0.7	7.74 ± 0.5
50	1.72 ± 0.3	1.48 ± 0.1	1.69 ± 0.4
Dark resp.	2.92 ± 0.2	2.15 ± 0.1	1.09 ± 0.0

Appendix III

Table 1. Components of chlorophyll fluorescence of two-year-old western redcedar seedlings, acclimated at the same PFD as the excitation PFD. (Mean ± SE, n=5).

PFD	Shade Treatment		
	Full sun [100%]	**Moderate shade** [49%]	**Deep shade** [27%]
sFo (relative units)			
25-->25*	8 ± 0.2c	11 ± 0.2a	10 ± 0.3b
50-->50	14 ± 0.6b	20 ± 0.7a	18 ± 0.3a
100-->100	30 ± 1.0b	49 ± 1.4a	46 ± 1.2a
200-->200	63 ± 1.8b	83 ± 1.8a	87 ± 1.4a
400-->400	128 ± 6.1b	170 ± 2.5a	159 ± 3.5a
sFp (relative units)			
25-->25	0.38 ± 0.02a	0.40 ± 0.01a	0.42 ± 0.01a
50-->50	0.49 ± 0.03a	0.46 ± 0.01a	0.46 ± 0.01a
100-->100	1.15 ± 0.12a	0.74 ± 0.04b	0.77 ± 0.04b
200-->200	2.07 ± 0.15a	1.53 ± 0.22b	1.25 ± 0.11b
400-->400	2.75 ± 0.19a	2.17 ± 0.30a	2.08 ± 0.19a

Appendix III
Table 1. Continued.

Treatment	Full sun	Moderate shade	Deep shade
sFt (relative units)			
25-->25	0.43 ± 0.07b	0.63 ± 0.05a	0.69 ± 0.05a
50-->50	0.39 ± 0.04b	0.66 ± 0.07a	0.71 ± 0.06a
100-->100	0.30 ± 0.03a	0.37 ± 0.07a	0.48 ± 0.04a
200-->200	0.24 ± 0.02b	0.31 ± 0.05ab	0.39 ± 0.03a
400-->400	-0.13 ± 0.05b	-0.002 ± 0.04ab	0.09 ± 0.02a
sFv/Fm (relative units)			
25-->25	0.28 ± 0.01a	0.29 ± 0.01a	0.30 ± 0.01a
50-->50	0.33 ± 0.02a	0.31 ± 0.01a	0.32 ± 0.01a
100-->100	0.53 ± 0.03a	0.43 ± 0.01b	0.43 ± 0.01b
200-->200	0.67 ± 0.02a	0.59 ± 0.04ab	0.55 ± 0.02a
400-->400	0.73 ± 0.01a	0.67 ± 0.03a	0.67 ± 0.02a

Below are mean sFv/Fm calculated from sFm where it was higher then sFp.

PFD	Full sun	Moderate shade	Deep shade
25-->25	0.57	0.51	0.51
50-->50	0.33	0.42	0.30
100-->100	0.53	0.46	0.47

Appendix III
Table 1. Continued.

PFD	Full sun	Moderate shade	Deep shade
Intensity of light absorbed (Iabs)			
25-->25	8 ± 0.1a	8 ± 0.1a	8 ± 0.3a
50-->50	24 ± 1.2b	31 ± 0.3a	29 ± 1.1ab
100-->100	59 ± 3.5a	62 ± 0.8a	57 ± 2.5a
200-->200	103 ± 5.2b	130 ± 2.4a	120 ± 2.8a
400-->400	206 ± 13.0b	249 ± 9.0a	239 ± 7.3a

Notes : Means with the same letter are not significantly different between treatments for a particular harvest date ($\alpha<0.05$, Student-Newman-Keuls test).

Within a treatment, means connected with the same vertical line are not significantly different ($\alpha<0.05$, Student-Newman-Keuls test).

* PFD during the 30 min light acclimation period ----> excitation PFD during fluorescence measurement.

Appendix III

Table 2. Components of variable fluorescence transient of 2-year-old western redcedar seedlings, acclimated at 300 $\mu mol.m^{-2}.s^{-1}$ and then measured at different PFD. (mean ± SE, n=5).

P F D	Shade Treatment		
	Full sun [100%]	**Moderate shade** [49%]	**Deep shade** [27%]
sFo (relative units)			
300-->25*	9 ± 0.5b	13 ± 0.4a	12 ± 0.4a
300-->50	17 ± 0.6c	24 ± 0.5a	22 ± 0.4b
300-->100	30 ± 2.2c	46 ± 1.0a	40 ± 0.7b
300-->200	66 ± 2.2c	92 ± 1.5a	83 ± 3.4b
300-->400	126 ± 6.1b	170 ± 2.5a	159 ± 3.2a
sFp (relative units)			
300-->25	0.41 ± 0.01a	0.40 ± 0.01a	0.39 ± 0.01a
300-->50	0.37 ± 0.03a	0.42 ± 0.01a	0.42 ± 0.01a
300-->100	0.98 ± 0.09a	0.69 ± 0.05b	0.64 ± 0.02b
300-->200	1.48 ± 0.07a	0.76 ± 0.02c	0.97 ± 0.09b
300-->400	3.31 ± 0.14a	2.44 ± 0.17b	2.25 ± 0.23b

Appendix III
Table 2. Continued.

P F D	Full sun	Moderate shade	Deep shade
sFt (relative units)			
300-->25	0.25 ± 0.03b	0.37 ± 0.065ab	0.45 ± 0.04a
300-->50	0.09 ± 0.02c	0.25 ± 0.052b	0.42 ± 0.04a
300-->100	0.09 ± 0.03b	0.19 ± 0.058b	0.36 ± 0.03a
300-->200	-0.002 ± 0.04a	0.04 ± 0.038a	0.09 ± 0.02a
300-->400	-0.030 ± 0.07a	0.002 ± 0.046a	0.07 ± 0.04a
sFv/Fm (relative units)			
300-->25	0.29 ± 0.01a	0.28 ± 0.01a	0.28 ± 0.01a
300-->50	0.27 ± 0.01a	0.30 ± 0.01a	0.30 ± 0.01a
300-->100	0.49 ± 0.03a	0.41 ± 0.02b	0.39 ± 0.01b
300-->200	0.60 ± 0.01a	0.43 ± 0.01b	0.49 ± 0.02b
300-->400	0.77 ± 0.01a	0.71 ± 0.02b	0.69 ± 0.02b

Below are mean sFv/Fm calculated from sFm where it was higher than sFp.

P F D	Full sun	Moderate shade	Deep shade
300-->25	0.57	0.51	0.51
300-->50	0.33	0.42	0.30

Appendix III
Table 2. Continued.

P F D	Full sun	Moderate shade	Deep shade
Intensity of light absorbed (Iabs)			
300-->25	10 ± 0.9b	15 ± 0.6a	15 ± 0.6a
300-->50	25 ± 1.1b	33 ± 1.1a	31 ± 1.9a
300-->100	50 ± 3.8b	64 ± 1.1a	62 ± 2.6a
300-->200	102 ± 4.2c	133 ± 2.7a	116 ± 3.4b
300-->400	204 ± 10.8b	258 ± 31.5a	250 ± 5.6a

Notes : Means with the same letter are not significantly different between treatments for a particular harvest date ($\alpha<0.05$, Student-Newman-Keuls test).

Within a treatment, means connected with the same vertical line are not significantly different ($\alpha<0.05$, Student-Newman-Keuls test).

* PFD during the 30 min light acclimation period, -----> excitation PFD during the fluorescence measurement.

Appendix IV

Table 1. Maximum, minimum and average green house temperature and relative humidity conditions during the drought experiment (06 August - 28 September 1991).

Date	Temperature			Relative humidity (%)		
	Max	Min	Avg	Max	Min	Avg
August						
6	30.0	13.5	21.8	60	31	45.5
7	23.0	16.5	19.8	72	30	51.0
8	20.5	11.0	15.8	71	40	55.5
9	19.5	13.5	16.5	75	56	65.5
10	12.4	11.0	11.7	80	57	68.5
11	18.5	10.5	14.5	80	74	77.0
12	20.0	12.8	16.4	75	44	59.5
13	33.9	13.0	23.5	80	24	52.0
14	36.9	17.0	27.0	67	21	44.0
15	38.5	18.0	28.3	65	21	43.0
16	32.2	18.0	25.1	64	31	47.5
17	31.9	17.0	24.5	74	30	52.0
18	32.0	17.5	24.8	75	27	51.0
19	32.5	16.0	24.3	61	26	43.5
20	30.0	15.5	22.8	76	26	51.0
21	32.0	16.5	24.3	72	25	48.5
22	30.0	16.0	23.0	72	27	49.5
23	18.5	12.0	15.3	73	40	56.5
24	25.0	10.0	17.5	80	26	53.0
25	25.5	11.6	18.6	79	26	52.5
26	15.0	12.0	13.5	80	55	67.5
27	14.0	10.0	12.0	80	68	74.0
28	11.8	10.5	11.2	80	76	78.0
29	16.7	10.5	13.6	80	57	68.5
30	14.5	12.0	13.3	79	75	77.0
31	15.0	9.5	12.3	81	64	72.5

Appendix IV
Table 1. Continued.

Date	Temperature			Relative humidity (%)		
	Max	Min	Avg	Max	Min	Avg
September						
1	22.5	8.0	15.3	75	27	51.0
2	30.0	15.9	23.0	55	26	40.5
3	29.0	13.0	21.0	64	24	44.0
4	31.5	14.9	23.2	59	24	41.5
5	31.0	15.5	23.3	65	26	45.5
6	23.5	14.0	18.8	71	41	56.0
7	14.0	11.0	12.5	76	56	66.0
8	22.6	9.8	16.2	77	29	53.0
9	26.0	22.0	24.0	50	25	37.5
10	27.0	25.5	26.3	51	22	36.5
11	26.0	25.0	25.5	46	24	35.0
12	15.9	11.5	13.7	65	32	48.5
13	18.0	8.5	13.3	80	30	55.0
14	21.0	9.0	15.0	74	29	51.5
15	23.5	11.5	17.5	72	26	49.0
16	32.5	13.0	22.8	50	27	38.5
17	27.5	25.5	26.5	61	25	43.0
18	-	-	-	68	27	47.5
19	28.5	13.0	20.8	78	55	66.5
20	18.0	9.5	13.8	80	30	55.0
21	12.9	10.0	11.5	74	35	54.5
22	15.0	10.5	12.8	73	45	59.0
23	27.0	11.0	19.0	71	25	48.0
24	28.0	26.0	27.0	60	25	42.5
25	30.5	27.5	29.0	51	23	37.0
26	30.2	29.0	29.6	65	29	47.0
27	14.5	11.7	13.1	79	64	71.5
28	15.0	11.5	13.3	79	64	71.5

Appendix IV

Table 2. Photosynthetic rate and components of variable fluorescence of 1-year-old western redcedar seedlings grown under three shade treatments experiencing water stress condition

Percent Soil Water Content	**Photosynthesis** (sFo basis)	**sFp**	**sFt**	**sFv/Fm**
	Full sun			
76	1.51 ± 0.09	1.06 ± 0.19	0.25 ± 0.03	0.50 ± 0.04
51	1.13 ± 0.05	1.65 ± 0.13	0.11 ± 0.02	0.62 ± 0.02
33	0.63 ± 0.11	1.74 ± 0.20	-0.14 ± 0.04	0.62 ± 0.03
30	0.33 ± 0.06	1.70 ± 0.20	-0.15 ± 0.04	0.62 ± 0.03
24	0.00 ± 0.00	1.40 ± 0.23	-0.27 ± 0.04	0.57 ± 0.04
76	0.75 ± 0.05	1.13 ± 0.08	-0.22 ± 0.05	0.53 ± 0.02
	Moderate shade			
60	1.25 ± 0.07	0.75 ± 0.07	0.54 ± 0.05	0.42 ± 0.02
36	0.78 ± 0.02	1.40 ± 0.08	0.15 ± 0.04	0.58 ± 0.01
29	0.75 ± 0.07	1.26 ± 0.08	-0.02 ± 0.04	0.56 ± 0.02
26	0.50 ± 0.05	1.66 ± 0.09	0.06 ± 0.04	0.63 ± 0.01
16	0.00 ± 0.00	1.13 ± 0.07	-0.12 ± 0.02	0.53 ± 0.02
55	0.60 ± 0.06	1.28 ± 0.08	-0.07 ± 0.04	0.56 ± 0.01

Appendix IV
Table 2. Continued.

Percent Soil Water Content	Photosynthesis	sFp	sFt	sFv/Fm
	Deep shade			
73	1.10 ± 0.12	1.36 ± 0.10	0.54 ± 0.05	0.58 ± 0.02
45	1.07 ± 0.07	1.86 ± 0.11	0.15 ± 0.04	0.65 ± 0.01
39	0.60 ± 0.05	1.74 ± 0.12	-0.02 ± 0.04	0.63 ± 0.02
31	0.09 ± 0.03	1.76 ± 0.24	0.06 ± 0.04	0.63 ± 0.04
24	0.00 ± 0.00	1.07 ± 0.16	-0.12 ± 0.02	0.50 ± 0.04
72	0.59 ± 0.12	0.97 ± 0.16	-0.07 ± 0.04	0.48 ± 0.04

Means connected with the same vertical line are not significant between rows for percent water content ($\alpha<0.05$, Student-Newman-Keuls test).