IS THE EFFICIENCY OF SUNFLECK UTILIZATION AN IMPORTANT DETERMINANT OF SHADE TOLERANCE? A CASE STUDY WITH WESTERN REDCEDAR AND COASTAL DOUGLAS-FIR IN THE UNDERSTORY OF RED ALDER

by

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ABSTRACT

To determine whether efficient photosynthetic utilization of sunflecks may be an important determinant of shade tolerance among sympatric conifer species, transient and steady-state photosynthetic responses to light were characterized for two conifers of contrasting shade tolerance growing under a closed canopy of red alder (*Alnus rubra* Bong.). Western redcedar (*Thuja plicata* Donn) is a very shade tolerant species which can survive for extended periods in deep understory shade, whereas coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) exhibits poorer survival and is considered shade intolerant. The requirement for photosynthetic induction initially limited photosynthesis in both species by about 70%. Given constant high light, times to reach 50% and 90% of full photosynthetic induction were 3.5 and 31.8 minutes for redcedar and 2.2 and 19.8 minutes for Douglas-fir. However, despite requiring more time to become fully induced, redcedar attained similar or higher absolute photosynthetic rates (on both area and mass bases) as Douglas-fir during the same induction time-course. Little loss of induction occurred in either species during 2 and 5 minutes in shade, but redcedar maintained induction better than Douglas-fir after 15 and 30 minutes. This was, however, unlikely to be important on sunny days when the time between most sunflecks was ≤30 seconds and only rarely exceeded 5 minutes. When given a fluctuating light regime consisting of five 30 second lightflecks (simulated sunflecks) separated by 2 minute intervals of low light, redcedar achieved a similar induction state as Douglas-fir because it maintained a high rate of stomatal opening between lightflecks which compensated for its longer initial lag period for stomatal opening. Lightfleck use efficiency and the contribution of net post-illumination CO₂ fixation to the overall carbon gain attributable to lightflecks did not differ significantly between species, nor did absolute carbon gain or rates of carbon gain in fluctuating light. However, while the two species did not clearly separate on the basis of photosynthetic induction characteristics, gas exchange measurements under steady-state conditions indicated that redcedar had an approximately two-fold lower foliar dark respiration rate and light compensation point than Douglas-fir. It is concluded that interspecific differences in the efficiency of sunfleck utilization are much less likely to be important in explaining the contrasting shade tolerance of these species than differences in dark respiration.

**Key words:** coastal Douglas-fir – *Pseudotsuga menziesii* var. *menziesii*, lightflecks, photosynthetic induction, photosynthesis, red alder – *Alnus rubra*, respiration, shade tolerance, sunflecks, western redcedar – *Thuja plicata*
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CHAPTER 1
INTRODUCTION

1.1 BACKGROUND

In forestry, knowledge of the ecological characteristics of tree species has become an important foundation for making scientifically sound decisions regarding the suitability of various tree species for given sites, silvicultural systems, and treatments (Klinka and Feller 1984). Among these characteristics, shade tolerance, the capacity to survive and grow under low light conditions, has been considered of foremost importance, e.g., “a knowledge of [shade] tolerance and its implications for competitiveness and growth is fundamental to good silviculture and should support every management decision” (Daniel et al. 1979; also Klinka et al. 1990). This is probably more true today than ever before.

In recent years, a diversification or shift in societal values for forest resources, as well as the recognition by forest researchers and practitioners of the potential ecological benefits of alternative forest practices on some sites, has led to a multi-value approach to forest management that places increasing emphasis on objectives other than timber production. As a result, conventional clear-cutting and plantation-based silviculture (e.g., Lavender et al. 1990) is being increasingly supplemented or replaced with partial cutting and/or mixed-species and mixedwood silviculture (Smith et al. 1996; e.g., Hansen et al. 1995; Comeau and Thomas 1996; Arnott and Beese 1997; Coates and Burton 1997; Beese 1998; Cameron et al. 1999; Vyse 1999). Unlike plantation-based silviculture which bears close resemblance to simple agricultural systems (Colombo and Parker 1999), silvicultural systems which require tree species to survive and grow under canopy influence and/or in mixture with other tree species are largely driven by light. Not only are the effects of canopy influence on the survival and growth of individual species largely related to light limitations (see listing of light-growth/survival studies below), but interactions among individuals, and thus the stratification of tree species in mixture, likewise appear strongly driven by the competition for light (e.g., Kobe 1996). Not surprisingly then, the importance of a good understanding of shade tolerance is now recognized in legislation governing forest practices in British Columbia, particularly for silvicultural prescriptions involving species mixtures (Province of British Columbia 1995).

Much work has recently been done to advance knowledge of the quantitative relationships between light availability and the survival and growth of tree species under field conditions in British Columbia (Carter and Klinka 1992; Klinka et al. 1992; Wang et al. 1994; Chen et al. 1996; Kayahara et al. 1996; Chen 1997; Mailly and Kimmins 1997; Chen and Klinka 1998; Wright et al. 1998; Coates and Burton 1999; Williams et al. 1999; see also Kobe and Coates 1997). From this body of work, and concurrent studies elsewhere in North America (e.g., Lieffers and Stadt 1994; Pacala et al. 1994; Kobe et al. 1995; Kobe 1996; Pacala et al. 1996; Beaudet and Messier 1998;
Groot 1999; Messier et al. 1999) it has become clear that tree species of mid- and high-latitude forests do in fact differ in light-dependent survival and growth (i.e., they separate along the light-resource axis), albeit species rankings for absolute growth at low light do not necessarily conform to expectations set-out by traditional shade tolerance categorizations. Presumably, species differences in survival and growth in relation to light (vis à vis shade tolerance) can be related to variation in structural (morphological) and/or functional (physiological) traits which determine the capacity to acquire and use carbon efficiently (Horn 1971; Boardman 1977; Bazzaz 1979; Björkman 1981; Givnish 1988). However, although the morphological responses to light of tree species from mid- and high-latitudes have received considerable attention in recent years (e.g., Canham 1988; Leverenz and Hinckley 1990; Klinka et al. 1992; Walters et al. 1993a, b; Lieffers and Stadt 1994; Wang et al. 1994; Chen et al. 1996; Kayahara et al. 1996; Walters and Reich 1996; Chen 1997; Mailly and Kimmins 1997; Beaudet and Messier 1998; Chen and Klinka 1998; Messier et al. 1999b; Williams et al. 1999), the physiological mechanisms underlying the differences among these species in light-dependent survival and growth remain poorly understood.

To date, physiological studies of shade tolerance have largely focused on photosynthetic rates, probably because it has been generally assumed that maximization of carbon gain is central to adaptation to shade (Givnish 1988). The converse condition, rates of carbon loss through dark respiration, has been largely ignored. This is somewhat surprising given that dark respiration generally contributes proportionately more to net carbon balance as light availability decreases (e.g., Field 1988). Although it was suggested early on that one of the most important adaptations of shade tolerant plants might be a low respiration rate (Shirley 1945; Grime 1965), strong evidence for this has never been established. Rather, the hypothesis that in shaded habitats shade tolerant species have lower dark respiration rates than shade intolerant species has effectively evolved into a paradigm over the years (Givnish 1988) without ever being sufficiently tested (see Reich et al. 1998).

The strict focus on photosynthetic rates has also been somewhat paradoxical insofar as only steady-state rates have usually been measured (Chazdon 1988; Pearcy 1994). While such measurements demonstrate the potential for photosynthesis of understory plants, the ecological relevance of such measures is clearly questionable. Realization of full photosynthetic potential, particularly at high light levels, depends on constant light conditions of sufficient duration to allow for the attainment of steady-state photosynthetic rates. Such a situation may be unlikely under closed forest canopies where light conditions fluctuate continuously between low levels of diffuse light and intermittently high, predominantly direct light in the form of ‘sunflecks’ (Pearcy et al. 1994). Given that sunflecks can make a considerable contribution to total daily understory light (see reviews by Chazdon and Pearcy 1991 and Lieffers et al. 1999) and that non-steady-state (transient) photosynthetic responses to light can differ substantially from steady-state expectations for the same light level (Pearcy et al. 1994; Pearcy et al. 1997; Naumburg et al. 2001), it is possible that the success or failure of understory plants may be dependent, at least in part, on their capacity for efficient photosynthetic utilization of sunflecks (Chazdon and Pearcy 1991; Pearcy 1994).

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1 Delineation of forests as low-, mid-, or high-latitude follows Strahler and Strahler (1997).
The capacity for photosynthetic use of sunflecks has been extensively studied for diverse species of low-latitude (tropical) forests and to a lesser extent for herbaceous species of higher-latitude forests. Species differences in performance have been reported (e.g., see review by Chazdon 1988), and in some cases the growth of understory plants has been correlated with the availability of sunflecks (Pearcy 1983; Oberbauer et al. 1988; Sims and Pearcy 1993; Watling et al. 1997). In contrast, although the potential importance of sunflecks to forest tree species from mid- to high-latitudes has also been recognized for some time (Shirley 1945; Hodges 1967; Hodges and Scott 1968), only limited information on certain aspects of this issue is currently available for these species (Literature Review, Chapter 2). Indeed, the importance of sunflecks in the understories of these forests (Lieffers et al. 1999) and whether or not and to what extent tree species from these forests may differ in their capacities to use sunflecks (Messier et al. 1999a) have recently been identified as knowledge gaps needing to be filled.

1.2 PURPOSE AND OBJECTIVES

To determine whether efficient photosynthetic utilization of sunflecks might be an important physiological determinant of shade tolerance among sympatric conifer species, this thesis documents an investigation into the sunfleck activity beneath a closed canopy of red alder (*Alnus rubra* Bong.) and the comparative transient and steady-state photosynthetic performances and dark respiration of the saplings of two understory conifers of contrasting shade tolerance: western redcedar (*Thuja plicata* Donn) which is considered very tolerant of shade (Baker 1949; Daniel et al. 1979) and the coastal variety of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) which is generally considered intolerant of shade (e.g., Mailly and Kimmins 1997)\(^2\). The specific objectives are:

(i) to describe the distribution of sunflecks under a closed canopy of red alder in terms of their duration, frequency, and maximum photosynthetic photon flux density;

(ii) to quantify, compare, and contrast the photosynthetic light use efficiency of understory saplings of western redcedar and coastal Douglas-fir under non-steady-state (transient) conditions, including an analysis of their photosynthetic performance in a series of simulated sunflecks representative of the duration of natural sunflecks measured in (i);

(iii) to quantify, compare, and contrast the photosynthetic responses to light of understory saplings of western redcedar and coastal Douglas-fir under steady-state conditions;

(iv) to quantify, compare, and contrast the foliar dark respiration rates of understory saplings of western redcedar and coastal Douglas-fir; and

(v) to evaluate the extent to which the physiological characteristics measured in (ii), (iii), and (iv) are consistent with the putative shade tolerances of western redcedar and coastal Douglas-fir.

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\(^2\) Two varieties of Douglas-fir are distinguished regionally and considered to differ in shade tolerance (Hermann and Lavender 1990). The coastal variety (var. *menziesii*) is considered intolerant of shade (e.g., Mailly and Kimmins 1997), whereas the continental or interior variety (var. *glauca*) is usually regarded as moderately or intermediately tolerant of shade (Chen et al. 1996; Chen 1997; Chen and Klinka 1997).
CHAPTER 2
LITERATURE REVIEW

2.1 INTRODUCTION

Fluctuations in light are ubiquitous in nature. At one extreme, light levels may change over months or longer due to seasonal changes in solar angle, annual deciduous canopy leaf-off, and gap formation/closure (Lassoie et al. 1983; Ross et al. 1986; Oberhuber and Bauer 1991; Constabel and Lieffers 1996; Skillman et al. 1996; Man and Lieffers 1997). Within forest gaps and in open or relatively open areas, daily changes in sun angle and intermittent cloud cover may cause fluctuations in light on the order of hours to minutes (e.g., Knapp and Smith 1987, 1988; Krause and Winter 1996). At the other extreme, light levels within tree crowns and in the forest understory may fluctuate on the order of minutes to seconds (e.g., Pearcy 1983; Roden and Pearcy 1993a). In the forest understory where fluctuations in light may be especially rapid, low levels of diffuse background light that characterize deep shade are intermittently and briefly punctuated by small, short bursts of higher intensity, predominantly direct light which penetrate through the canopy as sunflecks (Pearcy et al. 1994). These sunflecks result from the interaction between diurnal and seasonal changes in solar angle and weather conditions (wind, cloud cover) with the height, density, distribution, and flexibility of canopy elements and neighbouring vegetation (Reifsnyder et al. 1971; Pearcy 1983; Tang et al. 1988; Roden and Pearcy 1993a; Baldocchi and Collineau 1994). Sunflecks may, therefore, exhibit different characteristics in different forest types.

Technically, sunflecks are excursions in photosynthetic photon flux density (PPFD) just above a threshold PPFD which in turn is usually defined to be just above the background diffuse PPFD in the understory (Pearcy et al. 1994). As such, thresholds for identifying sunfleck events are normally determined on a site-specific basis. Once defined, sunflecks are often further characterized on the basis of their duration, frequency, and maximum (peak) PPFD. In closed canopy forests sunflecks are typically resident for no more than 10 minutes and do not provide full sun irradiance owing to the strong penumbral effects associated with tall, closed canopies (Smith et al. 1989). Sunflecks can, however, make a considerable contribution to total daily understory PPFD. Although this contribution will clearly be dependent on the threshold selected for defining a sunfleck event (e.g., Washitani and Tang 1991; Baldocchi and Collineau 1994), the upper limit reported is about 85–90% for both low-latitude and mid-to high-latitude forests (see reviews by Chazdon and Pearcy 1991 and Lieffers et al. 1999).

If tree species differ in their capacities to use sunflecks for photosynthesis, then such differences could conceivably contribute to the relative success or failure of these species in the forest understory. In this study it was hypothesized that, in an understory environment, as a very shade tolerant species western redcedar should exhibit

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3 Occasionally, sunflecks have alternatively been defined based on some observable photosynthetic response of a study species, such as its foliar light compensation point. Other times, thresholds for sunflecks have been selected arbitrarily.
more efficient transient photosynthetic responses to changing light conditions than shade intolerant coastal Douglas-fir. Because of recent interest in mixedwood silviculture (mixtures of broad-leaved deciduous trees and evergreen conifers), a red alder-conifer mixedwood stand was selected as a model system to test this hypothesis. The following literature review is arranged into two main divisions related to the study in question. Section 2.2 overviews what is known of transient photosynthetic responses of plants to dynamic light conditions, with particular reference to tree species from mid- to high-latitudes (including redcedar and Douglas-fir). Section 2.3 then provides an overview of coastal alder-conifer mixedwood forests, emphasizing what is known or inferred about understory light in these stands and the differential suitability of redcedar and Douglas-fir for growing in mixture with red alder.

2.2 PHOTOSYNTHETIC RESPONSE TO SUNFLECKS

To assess whether species differ in their capacities to use sunflecks for photosynthesis, both the theory of photosynthetic induction (see below) and methods for its quantitative measurement need to be understood. With the purpose of addressing these topics, this section, which forms the bulk of the literature review, has been divided into three subsections: i) photosynthetic induction theory; ii) an overview of the parameters conventionally used to quantify photosynthetic induction and its effects on carbon gain; and iii) a summarization of what is currently known about the capacity of tree species from mid- to high-latitude forests for photosynthesis in fluctuating light.

2.2.1 Photosynthetic induction theory

In forest understories where sunflecks are frequent, transient photosynthetic responses to light become of increased importance relative to the steady-state responses of the same. This is because photosynthesis has a light-dependent induction requirement that must be met before photosynthesis can proceed maximally at any given light level, as it does under steady-state conditions (Pearcy et al. 1994). For leaves that have been in low levels of diffuse light for prolonged periods of time, this requirement for induction can initially limit photosynthetic rates by as much as 80–90% (e.g., Chazdon and Pearcy 1986a; Ògren and Sundin 1996). Thus, measurements of steady-state photosynthesis (e.g., from light- and/or CO₂-response curves) reveal little about the capacity of a plant to utilize temporally variable light regimes, and transient photosynthetic responses to light must be examined wherever dynamic light conditions are important.

Because sunflecks occur on time-scales too short to elicit physiological acclimation (Chabot et al. 1979; Sims and Pearcy 1993; Watling et al. 1997; see also Yanhong et al. 1994), regulation is of primary importance where photosynthetic utilization of sunflecks is of issue (Pearcy et al. 1994). Photosynthetic induction is regulated by both a fast component and a slow component (Kirschbaum and Pearcy 1998b, c). The fast induction component is generally complete with 1–2 minutes upon transfer of a non-induced leaf to continuous high light (Kirschbaum and Pearcy 1988c; Pons et al. 1992; Sassenrath-Cole and Pearcy 1992; see also Han et al. 1999). It represents the removal of a light limitation on the regeneration of ribulose 1,5-bisphosphate (RuBP) which is caused by inactivation of key photosynthetic enzymes in low light (Kirschbaum and Pearcy 1988c; Sassenrath-Cole and Pearcy 1992, 1994; Krall et al. 1995).
In non-induced leaves the slow component of photosynthetic induction may require 10–60 minutes or more for completion upon transfer to continuous high light, depending on species, tissue age, and environmental conditions (e.g., Pearcy et al. 1985; Roden and Pearcy 1993b; Ögren and Sundin 1996; Küppers et al. 1996). The slow induction component represents both the light activation of the enzyme ribulose 1,5-bisphosphate carboxylase (Rubisco) and the light-induced opening of stomata (Kirschbaum and Pearcy 1988b; Seemann et al. 1988; Woodrow and Mott 1989). Rubisco activation is often completed before stomatal opening, but the relative role of stomata in limiting photosynthesis will be highly dependent on initial conductance and the time since the light increase (Kirschbaum and Pearcy 1988b; Tinoco-Ojanguren and Pearcy 1993b; Allen and Pearcy 2000; Tang and Liang 2000).

Continuous high light is however not necessarily required for photosynthetic induction to proceed. This is important because extended periods of continuous high light may be rare in the forest understory. Exposure to a series of sunflecks can also be effective in progressively increasing induction, so long as the time between sunflecks is not too long (e.g., Pearcy et al. 1985; Chazdon and Pearcy 1986a; Pfitsch and Pearcy 1989; Poorter and Oberbauer 1993; Roden and Pearcy 1993b; Sims and Pearcy 1993). The time between sunflecks is important because any photosynthetic induction gained by previous exposure to high light will decay in a time-dependent manner given a sufficient duration of low light between sunfleck events (Chazdon and Pearcy 1986a; Pfitsch and Pearcy 1989). Leaves which maintain induction only poorly during periods of low light will be less able to exploit subsequent sunflecks for photosynthesis, and growth may be compromised (Sims and Pearcy 1993). After long periods of shade, limitations due to the slow induction component are so great that the fast induction component imposes little additional limitation on carbon gain. Thus, the fast induction component is generally only important for fully or near fully induced leaves following shading intervals short enough that the decay of the slow component is minimal (Kirschbaum and Pearcy 1988c; Pons et al. 1992; Sassenrath-Cole and Pearcy 1992; see also Seemann et al. 1988).

In rapidly fluctuating light it is not only the maximum rate of photosynthesis achievable during a sunfleck (a function of the induction state of a leaf) that is important to leaf carbon gain, but also the capacity for continued fixation of CO₂ (photosynthesis) after the sunfleck has passed (Pearcy et al. 1985; Chazdon and Pearcy 1986b). Such ‘post-illumination CO₂ fixation’ is possible in shade leaves if, during sunflecks, the rate of electron transport transiently exceeds that of carbon fixation and large pools of photosynthetic carbon reduction cycle intermediates (especially triose-phosphate) accumulate (Laisk et al. 1984; Sharkey et al. 1986; Kirschbaum and Pearcy 1988a). Post-illumination CO₂ fixation is most evident following brief sunflecks (<1 min.; e.g., Chazdon and Pearcy 1986b) because following longer exposures to high light this effect can be masked by a post-illumination ‘photorespiratory burst’ (CO₂ evolution) which results from the buildup and subsequent decarboxylation of glycocolate pathway intermediates (Vines et al. 1983). In contrast to the buildup of photosynthetic intermediates (for post-illumination CO₂ fixation) which requires only about 5 s (Sharkey et al. 1986; Kirschbaum and Pearcy 1988a), the buildup of photorespiratory intermediates (for the photorespiratory burst) requires about 1 min to appear and up to 5 min to reach maximum (Vines et al. 1983). Post-illumination CO₂ fixation can in some cases make a considerable contribution to the total carbon gain attributable to sunflecks, compensating in part for induction limitations. In fact, for fully induced leaves, carbon gain in response to short, frequent, high intensity sunflecks may sometimes be even
greater than that expected during steady-state photosynthesis for a similar duration of exposure to high light (Pearcy et al. 1985; Chazdon and Pearcy 1986b; Kirschbaum and Pearcy 1988a; Pfitsch and Pearcy 1989; Pons and Pearcy 1992; Roden and Pearcy 1993b; Sims and Pearcy 1993; Ögren and Sundin 1996; Valladares et al. 1997).

Photosynthesis generally responds rapidly to changes in light, whereas stomatal conductance may or may not. Species with stomata which respond relatively quickly to fluctuating light have been termed ‘trackers’ and those with stomata that do not have been termed ‘nontrackers’ (Knapp and Smith 1990). Because stomata of nontracker species remain relatively more open during low light intervals between sunfleck events, nontracker species may be afforded with faster and more efficient photosynthetic responses to subsequent sunflecks (limitations imposed by stomata are reduced). However, this may come at the cost of greater water loss during periods of shade in which the stomata of these species close only slowly (Knapp and Smith 1990). Stomatal behaviour in fluctuating light could therefore have important implications for water loss as well as for carbon gain.

2.2.2 Parameters conventionally used to quantify photosynthetic induction and its effects on carbon gain

In consequence of the light-dependent induction requirement and its time-dependent decay in shade, in the understory leaves can be expected to be at various stages of induction throughout the day as they become partly induced by individual sunflecks of varying duration and maximum PPFD and then gradually lose some or all of this induction during the intervening, variable periods of low light between sunfleck events. Although the net result of this may be captured by measurements of time-integrated photosynthesis, such analyses reveal little about leaf function and the specific role of photosynthetic induction (versus light availability) in limiting carbon gain. Therefore, quantitative analysis of the effects of photosynthetic induction is required. The three principle parameters conventionally used to quantify these effects are i) photosynthetic induction potential; ii) photosynthetic induction state; and iii) sunfleck use efficiency. Methods for quantifying these parameters are outlined below.

The overall capacity for photosynthetic induction has typically been quantified in terms of one or more ‘induction potential’ parameters (A-19, A-90; Chazdon and Pearcy 1986a). These parameters are derived by abruptly exposing a non-induced leaf to continuous high light and following the time-course of the complete induction response, from steady-state photosynthesis at low light through the transition to steady-state photosynthesis at high light. From the response curve, times to reach 50% (A-19) and 90% (A-90) of the maximum photosynthetic rate are then computed. Although extended periods of continuous high light are generally not representative of understory conditions, analysis of the time required for photosynthetic induction under these conditions allows the optimal physiological capacity for induction to be gauged independent of the temporal pattern of light in the understory.

‘Photosynthetic induction state’ (A-IS) has conventionally been used to quantify the current level of photosynthetic induction in a leaf and, through repeated measurement, can be used to assess the rapidity with which induction can be both gained and lost in either constant or fluctuating high light (Chazdon and Pearcy 1986a). It is computed as the net photosynthetic rate at some pre-defined time after a light increase expressed relative to the fully induced (maximum) steady-state net photosynthetic rate in saturating light. Most frequently, it is measured 60 s
after a light increase (as A-IS\text{50} values) and considered an index of the capacity of a leaf to respond immediately to a light increase (Pearcy et al. 1994).

To describe the overall efficiency with which sunflecks can be used for photosynthetic carbon gain, a 'sunfleck use efficiency' parameter is often computed as the carbon gain attributable to a sunfleck expressed as a percentage of the carbon gain that would be expected assuming an instantaneous steady-state photosynthetic response to the same sunfleck (Chazdon and Pearcy 1986b). The carbon gain attributable to a sunfleck includes both that which occurs during the sunfleck-proper and any net post-illumination CO\textsubscript{2} fixation attributable to the same sunfleck. Because the absolute amount of post-illumination CO\textsubscript{2} fixation is maximum after about 5 s\textsuperscript{4} and thereafter remains constant as sunfleck duration increases (Sharkey et al. 1986; Kirschbaum and Pearcy 1988a), the proportional contribution of post-illumination CO\textsubscript{2} fixation to the overall carbon gain attributable to a sunfleck will decrease as sunfleck duration increases (Pons and Pearcy 1992; Küppers and Schneider 1993). Thus, for any given leaf, sunfleck use efficiency can be expected to be highest in a light regime characterized by frequent short sunflecks (Pearcy et al. 1985; Chazdon and Pearcy 1986b; Pfitsch and Pearcy 1989; Pons and Pearcy 1992; Tinoco-Ojanguren and Pearcy 1992; Roden and Pearcy 1993b; Ögren and Sundin 1996; see also Pollard 1970), as this results in minimal induction loss and maximal contribution from post-illumination CO\textsubscript{2} fixation.

Efficient photosynthesis under dynamic light conditions is thought to be characterized by i) rapid photosynthetic induction (low A-T\textsubscript{10} and A-T\textsubscript{30} values, indicative of short induction times); ii) a high capacity to maintain photosynthetic induction state during low light periods (high A-IS\text{50}, values after shading); and iii) a high capacity for post-illumination CO\textsubscript{2} fixation which, together with a high capacity to maintain induction state, leads to iv) a high sunfleck use efficiency (in fluctuating light). These characteristics of transient photosynthesis are thought to be differentially associated with shade tolerant versus shade intolerant species (Chazdon and Pearcy 1991).

2.2.3 Photosynthetic utilization of sunflecks by forest tree species of mid- to high-latitudes: the state of our knowledge

Whereas much information on photosynthetic utilization of sunflecks is available for tree species from low latitude (tropical) forests, comparatively little is known about the transient photosynthetic responses to dynamic light conditions for tree species from mid- and high-latitude forests (Table 2.1). This is particularly true for the conifers, and especially so if only studies of shade acclimated plants are considered. Also notable is that among the total sum of studies available for tree species from mid- and high-latitudes there has been large variation in both growth and measurement conditions and the physiological parameters measured. This alone renders the existing data difficult to interpret in a successional sense (e.g., are patterns of response evident between shade tolerant and shade intolerant tree species of these regions?), but there may also be some concern with the ecological relevance of individual studies.

\textsuperscript{4} Longer times (ca. 20 s) may be required if leaves have been held in darkness prior to illumination with high light, rather than at some ecologically relevant background level of diffuse light (Küppers and Schneider 1993).
Table 2.1 Summary of information available on transient photosynthetic responses to dynamic light conditions in forest tree species of mid- and high-latitudes. Studies are grouped under the headings 'deciduous angiosperms' or 'evergreen conifers' and listed within these categories in chronological order by date of publication. Species authorities are reproduced from the original work (where specified) and do not necessarily have a common source.

<table>
<thead>
<tr>
<th>Species</th>
<th>Study type/location and light levels during growth</th>
<th>Plant material</th>
<th>Parameters measured</th>
<th>Reference</th>
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<tbody>
<tr>
<td><em>Populus grandidentata</em> Michx, <em>P. tremuloides</em> Michx</td>
<td>glasshouse &amp; laboratory study growth light environment not quantified</td>
<td>rooted, presumably potted cuttings grown for an unspecified time (but &lt;1 year) in a glasshouse, then measured in the laboratory</td>
<td>• continuous measurement of photosynthesis in response to experimentally applied sunfleck regimes</td>
<td>Pollard 1970</td>
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<td><em>Fagus sylvatica</em> L., <em>Fraxinus excelsior</em> L., <em>Ulmus glabra</em> Huds.</td>
<td>field study, Cambridge, U.K. understory of mixed deciduous angiosperm forest; 1.5–6.1% full light</td>
<td>naturally established plants of unspecified age &amp; size</td>
<td>• photosynthetic induction during a 3 minute lightfleck at successively higher light intensities (initial induction state at each light level not taken into account)</td>
<td>Harbinson &amp; Woodward 1984</td>
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<tr>
<td><em>Acer saccharum</em></td>
<td>field study, Pellston, Michigan, U.S.A. understory of a mixed hardwood forest; light levels not specified</td>
<td>naturally established plants approx. 10 years old &amp; ≤40 cm tall</td>
<td>• continuous measurement of photosynthesis in response to a natural understory sunfleck regime</td>
<td>Weber et al. 1985</td>
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<td><em>Populus tremuloides</em></td>
<td>field study, Medicine Bow National Forest, Wyoming, U.S.A. &quot;open-understory&quot; (receiving &gt;2 h full sun per day) of a subalpine mixed species forest with a deciduous <em>P. tremuloides</em> component</td>
<td>naturally established seedlings or saplings 0.3–1.0 m tall</td>
<td>• photosynthetic response to 5 min simulated &quot;cloudflecks&quot; (fluctuations in light at high light)</td>
<td>Knapp &amp; Smith 1989</td>
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<td><em>Quercus macrocarpa</em> Michx.</td>
<td>field study, Manhattan, Kansas, U.S.A. relatively open-grown individuals at the &quot;forest-prairie edge&quot;</td>
<td>naturally established saplings or adult trees of unspecified size</td>
<td>• photosynthetic response to 6 min simulated &quot;cloudflecks&quot; (fluctuations in light at high light)</td>
<td>Knapp 1992</td>
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<td>Species</td>
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| *Fagus sylvatica* L.        | greenhouse study                                  | naturally established current-year seedlings transplanted into pots & grown for an unspecified time in a greenhouse under two experimental light treatments | - photosynthetic induction potential  
- maintenance of induction state in shade  
- lightfleck use efficiency, but from darkness | Küppers & Schneider 1993                                                  |
| *Populus fremontii* Wats.,  | field & glasshouse studies, Truckee & Davis, Calif. U.S.A. | field plants of unspecified origin, age, & size; leaves from the upper & lower crowns of individuals plants examined | - photosynthetic induction potential  
- maintenance of induction state in shade  
- lightfleck use efficiency | Roden & Pearcy 19936                                               |
| *Populus tremuloides* Michx. | field study in situ in presumably mono-specific *Populus* stands; natural lighting in the glasshouse; growth light environments not quantified | glasshouse plants from cuttings; grown for an unspecified time to an unspecified size |                                                                                     |                                  |
| *Quercus serrata* Thunb     | field & laboratory study, Tsukuba, Japan           | naturally established seedlings of unspecified age & size, transplanted under a glass canopy & then extracted after 5 months & analyzed in the laboratory | - maintenance of photosynthetic induction in shade | Yanhong et al. 1993             |
| *Quercus serrata* Thunb     | growth chamber study                               | seedlings grown from seed in pots in a growth chamber for 3 months under three experimental light treatments | - photosynthetic induction potential  
- lightfleck use efficiency | Yanhong et al. 1994             |
- maintenance of induction in shade  
- lightfleck use efficiency | Küppers et al. 1996             |
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<td><em>Betula pubescens</em> Ehb.</td>
<td>growth chamber study</td>
<td>naturally established seedlings transplanted into pots &amp; grown in a growth chamber for an unspecified time</td>
<td>• photosynthetic induction potential</td>
<td>Ögren &amp; Sundin 1996</td>
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<td><em>Acer macrophyllum</em> Pusch., <em>Acer platanoides</em> L., <em>Acer rubrum</em> L., <em>Acer saccharum</em> Marsh.</td>
<td>outdoor study with artificial shade, Montreal, Quebec, Canada two growth light environments: i) &quot;simulated gap edge&quot;, 30 μmol m⁻² s⁻¹ (ca. 1.5% full sun); ii) &quot;simulated gap centre&quot;, 400 μmol m⁻² s⁻¹ (ca. 20% full sun)</td>
<td>3–4 year-old potted seedlings reared from seed in a growth chamber &amp; subsequently grown outdoors under two artificial shading treatments until new leaves formed &amp; matured</td>
<td>• photosynthetic induction potential</td>
<td>Lei &amp; Lechowicz 1997</td>
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<td><em>Acer rubinerve</em> Siebold &amp; Zucc., <em>Fagus crenata</em> Blume</td>
<td>field study, Niigata Prefecture, Japan two unreplicated growth light environments within a <em>Fagus crenata</em> forest: i) &quot;undersory&quot;, 5.6% full light; ii) &quot;gap&quot;, 20.7% full light</td>
<td>6–8 year-old, 40–80 cm tall naturally established seedlings</td>
<td>• photosynthetic induction potential</td>
<td>Han et al. 1999</td>
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<td><em>Acer rubrum</em> L., <em>Cornus florida</em> L., <em>Liquidambar styraciflua</em> L., <em>Liriodendron tulipifera</em> L.</td>
<td>field study, North Carolina, U.S.A. understorey of a <em>Pinus taeda</em> plantation, with an abundant subcanopy &amp; understorey of hardwood tree species; 3–15% full light</td>
<td>2.0–4.5 m tall, 1.0–2.5 cm dbh naturally regenerated saplings</td>
<td>• photosynthetic induction potential • maintenance of induction in shade</td>
<td>Naumburg &amp; Ellsworth 2000</td>
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<td><em>Populus koreana</em> x <em>trichocarpa</em> cv. Peace</td>
<td>growth chamber study four light x soil moisture treatments: i) low light, 190 μmol m⁻² s⁻¹ (ca. 9.5% full sun) x well-watered; ii) low light x dehydrated; iii) high light, 550 μmol m⁻² s⁻¹ (ca. 27.5% full sun) x well-watered; &amp; iv) high light x dehydrated</td>
<td>seedlings grown for 2 months in pots, then transferred to the experimental treatments in a growth chamber</td>
<td>• photosynthetic induction potential</td>
<td>Tang &amp; Liang 2000</td>
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<td>Abies grandis Lind., Abies procera Rehd., Picea stichensis Bong., Pinus silvestris L., Pseudotsuga menziesii (Mirb.) Franco [variety unspecified], Tsuga heterophylla (Raf.) Sarg.</td>
<td>field study, LaGrande Washington, U.S.A. natural light gradient, from 100% full light in a clear-cut to approx. 1–2% full light beneath the adjacent stand</td>
<td>2-0 nursery seedlings planted in pots and/or out-planted along N-S transects from a clear-cut with vegetation control, to within the adjacent 35-40-year-old Douglas-fir stand; analyzed during the second growing-season in the field</td>
<td>continuous measurement of photosynthesis in response to a natural understory light regime</td>
<td>Hodges 1967; Hodges &amp; Scott 1968</td>
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<td>Pinus ponderosa Laws., Pseudotsuga menziesii (Mirb.) Franco [variety unspecified]</td>
<td>growth chamber study growth light environment roughly 175 μmol m⁻² s⁻¹ (ca. 9% full sun)</td>
<td>potted ca. 4-year-old seedlings grown for 4 months in a growth chamber at three day/night temperature regimes: i) 3/3°C; ii) 7/3°C; &amp; iii) 11/3°C</td>
<td>photosynthetic induction potential, but from darkness &amp; not explicitly quantified</td>
<td>Pharis et al. 1967</td>
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<td>Juniperus virginiana</td>
<td>field study, Ashland, Missouri, U.S.A. understory of a mixed deciduous (oak-hickory) forest</td>
<td>naturally established saplings of unspecified age &amp; size</td>
<td>continuous measurement of photosynthesis in response to a natural understory sunfleck regime</td>
<td>Laisoie et al. 1983</td>
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<td>Abies lasiocarpa, Pinus contorta, Pinus flexilis</td>
<td>field study, Medicine Bow National Forest, Wyoming, U.S.A. open-grown individuals (P. flexilis), or individuals within an &quot;open-understory&quot; (receiving &gt; 2 h full sun) of a subalpine mixed species forest</td>
<td>naturally established seedlings or saplings 0.3–1.0 m tall</td>
<td>photosynthetic response of exposed or relatively exposed individuals to simulated 'cloudflecks' (fluctuations in light at high light)</td>
<td>Knapp &amp; Smith 1989</td>
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<td>Thuja plicata Donn.</td>
<td>laboratory study unspecified growth light environment</td>
<td>1-year-old seedlings of unspecified origin, size, &amp; culture</td>
<td>continuous measurement of photosynthetic responses to relatively slow fluctuations in light at high light</td>
<td>Livingston 1994</td>
</tr>
<tr>
<td>Pinus taeda L.</td>
<td>field &amp; laboratory study, Athens, Georgia, U.S.A. nursery-grown seedlings, presumably relatively open-grown, later transferred &amp; held in a &quot;sheltered&quot; outdoor area prior to measurement</td>
<td>clonal material grafted onto root stocks &amp; grown in pots to an unspecified size for an unspecified time</td>
<td>continuous measurement of photosynthetic responses to relatively slow fluctuations in light at high light</td>
<td>Whitehead &amp; Teskey 1995</td>
</tr>
</tbody>
</table>
Table 2.1 (Continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Study type/location and light levels during growth a</th>
<th>Plant material</th>
<th>Parameters measured</th>
<th>Reference</th>
</tr>
</thead>
</table>
| *Pinus sitchensis* (Bong.) Carr., *Pinus sylvestris* L., *Tsuga heterophylla* (Raf.) Sarg. | growth chamber study, growth light environment 250 μmol m⁻² s⁻¹ (ca. 12.5% full sun) | potted nursery seedlings grown outdoors for 1–3 years, then transferred & grown under experimental conditions in a growth chamber until a new set of needles produced | • photosynthetic induction potential  
• maintenance of photosynthetic induction state in shade (*P. sylvestris* only)  
• lightfleck use efficiency (*P. sylvestris* only) | Ögren & Sundin 1996 |
| *Pseudotsuga menziesii* (Beissn.) Franco var. glauca | field study, Okanagan Falls, British Columbia, Canada (Dry Mild Interior Douglas-fir subzone)  
two growth light environments:  
i) a 2 ha clear-cut (100% full light); & ii) an adjacent understory (7.4% full light) of an immature "semi-open" conifer canopy | out-planted 1+0 nursery seedlings, analyzed *in situ* during the second growing-season | • maintenance of photosynthetic induction state during 10 minutes shading | Chen & Klinka 1997 |
| *Pseudotsuga menziesii* (Mirb.) Franco var. glauca, *Pseudotsuga menziesii* (Mirb.) Franco var. menziesii, *Thuja plicata* Donn, *Tsuga heterophylla* (Raf.) Sarg. | field & laboratory study, Victoria, British Columbia, Canada  
open-grown in a field with no shading | potted 1-year-old nursery seedlings grown outdoors for one season & then moved to the laboratory for analysis | • photosynthetic induction potential, but from darkness | Pepin & Livingston 1997 |

a. Where absolute light levels were reported in the original work, percentage of full sun (% full sun) has been estimated assuming a full sun irradiance of 2000 μmol m⁻² s⁻¹. Where light levels were instead reported as a percentage of a reference value measured in a nearby 'open' location, relative values are reported as a percentage of full light as they appear in the original work. Where appropriate, unit conversions for light follow the procedures of Thimijan and Heins (1983).
Concern over ecological relevance is particularly warranted where artificial environments have been employed (growth chambers, rearing of seedlings in pots, artificial shading). This is because from years of experimentation it has become increasingly evident that: i) the physiological responses of plants in artificial environments can in some cases be very different than that in the natural environment (e.g., Hinckley et al. 1989); ii) where plants are reared in pots, so-called ‘pot effects’ are not unlikely to develop (e.g., Thomas and Strain 1991; Will and Teskey 1997; see also Arnott 1975); and iii) failure in controlled studies to accurately reproduce ecologically relevant light levels can lead to erroneous conclusions regarding the fitness of different species for the understory environment because species rankings can reverse depending on the exact low light level selected for the comparison (Denslow et al. 1990; Walters and Reich 1996, 1999; Hättenschwiler 2001; and see also Minore 1988, Popma and Bongers 1988).

All three of these potential problems with controlled studies are suggested in published studies of photosynthetic induction. For example, photosynthetic induction times have been shown to be faster in the natural environment than in growth chamber environments (Gildner and Larson 1992). With regard to possible ‘pot effects’, seedlings of woody species reared for two growing-seasons in pots buried flush with the ground under a forest canopy had 2–7-fold longer induction times than naturally established understory plants of the same species (Kursar and Coley 1993). And, in reference to the selection of ecologically relevant light levels, species rankings for photosynthetic induction parameters have been shown to differ depending on whether 6% full light or 20% full light was selected as the ‘low light’ level for growth (Han et al. 1999). Furthermore, recent modeling experiments suggest that in some cases species differences in transient photosynthetic responses to sunflecks may in any case only really be significant, in terms of absolute daily carbon gain, in deep understory shade; at higher light levels (above about 10% full light for some hardwood tree species), induction limitations may become small and species differences in induction dynamics non-significant (Naumburg et al. 2001). If this latter point holds true for forest tree species more generally, it may help explain some of the contrasting evidence which currently exists regarding the importance of fluctuating light to the growth of tree species from mid- and high-latitude forests (Shirley 1945; Brix 1970; Wayne and Bazzaz 1993; Mitchell and Arnott 1995).

Although studies conducted in situ in the forest understory may ensure that experimental results apply over an ecologically relevant range of growth light conditions, the relevance of short-term field studies with newly planted seedlings may also be suspect if there is evidence of planting stress. For example, whereas it is known that stomatal responses to light can be altered by water stress (Willis and Balasubramaniam 1968; Davies and Kozlowski 1975; Barradas et al. 1994), newly planted seedlings may be unduly subject to water stress until their root systems become well established (Burdett 1990). Overall, it is therefore concluded that to study species differences in photosynthetic dynamics in an ecologically relevant context, field studies in relevant growth light environments with well-established plants of unrestricted rooting volume are best. Such studies are currently few for tree species from mid- and high-latitude forests (Table 2.1).

---

5 Both photosynthesis and growth have been shown to decrease with decreasing pot size owing to the restriction of rooting volume.
2.3 COASTAL RED ALDER-CONIFER MIXEDWOOD SYSTEMS

Over the last decade or so there has been a surge of interest in British Columbia (McLennan and Klinka 1990; Simard 1990; Comeau and Sachs 1992; Kabzems and Lousier 1992; Simard and Vyse 1994; and see research listing in Thomas et al. 1996) and elsewhere in North America (e.g., Lieffers and Beck 1994; Lieffers and Stadt 1994; Groot and Carlson 1996; Groot 1999; Man and Lieffers 1999a, b) in managing broad-leaved deciduous angiosperm species (hardwood species) in mixture with evergreen conifers (softwood species). This new or renewed interest in 'mixedwood' stands has occurred not only in response to improved markets for hardwood products, but also to trends toward more ecologically based silviculture (Lieffers and Beck 1994; Massie et al. 1994; Comeau and Thomas 1996; Man and Lieffers 1999a). In addition to the traditional focus on economy of timber production, maintenance and enhancement of the forest land base for wildlife habitat, water quality and fisheries, tourism and recreation potential, and cultural and spiritual values are increasingly of concern, as is the preservation of overall ecosystem integrity and sustainability through species- (biotic)-, structural-, and spatial-diversity. Maintaining a component of hardwood species across the landscape has been identified as a means to achieve some of these objectives (Province of British Columbia 1995).

Along the Pacific coast in northwestern North America, evergreen conifers are being increasingly grown in mixture with red alder (Alnus rubra Bong.), a broad-leaved deciduous angiosperm species abundant in the region. This section overviews the ecology of alder-conifer mixedwood forests, what is known or inferred about understory light in these stands, and the differential suitability of two conifers, western redcedar (Thuja plicata Donn) and coastal Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco var. menziesii), for growing in mixture with red alder.

2.3.1 Overview of ecology and successional dynamics

Red alder (Alnus rubra Bong.) is a shade intolerant (Baker 1949), fast-growing, short-lived deciduous broad-leaved species common to low elevation areas (generally <750 m) within about 200 km of the northern Pacific coast of North America (Harrington 1990). Although once regarded as an undesirable 'weed' species, red alder is now often considered an acceptable, and even sometimes desirable, tree species. Operationally, red alder is of interest because it is a potentially fast-growing species which may produce high value commodity (saw logs) in rotations of 25–40 years on good and medium sites (Massie et al. 1994; Peterson et al. 1996; Dobkowski 1997). However, it is not only the potential productivity of alder that is of interest to forest managers.

A number of potential ecological benefits have also been associated with red alder that may render it desirable for growing in mixture with conifers rather than just in monospecific plantations. Of primary interest among these benefits, is that red alder can maintain or enhance soil fertility (Tarrant and Trappe 1971) because of the fixation of atmospheric nitrogen in its root nodules by a symbiotic actinomycete (Frankia spp.). Thus, although broad-leaved deciduous angiosperm tree species can in general be useful for ameliorating environmental conditions and suppressing vegetation that may otherwise compete vigorously with regenerating conifers (e.g., McLennan and Klinka 1990; Kabzems and Lousier 1992; Lieffers and Stadt 1994; Groot and Carlson 1996; Man and Lieffers 1999b), the more important role of red alder as a nurse species may be to increase soil fertility (nitrogen, organic matter) on nitrogen-deficient or severely disturbed sites (Tarrant and Trappe 1971; Miller and Murray 1978).
Because red alder is relatively little affected by diseases and insects (Harrington 1990), its presence in a stand may also serve to inhibit the spread of infestations such as laminated root rot (Phellinus weirii) among susceptible conifers (Tarrant and Trappe 1971). Maintaining a component of red alder across the landscape can also contribute to species, structural, and spatial diversity (Peterson et al. 1996).

However, although red alder may provide several ecological benefits, this shade intolerant species exhibits very rapid juvenile height growth on large recently disturbed sites when given sufficient moisture (Harrington 1990). In consequence, where red alder establishes at roughly the same time as the conifers, the species mixture usually stratifies to the extent that red alder dominates the canopy and suppresses growth of the conifers, a condition that may last for 25–50 years or more depending on species and site quality (Peterson et al. 1996). If, then, the conifer component is expected to contribute incrementally to the merchantable yield from the site (Man and Lieffers 1999a) or to provide other long-term values, it must survive under the suppression of the alder canopy long enough to do so. In other words, to be compatible for growing in intimate mixture with red alder, conifers should be shade tolerant. It is of course also possible to grow more shade intolerant conifers with red alder, but such mixtures are likely to require more intensive initial and/or subsequent silviculture treatments to survive and/or exhibit acceptable growth; e.g., modification of initial species proportions, densities, and spatial arrangements and/or thinning of red alder to release the suppressed conifers (Miller and Murray 1978; Klinka and Feller 1984; Comeau and Sachs 1992; Shainsky and Radosevich 1992; Shainsky et al. 1992; Miller et al. 1993; Comeau et al. 1995).

2.3.2 Understory light environment

Both the relative light levels and sunfleck activity under red alder may be of interest where the performance of understory conifers is of concern. This is because both of these aspects of the light environment can be important to the photosynthesis of understory plants. In particular, total daily light (represented by canopy transmittance, % full sun) determines photosynthetic capacity (Chabot et al. 1979; Sims and Pearcy 1993; Watling et al. 1997; but see Wayne and Bazzaz 1993) and sunfleck activity (duration, frequency, and maximum intensity of sunflecks) governs the regulation of that photosynthetic capacity under non-steady-state conditions (Pearcy 1994; Pearcy et al. 1994). What is known or inferred about light levels and sunfleck activity in the understory of red alder is reviewed below.

2.3.2.1 Relative light availability

In stands dominated by red alder, understory light levels decrease exponentially as the basal area of red alder increases (Comeau 1996). However, light levels typical of the understory of closed canopy red alder stands are not known. In the Dry Maritime Coastal Western Hemlock (CWHdm) subzone of British Columbia, canopy transmittance was on the order of 11% in two slightly dry red alder stands that had established naturally after clearcutting and burning 6–8 years previously (Burton 1996), but it is not known whether closed canopy conditions existed in that study. No other measurements of light availability under closed canopy red alder appear to be available.
Given the general lack of information available on light conditions beneath red alder, the inference has been drawn that understory light levels must be relatively high because naturally established stands of red alder tend to be associated with a well developed understory (e.g., Klinka et al. 2000). Although not known, this observation may only apply to stands older than 15 years, which appears to be the minimum age at which the cover of understory vegetation initially begins to increase under red alder (Peterson et al. 1996). Regardless, basic principles of canopy influence do also suggest that for sites of comparable edaphic quality and climate, light availability under red alder may be relatively high in comparison with some other forest types. This is because, given closed canopy conditions or similarity in estimates of crown closure, light availability tends to be higher under more shade intolerant species than under more shade tolerant species among both deciduous and coniferous forest types (Vézina and Péch 1964; Horn 1971; Canham et al. 1994; Messier et al. 1998).

2.3.2.2 Sunfleck activity

No published information appears to be available regarding sunfleck activity or the contribution of sunflecks to total daily light in the understory of red alder. However, it might again be inferred that sunfleck activity under red alder is likely to be relatively high because within individual studies sunflecks tend to contribute relatively more light beneath shade intolerant species than beneath shade tolerant species (Canham et al. 1994). No such distinct pattern is evident across studies, but this is probably owing in large part to different thresholds used for defining sunflecks (Lieffers et al. 1999).

2.3.3 Differential suitability of western redcedar and coastal Douglas-fir for growing in mixture with red alder

With reference specifically to red alder-conifer mixedwood systems, the best means of providing a future stand of conifers is considered to be through conifers that establish with or prior to red alder (Peterson et al. 1996). Post-disturbance conifer regeneration is generally not of issue because it is normally absent in undisturbed red alder stands along the Pacific coast (Emmingham et al. 1989) and the under-planting of conifers in red alder thinnings (Emmingham et al. 1989) is not considered of operational interest at this time (Peterson et al. 1996). If, then, it is assumed that the goal is to establish conifers roughly simultaneously with red alder, their suitability for this purpose will depend on their capacity to survive once overtopped and suppressed by this faster-growing species (i.e., on their shade tolerance). Two commercially important conifers that exemplify the extremes in shade tolerance in the coastal range of British Columbia are western redcedar (Thuja plicata Donn) and the coastal variety of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco var. menziesii). Western redcedar is considered very shade tolerant (Baker 1949; Daniel et al. 1979) and coastal Douglas-fir is generally considered intolerant of shade (e.g., Mailly and Kiemens 1997).

Reports of the comparative performance of western redcedar and coastal Douglas-fir suggest that the differential suitability of these conifers for growing in mixture with red alder is consistent with their putative shade tolerance.
tolerances. On disturbed sites along the northwest Pacific coast, both western redcedar (Stein 1997) and coastal Douglas-fir (Cole and Newton 1986, 1987; Chan and Walstad 1987; Shainsky et al. 1992; Stein 1997) tend to be quickly overtopped and suppressed by red alder (see also retrospective study of Stubblefield and Oliver 1978). However, red alder tends to suppress the growth and reduce the survival of coastal Douglas-fir more than that of western redcedar (Miller and Murray 1978; see also Stubblefield and Oliver 1978), although exceptions are sometimes observed in short-term studies with planted seedlings (Burton 1996) or wherever extraneous factors such as browsing limit the performance of redcedar more than Douglas-fir (Stein 1997). Model simulations for mixtures of red alder, coastal Douglas-fir, and western redcedar in the Dry Maritime Coastal Western Hemlock (CWHdm) subzone of B.C. suggest that stemwood biomass yield of Douglas-fir will be reduced at alder densities above >100 stems ha\(^{-1}\) (Comeau and Sachs 1992) whereas >500 stems ha\(^{-1}\) of alder may be required to reduce the performance of redcedar (see Comeau et al. 1995). For management purposes, it has therefore been suggested that red alder and western redcedar could be established simultaneously in mixture each at full stocking whereas, in contrast, recommendations have been made to delay the establishment of red alder for 4–6 years to reduce competitive effects on coastal Douglas-fir (Peterson et al. 1996; see also Stubblefield and Oliver 1978; Comeau and Sachs 1992). Otherwise, where red alder and Douglas-fir establish at approximately the same time, follow-up operations will generally be necessary to release the Douglas-fir (Klinka and Feller 1984) before it becomes too severely suppressed for too long and does not respond (Helms 1964).

Presumably, western redcedar must have some physiological and/or morphological attributes which underlie its superior performance over coastal Douglas-fir under conditions of suppression. In the forest understory where low light strongly limits plant growth and survival, shade tolerant species such as western redcedar are expected to use light more efficiently for photosynthesis than more shade intolerant species (Boardman 1977; Bazzaz 1979) and this has been hypothesized to include more efficient utilization of sunflecks (Chazdon and Pearcy 1991). The photosynthetic characteristics of shade-grown individuals of redcedar and Douglas-fir have, however, not been directly compared under the same conditions, either on the basis of steady-state rates or non-steady-state transient photosynthetic responses to dynamic light conditions. Work with open-grown seedlings suggests that in sunny environments western redcedar may require roughly the same amount of time to become photosynthetically induced from darkness as coastal Douglas-fir (Pepin and Livingston 1997; base 22 °C air temperature, from equations in their Fig. 2a). However, it is not known whether or not species rankings for induction time would differ for individuals acclimated to shade and/or given some ecologically relevant initial background level of light (cf. darkness). Other observations on transient photosynthetic responses to light exist independently for redcedar and Douglas-fir, but are qualitative rather than quantitative in nature. These additional observations provide further evidence that i) photosynthesis of western redcedar responds to relatively slow fluctuations in light at high light (Livingston 1994); ii) photosynthesis of Douglas-fir responds to sunflecks (Hodges 1967; Hodges and Scott 1968) and exhibits an induction requirement when exposed to high light after darkness (Pharis et al. 1967); and iii) some temporal aspect of the growth light regime is important to the biomass growth of Douglas-fir (Brix 1970). Direct, quantitative comparisons of the steady-state and transient photosynthetic responses to light of well-established shade phenotypes of western redcedar and coastal Douglas-fir were made as part of the study which follows.
CHAPTER 3
MATERIALS AND METHODS

3.1 STUDY SITE AND PLANT MATERIAL

The mixedwood study site was located near the municipality of Maple Ridge within the University of British Columbia (U.B.C.) Malcolm Knapp Research Forest in southwestern British Columbia (49°16'N, 122°34'W). The site falls within the Dry Maritime Coastal Western Hemlock (CWHdm) biogeoclimatic subzone (Meidinger and Pojar 1991), in Section C.2 of the Coast Forest Region of Canada (Rowe 1972). The cool mesothermal climate of the CWHdm subzone is characterized by low evaporative demand, a large amount of precipitation, and a general lack of temperature extremes (Meidinger and Pojar 1991; Green and Klinka 1994). Summers are cool and relatively dry, winters are mild and wet, and the vegetative season and frost-free period relatively long. Based on 30-year climate normals from a station located within 2 km of the study site, mean annual temperature is approximately 9.4 °C and mean annual precipitation 2184 mm-year\(^{1}\), with a negligible amount falling as snow (Environment Canada 1993, Clim. Stn. # 1103332). Growing-season water deficits are unlikely (Klinka and Krajina 1986; Meidinger and Pojar 1991). Soils at the site were Ferric Podzols derived primarily from granitic glacial till (Klinka and Krajina 1986), and were sandy loam in texture with high coarse fragment content. Humus forms were of the Moder type. Based on the methods of Green and Klinka (1994), the site was classified as very moist and nutrient rich (indicating growing-season water surplus and relatively large amounts of available nitrogen and rapid turnover of organic matter).

The original forest consisted of a western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)\(^7\) – western redcedar (*Thuja plicata* Donn) – coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) mixture which had originated after fire in 1868 (Univ. B.C. Res. For. records). An approximately 35 ha area of this forest, including a 16 ha watershed (drained by a small stream), was clear-cut in fall/winter 1982/83. Logging slash was burned in the summer of 1983, and 2+1 western redcedar and 2+0 coastal Douglas-fir seedlings from local, low elevation seed sources (B.C. Min. For. seed lots #3934 and #964) were dibble-planted in intimate mixture over most of the cut-over area in spring 1984 (only redcedar was planted in wetter areas). After planting the site received no further silvicultural treatments and red alder (*Alnus rubra* Bong.) regenerated naturally.

Physiological studies were conducted on western redcedar and coastal Douglas-fir in the summer of 1996, 13 growing-seasons after planting. At this time, red alder had closed canopy above the conifers, but notable gap-formation had not yet begun. Both redcedar and Douglas-fir were well above a sparse shrub and herb layer, and no expired saplings of either conifer species were evident. Salmonberry (*Rubus spectabilis* Pursh) was the most

\(^7\) Species authorities follow Hitchcock and Cronquist (1991).
prominent understory associate of the planted conifers, whereas a few individuals of vine maple (*Acer circinatum* Pursh) were confined to the edge of the stand. Sword fern (*Polystichum munitum* (Kaulf.) Presl) and bracken fern (*Pteridium aquilinum* (L.) Kuhn) formed the herbaceous layer. A few, approximately 0.5 m tall, presumably naturally regenerated western hemlock and western redcedar were present, but no live or dead more recently established individuals of any conifer species were observed.

Six saplings each of western redcedar and coastal Douglas-fir were randomly selected for study from the sub-population of saplings from the original intimate mixture of the two species that i) occupied the west lower slope position of the site (saplings located at the bottom of the slope were avoided); and ii) exhibited relatively good overall vigour and the presence of branches orientated to the south aspect in the mid- to upper-crown at a pre-defined sampling height of 2.0-2.5 m. At this height, essentially the only vegetation influencing the light environment of the experimental foliage was the alder canopy. The average diameter at breast height (dbh, 1.3 m) of selected saplings was 11.7 ± 1.6 cm for western redcedar and 9.9 ± 1.5 cm for coastal Douglas-fir (mean ± SE). Species remained interspersed after saplings were selected for study. Physiological measurements were made during August because needles of Douglas-fir did not appear fully mature until approximately 25 July (based on subjective assessments of colour and texture). The alder canopy was in full leaf at this time.

Observations of morphology and leaf form suggested that the saplings of both western redcedar and coastal Douglas-fir were strongly shade acclimated. Western redcedar had a relatively full and long live crown, long lateral branches, and drooping flat foliar sprays arranged in a single planar layer as is characteristic of this species when grown in shade (Parker and Johnson 1987). In contrast, coastal Douglas-fir exhibited the short, sparse live crown (Cole and Newton 1986, 1987; Hermann and Lavender 1990) and effectively horizontal lateral branch growth and planar needle arrangement (Leverenz and Hinckley 1990) as is typical of this species when grown under heavy shade. Needle retention on Douglas-fir was visibly poor (cf. vigour criteria for shade-grown Douglas-fir in Carter and Klinka 1992), and inspection of needles present (by counting back growth increments) indicated that although as many as seven age classes were represented, only current-year, second-year, and third-year needles were present in abundance.

Weather data for the study period were obtained from an Environment Canada weather station (Clim. Stn. # 1103332, 147 m elevation) within 2 km of the site. Comparison of growing-season (June-Sept.) values of mean, minimum, and maximum air temperatures and precipitation for the study period with long-term climate normals for the same weather station (Environment Canada 1993) indicated that the 1996 growing-season was generally typical, except that precipitation was lower than average in June and July (Table 3.1). This suggests the possibility of a slight water deficit early in the growing-season. However, by July rainfall was very similar to the 53 mm average for the driest month in CWHdm subzone (Meidinger and Pojar 1991), and rainfall was above average in August during the period of physiological measurements (Table 3.1). No extended periods without precipitation occurred within any month.
Table 3.1 Comparison of long-term climate normals and current-year monthly averages for mean daily temperature, maximum daily temperature, minimum daily temperature, precipitation, and number of days per month with measurable precipitation. Also shown are comparisons of extreme maximum and minimum monthly temperatures.

<table>
<thead>
<tr>
<th>Environmental parameter</th>
<th>Long-term (30-year) climate normals for the June-September growing-season, U.B.C. Research Forest environmental monitoring station</th>
<th>Weather data for the 1996 June-September growing-season, U.B.C. Research Forest environmental monitoring station</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean daily temperature, °C</td>
<td>14.6</td>
<td>16.8</td>
</tr>
<tr>
<td>Maximum daily temperature, °C</td>
<td>19.6</td>
<td>22.5</td>
</tr>
<tr>
<td>Minimum daily temperature, °C</td>
<td>9.5</td>
<td>11.1</td>
</tr>
<tr>
<td>Extreme maximum temperature, °C</td>
<td>33.0</td>
<td>34.4</td>
</tr>
<tr>
<td>Extreme minimum temperature, °C</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Total precipitation, mm</td>
<td>93.1</td>
<td>80.9</td>
</tr>
<tr>
<td>Number of days with measurable precipitation (≥0.2 mm)</td>
<td>13</td>
<td>9</td>
</tr>
</tbody>
</table>

b. Source: U.B.C. Research Forest records.

Sky conditions during the summer of 1996 are shown in Table 3.2 based on observations at the same weather station. Longer-term cloud cover data are not available for direct comparison, but frequent cloudiness is considered characteristic of this location (Klinka and Krajina 1986) and the Pacific coastal region more generally (Waring and Franklin 1979).

3.2 UNDERSTORY ENVIRONMENT

The understory environment was characterized in terms of mid-day temperature, mid-day humidity, relative light availability, and potential sunfleck activity. Some of these measures also served as a basis against which to evaluate the relevancy of the measurement conditions used in gas exchange analysis.
Table 3.2  Sky conditions during the 1996 growing-season. Daily light index ranges from 1.0 (both morning and afternoon mainly overcast) to 3.0 (both morning and afternoon mainly sunny). Values >1.0 but <3.0 represent variable or changing sky conditions (derived from U.B.C. Research Forest records) 

<table>
<thead>
<tr>
<th>Parameter</th>
<th>June</th>
<th>July</th>
<th>August</th>
<th>September</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean daily light index (scale 1.0–3.0)</td>
<td>1.80</td>
<td>2.48</td>
<td>2.15</td>
<td>2.02</td>
</tr>
<tr>
<td>Percent of days with light index 3.0 (both morning and afternoon mainly sunny)</td>
<td>7%</td>
<td>65%</td>
<td>35%</td>
<td>17%</td>
</tr>
<tr>
<td>Percent of days with light index 1.0 (both morning and afternoon mainly overcast)</td>
<td>23%</td>
<td>16%</td>
<td>16%</td>
<td>0%</td>
</tr>
<tr>
<td>Percent of days with light index &gt;1.0 and &lt;3.0 (variable or changing sky conditions)</td>
<td>70%</td>
<td>19%</td>
<td>49%</td>
<td>83%</td>
</tr>
<tr>
<td>Percent of days with mainly sunny conditions in either morning or afternoon or both</td>
<td>27%</td>
<td>74%</td>
<td>52%</td>
<td>43%</td>
</tr>
<tr>
<td>Percent of days with mainly overcast conditions in either morning or afternoon or both</td>
<td>50%</td>
<td>26%</td>
<td>42%</td>
<td>57%</td>
</tr>
</tbody>
</table>

a. Sky conditions were recorded subjectively by Research Forest staff twice daily, once in the morning at 08:00 h and once in the afternoon at 16:00 h Pacific standard time. These qualitative data were then converted into a numerical three point light index: 3, 'mainly sunny'; 2, 'intermediate cloud cover'; and 1, 'mainly overcast'. The daily light index was then computed as the mean of the morning and afternoon values (scale 1.0–3.0), and the data summarized by month as shown.

3.2.1 Temperature, humidity, and vapour pressure deficit

Throughout the period of gas exchange analysis, a hand-held probe containing a thermocouple and Vaisala sensor was used to measure understory air temperature (T<sub>air</sub>) and relative humidity (RH) at approximately 2.0–2.5 m from the ground surface at mid-day (ca. 12:00 h, Pacific standard time). Mid-day understory vapour pressure deficit of the air (VPD<sub>air</sub>) was calculated as:

\[
\text{VPD}_{\text{air}} = \text{VP}_{\text{sat}} - \text{VP}_{\text{air}}
\]

where, \(\text{VP}_{\text{sat}}\) is the saturation vapour pressure over water at the measured air temperature (from standard tables) and \(\text{VP}_{\text{air}}\) is the corresponding vapour pressure of the air (\(\text{VP}_{\text{air}} = \text{VP}_{\text{sat}} \times \text{RH} / 100\)).

3.2.2 Light

Understory light was characterized both in terms of relative light availability and potential sunfleck activity. Relative light availability was assayed with quantum sensors as % canopy transmittance and sunfleck activity was measured using photodiode sensors.
3.2.2.1 Canopy transmittance

The light environment associated with each understory conifer sapling studied was characterized in terms of the percent transmittance of light through the red alder canopy in the photosynthetically active range (400–700 nm):

\[
\text{% canopy transmittance} = \frac{Q_i}{Q_o} \times 100\% \quad [2]
\]

where, \(Q_i\) is photosynthetic photon flux density (PPFD) at the location of a sapling in the understory and \(Q_o\) is the unattenuated reference PPFD measured in a nearby clearing (e.g., Pierce and Running 1988; Carter and Klinka 1992; Lieffers and Stadt 1994; Parent and Messier 1996).

The procedure was as follows. A datalogger (CR-10, Campbell Scientific, Shepshed, England) was set-up in a nearby clearing to continuously measure the reference PPFD \(Q_o\) from a quantum sensor (LI-190SA, Li-Cor, Lincoln, Nebr.) at 5 second intervals. Using a second quantum sensor and a hand-held light meter (LI-189, Li-Cor, Lincoln, Nebr.), corresponding measurements of understory PPFD \(Q_i\) were then made in the south aspect of each sample tree at approximately 2.0–2.5 m height. The percent canopy transmittance associated with each sapling was computed as in Equation 2 above. To avoid variation introduced by sunfleck activity in the understory, measurements were made under completely overcast and uniform sky conditions (Parent and Messier 1996), which is appropriate as long as canopies are relatively uniform in composition and cover (Stadt et al. 1997; Comeau et al. 1998; and cf. Messier and Parent 1997) as was the case here. Measurements were made in August during the period when canopy leaves were fully expanded and conifer saplings were being assessed for photosynthetic performance.

3.2.2.2 Sunfleck activity

Direct, high frequency sampling of sunfleck activity in the understory was accomplished using 12 individual gallium arsenide phosphide (GaAsP) photodiode sensors (G1118, Hamamatsu Corp., Bridgewater, N.J) (Pontailler 1990) connected to two dataloggers (CR-10, Campbell Scientific, Inc., Shepshed, England). All photodiodes were individually calibrated (680 Ω resistors) against a quantum sensor (LI-190SA, Li-Cor, Lincoln, Nebr.) prior to use in the field. Photodiodes were not modified for cosine response because sampling was restricted a priori to a 6 h interval centred around local noon (Pacific standard time), from 09:00 to 15:00 h on completely clear-sky days. Photodiode sensors have good cosine response up to zenithal beam angles of 70° (above a 20° angle of incident light) (Pontailler 1990).

In the field, each of the 12 photodiodes was mounted horizontally on a post in the south aspect of one of the 12 sample trees, at a height of roughly 2 m. For mounting, the sensors were first bound flush with epoxy over-top small holes drilled centrally on 5.0 x 5.0 x 2.0 cm blocks of pressure-treated wood. Three additional holes were then drilled equi-distant around each diode, and each hole fitted with a 3.0 cm square-ended screw. The heads of the screws were positioned in surface depressions drilled in the block well below the ‘view’ of the photodiode, and the square ends of the protruding screws were then set in corresponding depressions drilled on the top surface of the
post. This arrangement provided enough space between the block and the post for the wire to freely pass (to connect the photodiode to the datalogger), and permitted the photodiodes to be easily leveled in the field by means of differential adjustment of the three screws.

A datalogger program was written (Appendix 1) which could evaluate the output from the sensors every 2 s, count all detected sunfleck events, and evaluate and score them in discrete categories of interest. In the program a sunfleck event was defined to be an excursion of photosynthetic photon flux density (PPFD) above a threshold of 40 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \) (individual calibration factors were entered into the program so that the output from the photodiodes was read in terms of absolute PPFD). This threshold value was just above measured levels of diffuse light in the understory at mid-day on clear days (ca. 10–30 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \)) (Pearcy et al. 1994). From the categorical output of the dataloggers, histograms were generated to describe sunfleck activity in terms of i) sunfleck duration; ii) time between sunfleck events; and iii) maximum (peak) sunfleck PPFD. If a sensor was not functioning properly, data for this sensor were disregarded and categorical proportions of sunflecks adjusted accordingly.

3.3 TRANSIENT PHOTOSYNTHETIC RESPONSES TO DYNAMIC LIGHT CONDITIONS

3.3.1 Instrumentation, set-up, and approach

3.3.1.1 Instrumentation and settings

Transient photosynthetic responses to changing light conditions were analyzed \textit{in situ} in the field on attached mature current-year foliage of both species. Measurements were made using a regularly calibrated fast-responding (specification <0.1 s) field portable open-flow gas exchange system (LI-6400, Li-Cor, Lincoln, Nebr.) with a CO\(_2\) injector and a small volume 6 cm\(^2\) leaf chamber. The leaf chamber was fitted with an internal GaAsP photodiode and two thermoelectric Peltier coolers, and also contained the system’s dual infra-red gas analyzers, thereby eliminating time delays due to tubing. Data were logged to portable computer because the capacity of the internal data acquisition system of the LI-6400 was insufficient for extended high frequency sampling. The maximum rate of data acquisition was 2 s\(^{-1}\). Gas exchange parameters were computed from the raw data after von Caemmerer and Farquhar (1981).

Light in all tests was supplied by a 35 W halogen lamp and delivered to the leaf chamber by a rectangular mylar ‘light tunnel’ (7.2 x 8.0 x 30.0 cm). The light tunnel was fixed in place between the light source and the leaf chamber (but with sufficient headroom for airflow) and used to improve the uniformity of light delivered to the foliage (all three components were bolted to a tripod). The GaAsP photodiode within the leaf chamber was calibrated against a quantum sensor placed in the position normally occupied by the sample, and used as a measure of light received by the foliage. To vary the intensity of incident light, sections of spectrally neutral shade cloth were interposed between the distal end of the light tunnel and the leaf chamber. A single shade screen was required to reduce incident PPFD from the source to the selected high light (HL) level of 470 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \) used in all tests. The selected low light (LL) level of 30 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \) was then achieved by further shading the leaf chamber with a layer of four neutral density shade screens held taught on a Plexiglas frame. The frame was designed so that it could...
be easily slipped on and off of the leaf chamber window, thereby providing also for rapid manual control of transitions between high and low light. The high light level was selected to be effectively saturating for the foliage of both species without being so high as to cause photoinhibition. The low light level was representative of the level of diffuse light in the understory on sunny days.

Leaf chamber and reference air conditions were controlled so as to maintain leaf temperature (\(T_{\text{leaf}}\)) at 22 °C (set-point control via the Peltier coolers), leaf-to-air vapour pressure deficit (\(\text{VPD}_{\text{leaf-air}}\)) at 1.0 kPa (manual control), and the concentration of \(\text{CO}_2\) in the reference air stream ([\(\text{CO}_2\])_\text{Ref}) at 360 \(\mu\text{mol}\cdot\text{mol}^{-1}\) (set-point control via the \(\text{CO}_2\)-injector). It was necessary to control the leaf-air vapour pressure deficit (\(\text{VPD}_{\text{leaf-air}}\)) manually rather than by set-point control, so that a constant high flow rate rather than a variable flow rate could be used (the LI-6400 controls VPD by varying the flow rate). Because the LI-6400 had no on-board capabilities for humidifying the reference air, humidity was controlled manually as follows. Ambient air extracted from about 4 m height was first drawn through a tube containing a moist sponge, and then routed through a column of soda lime on the instrument console. The primary purpose of the soda lime column was to remove \(\text{CO}_2\) (later added-back as required by means of the \(\text{CO}_2\)-injector), but a small amount of water (<10 ml) was often added to the soda lime to aid in humidification. Humidified air was then dried to the desired level by manually diverting an appropriate portion of the flow through a tube of drierite on the instrument console. Flow rate was maintained at 400 mL min\(^{-1}\) and the fan speed set to fast. Higher flow rates were rejected because of insufficient signal size.

### 3.3.1.2 Field set-up

The field set-up used for in situ gas exchange analysis is shown in Figure 3.1. Industrial construction scaffolding was erected and used to support the gas exchange system, tripod, light source, and computer on a platform roughly 2 m in height (base unit 1.8 m high x 0.9 m wide, with screw jacks for leveling and extension to an additional 0.75 m; Canada Scaffold Supply Co. Ltd., Richmond, B.C.). A tall wooden frame was built to fit over the platform and used to support a poly-tarp that excluded any rain when present. Ambient air was extracted from above the poly-tarp. Power requirements for the gas exchange system were met by eight 12 V rechargeable batteries, and a gas generator (650 W, EX650, Honda Motor Company Ltd., Japan) was used to power both the light source and computer.
3.3.1.3 Sampling approach

One of the 12 saplings was randomly selected for sampling each day. Various tests (detailed in subsequent subsections) were performed on each sapling to examine three main features of the photosynthetic response to fluctuating light:

1) photosynthetic induction potential (the time required for photosynthetic induction under continuous high light);
2) the decay of photosynthetic induction state in low light; and
3) the capacity for photosynthetic induction and carbon gain in rapidly fluctuating light (photosynthetic response to simulated sunflecks).
Species comparisons based on relative measures of performance (induction potential, induction state, lightfleck use efficiency) were in all cases checked against those made more simply on the basis of absolute photosynthetic rates or absolute total carbon gain. In each of the three types of analysis, biochemical and stomatal limitations to photosynthesis were also explored and intrinsic water use efficiency (A/gs) was computed as a measure of the effect of photosynthetic induction dynamics on the tradeoff between maximizing photosynthesis and minimizing water loss.

Following gas exchange analysis, the experimental foliage was clipped from the tree and transported in moist paper towel to a laboratory at U.B.C. Projected leaf area was then measured on fronds (western redcedar) or freshly detached needles (coastal Douglas-fir) using an integrating, scanning leaf area meter fitted with a 105 mm lens calibrated and operated at 0.1 mm² resolution (LI-3100, Li-Cor Inc., Lincoln, Nebr.). The photosynthetic leaf area of each sample was taken to be the mean of five projected area measurements, and was used to correct gas exchange data for the true leaf area of the sample.

3.3.2 Photosynthetic induction in continuous high light

3.3.2.1 Photosynthetic induction potential

For quantification of photosynthetic induction potential, the time required for each species to reach 50% (A-T₅₀) and 90% (A-T₉₀) of full photosynthetic induction, from steady-state net CO₂ assimilation at low light to steady-state net CO₂ assimilation at saturating high light was determined. Foliage was first held in the leaf chamber for a minimum of 1 hour under low light (30 μmol·m⁻²·s⁻¹) and otherwise standard test conditions (Section 3.3.1.1). Steady-state conditions at low light were then autologged at 2 s⁻¹ for a minimum of 3 minutes, the shading device abruptly removed, and gas exchange responses to the rapid increase in light were followed to the steady-state at high light (470 μmol·m⁻²·s⁻¹). Sampling rate was maintained at 2 s⁻¹ for the first 20 minutes or so after the abrupt increase in light, and then usually reduced to 10 s⁻¹ for the remainder of the test.

For determination of A-T₅₀ and A-T₉₀, net CO₂ assimilation data for each individual sapling were input and fit independently to a two-parameter rectangular hyperbola using an automated iterative nonlinear least squares curve-fitting procedure (TableCurve, v. 1.0, Jandel Scientific, San Rafael, Calif.). The function took the form:

\[ A_t = \frac{(A_{HL} * b * t)}{(A_{HL} + b * t)} \]  

where, \( A_t \) is the net CO₂ assimilation rate (μmol·CO₂·m⁻²·s⁻¹) at any given time, \( t \) (s); \( A_{HL} \) is the steady-state rate of net CO₂ assimilation at high light; and \( b \) is the initial slope of the response. This function has previously been used in some other studies of the gas exchange kinetics of forest tree species (Poorter and Oberbauer 1993), and here provided the best overall fit for both species from among six equations that i) closely matched the data; ii) were relatively simple (with a small number of parameters); and iii) biologically meaningful (with parameters easily interpreted within the context of photosynthetic induction).
Prior to curve-fitting the data, the net CO₂ assimilation value at time zero (upon transfer to high light) was changed to the value of the mean steady-state rate at low light to provide a more accurate starting estimate for the routine. Assimilation data were then normalized with respect to this starting estimate and subject to curve-fitting as described. Times to reach 50% (A-T₅₀) and 90% (A-T₉₀) of full photosynthetic induction were determined by setting Aᵢ to 50% or 90% of the AᵢHL estimate, respectively, in the fitted function.

To assess the relative importance of the light activation of Rubisco enzyme (ribulose 1,5-bisphosphate carboxylase) versus light-induced stomatal opening in the photosynthetic induction response, T₅₀ and T₉₀ values were also computed for photosynthetic CO₂ use efficiency (A/Cᵢ-T₅₀, A/Cᵢ-T₉₀) and stomatal conductance (gs-T₅₀, gs-T₉₀) for the same time-course of photosynthetic induction. Photosynthetic CO₂ use efficiency (A/Cᵢ) is useful as an index of photosynthetic utilization of leaf internal (intercellular space) CO₂ (Cᵢ) and thus Rubisco activation, because it factors out the influence of stomata on CO₂ flux. That A/Cᵢ reflects Rubisco activation during photosynthetic induction has been verified elsewhere with direct enzymatic measurements (Ögren and Sundin 1996). Stomatal patchiness does not appear to affect the calculation of Cᵢ in shade-grown leaves of woody species (Küppers et al. 1999), and initial stomatal conductances were high enough that cuticular conductance was also unlikely to introduce errors in Cᵢ.

Values of T₅₀ and T₉₀ for both A/Cᵢ and gs were determined according to the general procedure outlined above for net CO₂ assimilation. However, whereas A/Cᵢ-T₅₀ and A/Cᵢ-T₉₀ values were derived by fitting the A/Cᵢ data to the same equation as net CO₂ assimilation (Equation 3), the stomatal conductance data (for derivation of gs-T₅₀ and gs-T₉₀ values) were better fit to a cumulative model of the form (TableCurve, v. 1.0, Jandel Scientific, San Rafael, Calif.):

\[ gs_t = a + b \times 0.5 \times (1 + erf((t - c)/(2^{0.5} \times d))) \]  

where, gsᵢ is stomatal conductance (mol H₂O m⁻² s⁻¹) at any given time, t (s); a is the lower plateau of the response; b is the height of the transition; c is the centre of the transition, and d is a descriptor of the steepness of the transition.

### 3.3.2.2 Absolute photosynthetic rates during induction

Absolute rates of net carbon exchange (A, µmol CO₂ m⁻² s⁻¹) were compared between species at various points during the time-course of photosynthetic induction.

### 3.3.2.3 Intrinsic water use efficiency during induction

To determine whether any differences between species in photosynthetic induction dynamics may have implications for water use efficiency, changes in intrinsic water use efficiency (A/gs, µmol CO₂ mol H₂O⁻¹) were examined for each species during the time-course of photosynthetic induction.
3.3.3 The loss of photosynthetic induction with shading

3.3.3.1 The decay of photosynthetic induction state

The effect of shading on the loss of photosynthetic induction in western redcedar and coastal Douglas-fir was examined by quantifying the relative depression (from maximum) in the photosynthetic rate of each species following exposure of fully induced foliage to shading intervals of 2, 5, 15, and 30 minutes. The procedure was as follows. Foliage was first brought to steady-state gas exchange at saturating high light (470 μmol·m⁻²·s⁻¹) and then abruptly shaded (30 μmol photons·m⁻²·s⁻¹). After maintaining the shading treatment for one of the pre-selected times (2, 5, 15, or 30 minutes), the shading device was abruptly removed and the sample returned to high light. The four shading intervals were applied in random order in this manner to each sapling, allowing sufficient time between shading intervals such that a steady-state was always re-achieved at high light before the next shading interval was applied. Gas exchange data were logged to computer at 2 s⁻¹, except during the longest shading intervals when logging frequency was temporarily reduced to 10 s⁻¹ until about 5 minutes prior to the return to high light.

The relative depression in photosynthetic rate following each period of shading was quantified in terms of the photosynthetic induction state (a measure of the capacity of a leaf to respond immediately to a light increase), computed after Chazdon and Pearcy (1986a) as the net CO₂ assimilation rate 60 s after the light increase expressed relative to the maximum steady-state rate of net CO₂ assimilation in saturating light. Or, in mathematical terms:

$$A-IS_{60} = \frac{(A_{60} - A_{LL})}{(A_{HL} - A_{LL})}$$

where, $A-IS_{60}$ is the photosynthetic induction state 60 s after return to high light (relative units); $A_{60}$ is the net CO₂ assimilation rate 60 s after return to high light (μmol CO₂·m⁻²·s⁻¹); and $A_{LL}$ and $A_{HL}$ are the steady-state rates of net CO₂ assimilation at low light and saturating high light, respectively (μmol CO₂·m⁻²·s⁻¹).

Values of $A_{60}$ input into Equation 5 were determined by curve-fitting the photosynthetic response during the first 120 s after return to high light and extracting the value predicted at 60 s. Because the function used earlier to fit the photosynthetic induction response of non-induced foliage (Equation 3) did not produce acceptable fits for foliage undergoing incomplete transitions to the steady-state at high light, a four parameter transition function (logistic dose-response) was used to fit the initial response after all shading intervals. The function took the form:

$$A_t = a + b / (1 + (t/c)^d)$$

where, $A_t$ is the net CO₂ assimilation rate (μmol CO₂·m⁻²·s⁻¹) at any given time, $t$ (s) after the light increase; $a$ is the lower plateau of the response; $b$ is the height of the transition; $c$ is the centre of the transition; and $d$ is a descriptor of the slope of the transition. Data were normalized with respect to the starting value prior to curve-fitting.
To examine the relative role of the loss of Rubisco activity versus the closing of stomata in the decay of photosynthetic induction, induction state (IS$_{60}$) values were also determined for photosynthetic CO$_2$ use efficiency (A/C$_i$-IS$_{60}$) and stomatal conductance (gs-IS$_{60}$) by substituting the corresponding values of A/C$_i$ or gs for A in Equation 5. As with the A$_{60}$ values input into Equation 5, A/C$_i$ and gs$_{60}$ values input into the same equation were extracted from the fit of the appropriate data to Equation 6.

3.3.3.2 Effect of shading intervals on absolute photosynthetic rates

Species were also compared on the basis absolute photosynthetic rates 60 s after the light increase, i.e., on the basis of A$_{60}$ values (photosynthetic rates measured at the same time induction state values were determined).

3.3.3.3 Intrinsic water use efficiency during shade periods

To determine the extent to which slow stomatal closing in shade may impact the water use efficiency of western redcedar and coastal Douglas-fir in the low light periods between high light events, intrinsic water use efficiency (A/gs, μmol CO$_2$-mol H$_2$O$^{-1}$) was computed for both species at the end of each shading interval.

3.3.4 Photosynthetic induction in fluctuating light

Non-induced foliage was exposed to a series of simulated sunflecks ('lightflecks') to determine the effects of a fluctuating light regime (rapidly alternating periods of high and low light) on the photosynthetic induction state, carbon gain, and water use efficiency of western redcedar and coastal Douglas-fir. The lightfleck series consisted of five 30 second lightflecks (470 μmol-m$^{-2}$s$^{-1}$) separated by 2 minute intervals of low light (30 μmol-m$^{-2}$s$^{-1}$). A lightfleck duration of 30 s was selected based on early observations that the residence time of the majority of sunflecks in the understory was 30 s or less. A low light interval of 2 min was used to separate individual lightfleck events to ensure that any post-lightfleck responses (post-illumination CO$_2$ fixation and photorespiratory bursts) were complete before subsequent lightflecks were administered (Pearcy et al. 1985; Chazdon and Pearcy 1986b).

For the test, foliage was first brought to steady-state gas exchange at low light (30 μmol-m$^{-2}$s$^{-1}$) and this condition was logged to computer at 2 s$^{-1}$ for a minimum of 3 minutes. While continuing datalogging at the same rate, the lightfleck series was then applied beginning with the first 30 s lightfleck and ending with the fifth 2 min post-lightfleck shading interval. The total elapsed time for the test was thus 750 s or 12.5 min (5*30 s lightflecks + 5*120 s post-lightfleck shading intervals = 750 s). Gas exchange data from the test were used to compute the parameters described in the following sections.

3.3.4.1 Photosynthetic induction state

Photosynthetic induction state was determined according to the equation given previously (Equation 5), except that in this case it was computed 30 s after the light increase (as A-IS$_{30}$ values), at the end of each lightfleck in the series. Induction state values were determined similarly for photosynthetic CO$_2$ use efficiency (A/C$_i$-IS$_{30}$) and stomatal conductance (gs-IS$_{30}$).
To gauge the degree to which photosynthetic induction could proceed in fluctuating light in comparison with continuous high light, photosynthetic induction state (A-IS₃₀) at the end of lightfleck #5 was then compared to i) A-IS₆₃₀, the induction state achieved after exposure of non-induced foliage to a comparable total elapsed time under continuous high light (630 s, to the end of the fifth lightfleck); and ii) A-IS₁₅₀, the induction state achieved after exposure of non-induced foliage to a comparable cumulative photon exposure to continuous high light (70.5 mmol photons-m⁻², equivalent to exposure to five lightflecks of 30 s duration). The former comparison illustrated the light-dependency of photosynthetic induction and the latter comparison the extent to which photosynthetic induction may proceed either faster or slower in fluctuating light than under continuous illumination with the same amount of high light. The A-IS₆₃₀ and A-IS₁₅₀ values required for these comparisons were obtained by curve-fitting the first 750 s of induction potential data from Section 3.3.2.1 to the logistic dose-response function used to describe incomplete transitions to the steady-state (Equation 6). Corresponding IS₆₃₀ and IS₁₅₀ values for photosynthetic CO₂ use efficiency (A/Cᵣ) and stomatal conductance (gs) were computed similarly.

3.3.4.2 Lightfleck use efficiency

The efficiency with which lightflecks were used for photosynthetic carbon gain was examined for each species by computing an index of ‘lightfleck use efficiency’ (LUE) after (Chazdon and Pearcy 1986b):

\[
LUE = \frac{\text{measured carbon gain}}{\text{predicted carbon gain}} \times 100
\]  \[7\]

where, ‘measured carbon gain’ is the absolute net amount of carbon gain attributable to a lightfleck; and ‘predicted carbon gain’ is the absolute net amount of carbon gain hypothetically expected if an instantaneous steady-state response were assumed for the duration of the lightfleck (30 s). Both terms in the equation represent absolute amounts of CO₂ fixed (µmol CO₂-m⁻²) rather than rates of CO₂ fixation (µmol CO₂-m⁻²-s⁻¹).

To derive the appropriate terms for the calculation of LUE, photosynthesis data were first normalized with respect to the mean steady-state rate of CO₂ fixation at low light prior to the lightfleck series. Numerical integration of the net CO₂ assimilation rate was then carried out from the beginning of each lightfleck until the end of the 2 minute shading interval following the same lightfleck (over a period of 150 s). This gave the carbon gain attributable to individual lightflecks (numerator terms for LUE), which included not only the photosynthetic response to the lightfleck-proper (interval between when the high light was switched on and off) but also that due to the net post-lightfleck response (post-illumination CO₂ fixation less any CO₂ lost to post-illumination photorespiratory bursts). Predicted carbon gain (denominator term for LUE) was computed by subtracting from the maximum steady-state photosynthetic rate at saturating high light the steady-state photosynthetic rate at low light (A₇Hₗ - A₇Lₗ) and multiplying this value by the lightfleck duration (30 s).

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8 Photon exposure (photons-m⁻²), which is a measure of light dosage or quantity, is the product of irradiance and duration of illumination (Anderson et al. 1997). Thus, the photon exposure to high light here was: 470 µmol photons m⁻² s⁻¹ * 150 s = 70.5 mmol photons-m⁻².
To assess the contribution of net post-lightfleck CO\textsubscript{2} fixation to the total carbon gain attributable to a lightfleck, any positive net post-lightfleck CO\textsubscript{2} fixation was separated out from that carbon gain due to the lightfleck-proper and then expressed as a percentage of the total carbon gain attributable to a lightfleck.

### 3.3.4.3 Absolute carbon gain in fluctuating light

Species were also compared on the basis of the absolute amount of carbon gained (\(\mu\text{mol CO}_2\cdot\text{m}^2\)) and absolute rates of photosynthesis achieved (\(A, \mu\text{mol CO}_2\cdot\text{m}^2\cdot\text{s}^{-1}\)) during the lightfleck series. To demonstrate the extent to which low foliar induction state might limit, and post-lightfleck CO\textsubscript{2} fixation might enhance, absolute carbon gain in fluctuating light, comparisons were drawn among: i) for non-induced foliage, the absolute carbon gain owing to the five 30 s lightflecks given in series (summed over the lightfleck series, so as to include any net post-illumination CO\textsubscript{2} fixation); ii) for non-induced foliage, the absolute carbon gain achieved during a comparable cumulative photon exposure to continuous high light (70.5 mmol photons\cdot m\textsuperscript{-2} dose, given as a 150 s exposure to 470 \(\mu\text{mol photons}\cdot\text{m}^2\cdot\text{s}^{-1}\)); and iii) the absolute carbon gain that would hypothetically be achieved during the same cumulative photon exposure to continuous high light (150 s at 470 \(\mu\text{mol photons}\cdot\text{m}^2\cdot\text{s}^{-1}\)) if an instantaneous steady-state photosynthetic response to the high light dose was assumed (as for fully induced leaves with no induction requirement). As before, absolute carbon gain (\(\mu\text{mol CO}_2\cdot\text{m}^2\)) was in all cases determined by numerical integration over the appropriate time interval after normalizing with respect to the steady-state photosynthesis rate at low light, so that any residual carbon gain was then due specifically to the exposure to high light. For each species, comparison of case iii (fully induced foliage) with cases i and ii (non-induced foliage) demonstrated the extent to which low foliar induction state can limit photosynthetic carbon gain. Comparison of case i (non-induced leaves given the 70.5 mmol-m\textsuperscript{-2} high light dose in a fluctuating light regime) and case ii (non-induced leaves given the same high light dose by continuous illumination) demonstrated the enhancement in carbon gain that can occur in fluctuating light at least in part as a result of post-lightfleck CO\textsubscript{2} fixation.

### 3.3.4.4 Intrinsic water use efficiency in fluctuating light

To determine what impact any interspecific differences in the dynamics of photosynthesis and stomatal conductance in fluctuating light might have on water use efficiency, intrinsic water use efficiency (\(A/\text{gs}, \mu\text{mol CO}_2:\text{mol H}_2\text{O}\textsuperscript{-1}\)) was computed for each species at the end of each lightfleck and at the end of each post-lightfleck shading interval in the series.

### 3.4 STEADY-STATE PHOTOSYNTHESIS AND DARK RESPIRATION

#### 3.4.1 Instrumentation and settings

In mid-August, curves representing the steady-state response of net CO\textsubscript{2} assimilation (\(A\)) to light (PPFD) and intercellular carbon dioxide concentration (\(C_i\)) were constructed in the laboratory using shoots detached from
the same field plants. Shoots were collected from individual saplings in the morning, transported to the laboratory with cut ends submerged in water, stored at room temperature under dim light (ca. <5 \mu mol-m^{-2}-s^{-1}), and analyzed within a day. Stems were always recut under water just prior to measurement. This manner of use of excised shoots has been well tested and validated for conifer species (e.g., Brix and Ebell 1969; Brix 1971; Neilson et al. 1972; DeLucia and Smith 1987; Zhang et al. 1993).

The gas exchange system and light system detailed in Section 3.3.1.1 were used for construction of both photosynthetic light-response (A/PPFD) and \( C_t \)-response (A/C\(_t \)) curves, except that the light source in this case was a 150 W quartz-halogen bulb. Measurement conditions were identical to those used for kinetic gas exchange analyses (i.e., 22 °C \( T_{leaf} \), 1.0 kPa \( VPD_{leaf-air} \), and either 360 \( \mu \)mol CO\(_2\)-mol\(^{-1}\) or 470 \( \mu \)mol photons m\(^{-2}\)-s\(^{-1}\) as appropriate), except that the air flow rate was reduced to 200 mL-min\(^{-1}\).

For both types of analysis, 20 minutes equilibration time was allowed after the foliage was initially sealed in the cuvette before any measurements were recorded and eight to 15 minutes equilibration time was allowed following each step-change in PPFD or \( C_t \), until A, \( C_t \), and gs were at steady-state as viewed graphically on the LI-6400. At each PPFD or \( C_t \) level steady-state gas exchange data were automatically logged to computer for 2–3 minutes at 5 s\(^{-1}\). Mean steady-state values were then calculated for each 2–3 minute autologging interval, and these mean values were then input and used in curve-fitting the A/PPFD or A/\( C_t \) response (see below). Sample size was initially six saplings per species for A/PPFD curves and three saplings per species for A/\( C_t \) curves. However, the electronic data file for one A/PPFD curve for Douglas-fir was corrupted and not retrievable.

### 3.4.2 Response to photosynthetic photon flux density

To construct light-response curves of steady-state net CO\(_2\) assimilation (A/PPFD curves), photosynthetic photon flux density (PPFD) was varied by interposing neutral density shade screens between the leaf chamber and the end of the mylar light tunnel distal to the light source, in seven steps from dark to beyond light saturation. Dark respiration (\( R_d \)) was always measured first so as to avoid generating artifactually high respiration rates (and light compensation points) typically observed after a period of active photosynthesis (Heichel 1970; Azcon-Bieto and Osmond 1983). The PPFD was then incrementally increased so that the onset of any photoinhibition would not affect measurements made in the quantum yield region of the photosynthetic light-response.

An iterative non-linear least squares curve-fitting program (TableCurve, v. 1.0, Jandel Scientific, San Rafael, Calif.) was used to fit the A/PPFD response to the form of the non-rectangular hyperbola given by Leverenz (1987)\(^9\). The function took the form:

\[
A + R_d = \frac{PPFD \times \Phi_1 + A_{sat} - [(PPFD \times \Phi_1 + A_{sat})^2 - 4 \times PPFD \times \Phi_1 \times A_{sat} \times \theta]^{0.5}}{2 \times \theta} \tag{8}
\]

---

\(^9\) The Leverenz function provided a significantly better fit to the data than did the rectangular hyperbola commonly used in studies of photosynthetic light-response (e.g., Long and Hallgren 1993).
where, $A$ is the net $\text{CO}_2$ assimilation rate in the light ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$); $R_d$ is the dark respiration rate ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$); PPFD is the incident photosynthetic photon flux density ($\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$); $\Phi_i$ is the apparent quantum yield (mol $\text{CO}_2 \cdot \text{mol incident photons}^{-1}$); $A_{\text{sat}}$ is $A$ when PPFD is saturating; and $\theta$ is the rate of bending or apparent convexity of the light-response curve ($0 \leq \theta \leq 1$, unitless). The maximum photosynthetic rate ($A_{\text{max}}$) of each species was reported as 90% of its curve-fit maximum value ($A_{\text{sat}}$) because, much like other models, the Leverenz function has a high asymptote that may not be reached for intact shoots even at full sun. Photosynthetic light compensation points (LCP, $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) were determined by setting $A=0$ in the fitted function. Values of $R_d$, LCP, and $\Phi_i$ were checked for apparent bias against values for the same parameters computed using the two points measured at 0 and approximately 30 $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (see Leverenz 1995). No bias was evident.

To determine if any interspecific differences in photosynthesis and dark respiration were consistent across measurement units, area-based net $\text{CO}_2$ assimilation rates ($A^*$, $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) were converted to mass-based values ($A_{\text{mass}}$, $\text{nmol CO}_2 \cdot \text{g}^{-1} \cdot \text{s}^{-1}$) and refit to Equation 8.

### 3.4.3 Response to intercellular carbon dioxide concentration

For construction of $A/C_i$ curves, foliage was first fully induced to the steady-state at 700 $\mu\text{mol} \cdot \text{mol}^{-1}$ atmospheric $\text{CO}_2$ concentration ($[\text{CO}_2]_{\text{atm}}$) and saturating but not excessive PPFD (470 $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). The $[\text{CO}_2]_{\text{atm}}$ was then incrementally decreased in 9 or 10 steps so that the corresponding range of $C_i$ achieved was roughly 50–500 $\mu\text{mol CO}_2 \cdot \text{mol}^{-1}$. Data for each species were then pooled, and an iterative non-linear least square curve-fitting package (TableCurve, v. 1.0, Jandel Scientific, San Rafael, Calif.) was used to fit the $A/C_i$ response. Data were best fit to the same function as the photosynthetic light response (Equation 8), with terms redefined to describe the $A/C_i$ response. The function took the form:

$$A + R_{pd} = \left\{ C_i \cdot \alpha + A_{sat} - \left[ (C_i \cdot \alpha + A_{sat})^2 - 4 \cdot C_i \cdot A_{sat} \cdot \phi \right]^{0.5} \right\} / 2 \cdot \phi$$

where, $A$ is the net $\text{CO}_2$ assimilation rate in the light ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$); $R_{pd}$ is an estimate of the combined rate of photorespiration and dark respiration in the light ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$); $C_i$ is the intercellular carbon dioxide concentration ($\mu\text{mol CO}_2 \cdot \text{mol}^{-1}$); $\alpha$ is the initial slope of the response (mol $\cdot \text{m}^{-2} \cdot \text{s}^{-1}$); $A_{sat}$ is $A$ when $C_i$ is saturating; and $\phi$ is the rate of bending toward saturation ($0 \leq \phi \leq 1$, unitless). Electron transport capacity was considered to be represented by the photosynthetic rate at high $C_i$ (where RuBP regeneration is limiting) and the amount (activity) of Rubisco by the initial slope of the response (von Caemmerer and Farquhar 1981; Farquhar and Sharkey 1982).

### 3.5 OTHER MEASUREMENTS (SUPPORTING DATA)

Xylem water potential and chlorophyll fluorescence parameters were examined for each sapling at mid-day (ca. 12:00 h Pacific standard time) on the same day that its gas exchange kinetics were being assayed in the field.
3.5.1 Mid-day xylem water potential

Mid-day xylem water potential was quantified using the pressure chamber technique (Ritchie and Hinckley 1975). For each sapling, one lateral shoot was excised from the distal end of each of two branches located directly above and below the branch used for gas exchange analysis. Shoots were immediately placed in plastic bags to inhibit transpirational water loss, and then transported a short distance to the pressure chamber for analysis. Xylem water potential was determined independently on the two shoots and reported for each sapling as the average of the two measurements.

3.5.2 Chlorophyll fluorescence

Chlorophyll fluorescence parameters were measured in situ at mid-day on attached current-year foliage using a field portable modulated fluorometer (OS-500, PP Systems Opti-Sciences Inc., Tyngsboro, Mass.). Instrument settings were optimized independently for each species, and a standard 30 minute dark adaptation period and subsequent pulse of low intensity far-red light were applied before each individual measurement. Fluorescence parameters measured included i) $F_v/F_m$, the ratio between variable yield ($F_v$) and maximal yield ($F_m$) chlorophyll $a$ fluorescence; and ii) the fluorescence half-rise time ($T'_{1/2}$) between minimal ($F_0$) and maximal yield fluorescence. The former was used as a measure of the photochemical efficiency of photosystem II (Kitajima and Butler 1975) or, more generally, to assess the stress level of the foliage. The latter was used as an estimate of the size of the plastoquinone pool as indicative of electron transport capacity (see Krause and Weis 1991). For each sapling, $F_v/F_m$ and $T'_{1/2}$ were reported as the average of three measurements made on the same or adjacent branches as used for gas exchange.

3.6 STATISTICAL ANALYSIS

The single-factor experiment was of a completely randomized design, with two levels of species and usually six replications (sample size was six saplings per species unless otherwise indicated). The corresponding linear model was:

$$Y_{ij} = \mu + \tau_j + \epsilon_{ij}$$

where $\mu$ is the population mean, $\tau_j$ is the effect of species, and $\epsilon_{ij}$ is the random error.

One-way analysis of variance (ANOVA) tests were carried-out to test the generalized null hypothesis that there was no effect of species on any parameter measured, i.e., that $\tau_j = 0$ in all cases. All statistical analyses were performed using the GLM procedure of SAS (SAS Institute Inc., Cary, N.C.), with species considered a fixed effect factor and replicates a random effect factor. Results were considered significant at $\alpha<0.05$. A sample ANOVA is shown in Table 3.3.
Table 3.3 Sample analysis of variance (ANOVA) for the comparison of western redcedar and coastal Douglas-fir. Results for photochemical efficiency of photosystem II ($F_v/F_m$) are shown by way of example.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of square errors</th>
<th>Mean square error</th>
<th>F-Value</th>
<th>Pr &gt; F_{1.10}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between species, $\tau_j$</td>
<td>1</td>
<td>0.00016875</td>
<td>0.00016875</td>
<td>1.12</td>
<td>0.3149</td>
</tr>
<tr>
<td>Within species or error, $\epsilon_{ij}$</td>
<td>10</td>
<td>0.00150750</td>
<td>0.00015075</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>0.00167625</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


CHAPTER 4
RESULTS

4.1 UNDERSTORY ENVIRONMENT

4.1.1 Temperature, humidity, and vapour pressure deficit

Mean mid-day values of air temperature, relative humidity, and vapour pressure deficit in the understory during the period of gas exchange sampling are shown in Table 4.1. Relative humidity never fell below 58% (minimum) and air temperature did not exceed 24.7 °C (maximum), even on mainly sunny days. Consequently, understory vapour pressure deficits remained low to moderate throughout.

Table 4.1 Mean mid-day air temperature, relative humidity, and vapour pressure deficit in the understory during the measurement period for gas exchange analyses. Standard deviations are shown in parentheses.

<table>
<thead>
<tr>
<th>Atmospheric parameter</th>
<th>Overall mean for all days</th>
<th>Mean for mainly sunny days (light index 3.0) a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature (T_{air}), °C</td>
<td>20.2 (3.3)</td>
<td>22.6 (1.8)</td>
</tr>
<tr>
<td>Relative humidity (RH), %</td>
<td>69.1 (11.2)</td>
<td>63.5 (4.0)</td>
</tr>
<tr>
<td>Vapour pressure deficit of the air (VPD_{air}), kPa</td>
<td>0.78 (0.38)</td>
<td>1.01 (0.17)</td>
</tr>
</tbody>
</table>

a. See footnote a in Table 3.2 (Materials and Methods) for an explanation of light index.

The reference levels of 22 °C leaf temperature (T_{leaf}) and 1.0 kPa leaf to air vapour pressure deficit (VPD_{leaf-air}) selected earlier in the season for use in both transient and steady-state gas exchange analyses (Materials and Methods) agreed favourably with measured air temperatures and vapour pressure deficits in the understory. The selected T_{leaf} of 22 °C was representative of the average air temperature (T_{air}) under the canopy on mainly sunny days when sunflecks were likely to be important (Table 4.1). The selected VPD_{leaf-air} of 1.0 kPa was also representative of understory conditions on mainly sunny days, and co-incidentally exactly that VPD predicted at 22 °C from the observed relationship between VPD_{air} and T_{air} (VPD_{air} = -1.42 + 0.11 * T_{air}; r^2=0.88).
4.1.2 Light

4.1.2.1 Canopy transmittance

Low values of \% canopy transmittance indicated that the understory was deeply shaded (Table 4.2). Light environments did not differ significantly between western redcedar and coastal Douglas-fir, although the result was marginal (Table 4.2).

<table>
<thead>
<tr>
<th>Relative measure of light availability</th>
<th>Western redcedar</th>
<th>Coastal Douglas-fir</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy transmittance, %</td>
<td>2.8 (0.3)</td>
<td>3.6 (0.2)</td>
<td>0.073</td>
</tr>
</tbody>
</table>

4.1.2.2 Sunfleck activity

The clear-sky restriction for measuring sunfleck activity was met on only three days during the study period (01 August, 12 August, and 31 August 1996). Histograms of sunfleck activity were qualitatively similar for all dates, and are illustrated by way of example for 12 August in Figures 4.1, 4.2, and 4.3. If there was any seasonal variation in sunfleck activity between the first and last measurement date, point-to-point variability and/or daily differences in windspeed masked this.

Most sunflecks were short, frequent, and of low peak intensity, but variation in sunfleck characteristics was still considerable. The overwhelming majority of sunflecks were 30 s or less in duration, and only rarely was the residence time of individual sunflecks longer than about 2.0–2.5 minutes (121–150 s category, Figure 4.1). However, sunflecks occasionally persisted for 5 or 6 minutes. The time between sunflecks was also most frequently ≤ 30 s, but sometimes as long as 29 minutes (1741–1770 s category, Figure 4.2). The peak PPFD of more than half of all sunflecks was ≤ 90 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \), but ranged up to 1340 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) (Figure 4.3).
Total number of sunflecks recorded: 2608

Figure 4.1 Duration (residence time) of sunflecks recorded under red alder between 09:00 h and 15:00 h under completely clear-sky conditions on 12 August 1996. No sunflecks were measured in the 601-1800 s range (not shown). Numerical values above the bars indicate the number of sunflecks associated with each category.

Total number of shade intervals recorded: 2608

Figure 4.2 Duration of shading intervals between sunflecks as recorded under red alder between 09:00 h and 15:00 h under completely clear-sky conditions on 12 August 1996. For clarity of presentation, the range of shading duration is indicated only for every other category considered (each category spans 30 s). Numerical values above the bars indicate the number of shading intervals associated with each category.
Total number of sunflecks recorded: 2608

Figure 4.3 Maximum (peak) photosynthetic photon flux density (PPFD) of sunflecks recorded under red alder between 09:00 h and 15:00 h under completely clear-sky conditions on 12 August 1996. Numerical values above the bars indicate the number of sunflecks associated with each category.

4.2 TRANSIENT PHOTOSYNTHETIC RESPONSES TO DYNAMIC LIGHT CONDITIONS

4.2.1 Photosynthetic induction and carbon gain in continuous high light

4.2.1.1 Photosynthetic induction potential

Western redcedar showed a significantly lower potential for rapid photosynthetic induction under continuous high light than did coastal Douglas-fir (Table 4.3). Times required to reach 50% ($A_{T50}$) and 90% ($A_{T90}$) of the steady-state rate of net CO$_2$ assimilation at high light from steady-state net CO$_2$ assimilation at low light were 3.5 ± 0.3 minutes and 31.8 ± 2.7 minutes for redcedar, and 2.2 ± 0.2 minutes and 19.8 ± 1.8 minutes for Douglas-fir. Species differences in induction time did not appear to be related to differences in the activation of ribulose 1,5-bisphosphate carboxylase (Rubisco) because times to reach 50% and 90% of the steady-state value of photosynthetic CO$_2$-use efficiency ($A/C_i-T_{50}$, $A/C_i-T_{90}$) did not differ between species (Table 4.3). However, while photosynthesis closely paralleled photosynthetic CO$_2$-use efficiency in Douglas-fir (indicating that induction in Douglas-fir was largely determined by Rubisco activation), in redcedar the increase in photosynthesis lagged behind (Figure 4.4). The additional limitation to photosynthetic induction in redcedar was taken to represent the opening of stomata, as supported by significantly longer times for stomatal opening in redcedar than in Douglas-fir ($gs-T_{50}$, $gs-T_{90}$, Table 4.3; see also stomatal conductance responses in Figure 4.4).
**Table 4.3** Induction potential parameters for western redcedar and coastal Douglas-fir from the understory of red alder. Shown are the times for net CO₂ assimilation (A), photosynthetic CO₂ use efficiency (A/Q), and stomatal conductance (gs) to reach 50% (T₅₀) and 90% (T₉₀) of the complete response to a sudden increase in light from 30 to 470 μmol·m⁻²·s⁻¹. Foliage was at steady-state conditions at low light prior to the abrupt increase in light. Values are means with standard errors in parentheses.

<table>
<thead>
<tr>
<th>Induction potential parameter</th>
<th>Western redcedar</th>
<th>Coastal Douglas-fir</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-T₅₀, minutes</td>
<td>3.53 (0.30)</td>
<td>2.20 (0.20)</td>
<td>0.004</td>
</tr>
<tr>
<td>A-T₉₀, minutes</td>
<td>31.78 (2.65)</td>
<td>19.77 (1.81)</td>
<td>0.004</td>
</tr>
<tr>
<td>A/Cₗ-T₅₀, minutes</td>
<td>2.00 (0.19)</td>
<td>1.91 (0.15)</td>
<td>0.720</td>
</tr>
<tr>
<td>A/Cₗ-T₉₀, minutes</td>
<td>17.99 (1.71)</td>
<td>17.20 (1.35)</td>
<td>0.720</td>
</tr>
<tr>
<td>gs-T₅₀, minutes</td>
<td>13.22 (0.68)</td>
<td>5.32 (0.59)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>gs-T₉₀, minutes</td>
<td>29.12 (2.40)</td>
<td>14.36 (1.25)</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

The relatively longer stomatal opening time for western redcedar than for Douglas-fir could not be attributed to species differences in initial conductance during the low light period prior to induction (Table 4.4). Rather, there was a tendency for greater overall change in conductance in redcedar (Table 4.4) and redcedar also exhibited a significantly longer lag period prior to stomatal opening than did Douglas-fir (Figure 4.5).
Figure 4.4 Representative time-courses of photosynthetic induction under constant high light in A) western redcedar and B) coastal Douglas-fir. Shown are the transitions in net CO₂ assimilation, photosynthetic CO₂-use efficiency, and stomatal conductance from steady-state conditions at low light (30 μmol·m⁻²·s⁻¹) to steady-state conditions at saturating high light (470 μmol·m⁻²·s⁻¹), upon the sudden increase in light. Data represent predicted values derived from fitted response-curves, and have been normalized on steady-state values at high light.
Table 4.4 Absolute stomatal conductance of western redcedar and coastal Douglas-fir. Shown are mean values for initial stomatal conductance \( (g_{SLL}) \), final stomatal conductance \( (g_{SHL}) \), and the transition in stomatal conductance \( (g_{SHL} - g_{SLL}) \) upon a sudden increase from low light \( (30 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}) \) to high light \( (470 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}) \). Standard errors are given in parentheses.

<table>
<thead>
<tr>
<th>Gas exchange parameter</th>
<th>Western redcedar</th>
<th>Coastal Douglas-fir</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>( g_{SLL} ), ( \text{mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1} ) ( (30 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}) )</td>
<td>0.044 (0.007)</td>
<td>0.053 (0.005)</td>
<td>0.349</td>
</tr>
<tr>
<td>( g_{SHL} ), ( \text{mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1} ) ( (470 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}) )</td>
<td>0.129 (0.024)</td>
<td>0.096 (0.009)</td>
<td>0.133</td>
</tr>
<tr>
<td>( g_{SHL} - g_{SLL} ), ( \text{mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1} )</td>
<td>0.084 (0.020)</td>
<td>0.043 (0.008)</td>
<td>0.073</td>
</tr>
</tbody>
</table>

Figure 4.5 Representative stomatal opening responses in western redcedar and coastal Douglas-fir. For the individual sapling responses illustrated, the lag time prior to stomatal opening was 83.8 s for redcedar and 27.3 s for Douglas-fir, as determined from curve fitting and denoted by the downward pointing arrows. Based on six saplings per species, mean lag time was significantly longer for redcedar \( (80.7 \pm 5.7 \text{ s}) \) than for Douglas-fir \( (35.8 \pm 3.8 \text{ s}) \) \( (p=0.001) \).
4.2.1.2 Absolute photosynthetic rates during induction

When species were compared instead on the basis of absolute photosynthetic rates during the same course of photosynthetic induction, western redcedar performed at the same level or higher than Douglas-fir (Table 4.5), despite taking longer to become fully induced (Table 4.3, Figure 4.4). Starting net CO₂ assimilation rates were similar for the two species, but the amplitude of increase in photosynthesis was greater for redcedar. Maximum photosynthetic rates (A_max) can be estimated from the time-courses of photosynthetic induction as 90% of the curve-fit maxima and, when determined in this manner, were significantly higher for redcedar (5.50 ± 0.27 μmol CO₂ m⁻² s⁻¹) than for Douglas-fir (4.29 ± 0.36 μmol CO₂ m⁻² s⁻¹) (p=0.023).

Table 4.5 Absolute net CO₂ assimilation rates for western redcedar and coastal Douglas-fir during photosynthetic induction under constant high light. Starting values (at time zero) represent mean steady-state rates at low light (30 μmol m⁻² s⁻¹) prior to the transfer to high light (470 μmol m⁻² s⁻¹). Values between 0.5-50 minutes represent predicted values from the curve-fit induction responses of six individuals per species. Standard errors are in parentheses.

<table>
<thead>
<tr>
<th>Time, minutes</th>
<th>Net CO₂ assimilation (A), μmol CO₂ m⁻² s⁻¹</th>
<th></th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Western redcedar</td>
<td>Coastal Douglas-fir</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>1.28 (0.24)</td>
<td>1.19 (0.07)</td>
<td>0.742</td>
</tr>
<tr>
<td>0.5</td>
<td>1.90 (0.26)</td>
<td>1.89 (0.12)</td>
<td>0.967</td>
</tr>
<tr>
<td>1</td>
<td>2.38 (0.28)</td>
<td>2.35 (0.17)</td>
<td>0.944</td>
</tr>
<tr>
<td>2</td>
<td>3.06 (0.30)</td>
<td>2.94 (0.24)</td>
<td>0.755</td>
</tr>
<tr>
<td>5</td>
<td>4.14 (0.32)</td>
<td>3.71 (0.32)</td>
<td>0.358</td>
</tr>
<tr>
<td>10</td>
<td>4.87 (0.32)</td>
<td>4.14 (0.36)</td>
<td>0.159</td>
</tr>
<tr>
<td>15</td>
<td>5.20 (0.31)</td>
<td>4.32 (0.37)</td>
<td>0.100</td>
</tr>
<tr>
<td>20</td>
<td>5.39 (0.31)</td>
<td>4.42 (0.38)</td>
<td>0.075</td>
</tr>
<tr>
<td>25</td>
<td>5.52 (0.31)</td>
<td>4.48 (0.38)</td>
<td>0.062</td>
</tr>
<tr>
<td>30</td>
<td>5.61 (0.31)</td>
<td>4.53 (0.39)</td>
<td>0.054</td>
</tr>
<tr>
<td>35</td>
<td>5.67 (0.31)</td>
<td>4.56 (0.39)</td>
<td>0.048</td>
</tr>
<tr>
<td>40</td>
<td>5.72 (0.30)</td>
<td>4.58 (0.39)</td>
<td>0.044</td>
</tr>
<tr>
<td>45</td>
<td>5.76 (0.30)</td>
<td>4.60 (0.39)</td>
<td>0.041</td>
</tr>
<tr>
<td>50</td>
<td>5.79 (0.30)</td>
<td>4.62 (0.39)</td>
<td>0.039</td>
</tr>
</tbody>
</table>
4.2.1.3 Intrinsic water use efficiency during induction

When non-induced foliage was transferred from low light to high light, intrinsic water use efficiency (A/gs) initially increased rapidly in both species, but was elevated relatively more over the steady-state value at high light in redcedar than in Douglas-fir (Figure 4.6). For example, at 2.5 min (stippled line in Figure 4.6) mean A/gs was 67.11 ± 2.31 and 52.43 ± 3.92 for redcedar and Douglas-fir, respectively (p=0.012). This was a result of similar photosynthetic rates but lower conductance values for redcedar than for Douglas-fir at this time.

![Graph showing intrinsic water use efficiency during the course of photosynthetic induction in representative individuals of western redcedar and coastal Douglas-fir.](image)

**Figure 4.6** Intrinsic water use efficiency during the course of photosynthetic induction in representative individuals of western redcedar and coastal Douglas-fir. The dashed line at 2.5 min (150 s) indicates the time for which mean species values of water use efficiency are reported in the text.

In contrast, under steady-state conditions intrinsic water use efficiency did not differ between species at either low light or high light (Table 4.6). Water use efficiency was similar for the two species at low light because both photosynthesis and conductance values were similar (Table 4.4, Table 4.5). At high light similarity in water use efficiency was observed because although redcedar tended to have higher maximum assimilation rates than Douglas-fir, redcedar also tended to have higher maximum conductances (Table 4.4, Table 4.5). The covariance observed between steady-state values of photosynthesis (A) and stomatal conductance (gs) was reflected in corresponding steady-state ratios of intercellular to atmospheric CO₂ concentration (C/Cₐ) which were similar for the two species at both light levels (Table 4.6).
Table 4.6 Intrinsic water use efficiency (A/gs) of western redcedar and coastal Douglas-fir under steady-state conditions at low light and steady-state conditions at high light. Also shown are the corresponding ratios of intercellular to atmospheric carbon dioxide concentration (C_i/C_a). Values are means with standard errors in parentheses.

<table>
<thead>
<tr>
<th>Steady-state gas exchange parameter</th>
<th>Western redcedar</th>
<th>Coastal Douglas-fir</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low light, 30 µmol photons m^{-2} s^{-1}</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A/gs, µmol CO_2·mol H_2O^{-1}</td>
<td>27.97 (2.42)</td>
<td>24.22 (3.75)</td>
<td>0.420</td>
</tr>
<tr>
<td>C_i/C_a, unitless</td>
<td>0.847 (0.013)</td>
<td>0.862 (0.017)</td>
<td>0.480</td>
</tr>
<tr>
<td>High light, 470 µmol photons m^{-2} s^{-1}</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A/gs, µmol CO_2·mol H_2O^{-1}</td>
<td>50.28 (6.34)</td>
<td>47.24 (3.87)</td>
<td>0.691</td>
</tr>
<tr>
<td>C_i/C_a, unitless</td>
<td>0.700 (0.024)</td>
<td>0.718 (0.021)</td>
<td>0.574</td>
</tr>
</tbody>
</table>

4.2.2 The loss of photosynthetic induction with shading

4.2.2.1 General observations

Representative photosynthetic responses to shading are shown for western redcedar in Figure 4.7. The steady-state rate of net CO_2 assimilation at high light was regained readily after a brief 2 minute interval of shading, but more time was required for this as the duration of shading increased. Photorespiratory bursts were evident at the start of a shading interval as transient depressions below the steady-state rate at low light (Vines et al. 1983). Although not shown in Figure 4.7, a reduction in C_i accompanied the recovery of net CO_2 assimilation following photorespiratory bursts. Responses of coastal Douglas-fir were qualitatively similar.

4.2.2.2 The decay of photosynthetic induction state

For both species, photosynthetic induction state (A-IS_{60}) decreased with increasing duration of shading but the rate of decay was slow (Table 4.7). Photosynthetic induction state decayed little during 2 or 5 minute shading intervals, but during the longer 15 and 30 minute shading intervals the reduction was considerable. Photosynthetic induction state did not differ between species after 2 or 5 minutes of shading, but western redcedar was better able than coastal Douglas-fir to maintain photosynthetic induction during 15 and 30 minute intervals of continuous shade (Table 4.7). Following prolonged shading (≥1 h), A-IS_{60} once again did not differ between species because foliage was non-induced. Similarity of A-IS_{60} values for Douglas-fir after 30 minutes of shade with those observed for this species after a prolonged time in shade suggested that at the background low light intensity of 30 µmol photons m^{-2} s^{-1}, the photosynthetic induction state of this species was largely lost within 30 minutes. In contrast, the A-IS_{60} of redcedar was notably higher after 30 minutes of shade than it was after prolonged shading.

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Figure 4.7 Representative photosynthetic responses of western redcedar to various intervals of shading. Upward arrows indicate times when continuous high light was applied. Downward arrows indicate the start of a shading interval. High light was first applied after a prolonged period in shade (≥1 h). In this illustration, subsequent shading intervals are 2, 5, 15, and 30 minutes respectively, applied following the attainment of steady-state conditions at high light in each case. The transient depressions below the steady-state rate at low light evident at the beginning of shading intervals indicate photorespiratory bursts. The break in the time axis occurs during a period when data logging was interrupted for instrument battery changes, IRGA matching, and VPD_{leaf-air} adjustments (two other instrument check periods are evident as gaps in the data at 125-137 min. and 163-167 min).

In both western redcedar and coastal Douglas-fir, the loss of photosynthetic induction was accompanied by reductions in both photosynthetic CO₂ use efficiency (A/C\text{\textsubscript{T-IS}}{\text{\textsubscript{60}}}) and stomatal conductance (gs-IS\text{\textsubscript{60}}) (Table 4.7). However, given the closer correspondence between A-IS\text{\textsubscript{60}} and A/C\text{\textsubscript{T-IS}}{\text{\textsubscript{60}}} responses than between A-IS\text{\textsubscript{60}} and gs-IS\text{\textsubscript{60}} responses, deactivation of Rubisco (represented by the reduction in A/C\text{\textsubscript{T-IS}}{\text{\textsubscript{60}}}) was probably the primary cause of the decay of photosynthetic induction state in both species. Species differences in deactivation of Rubisco appeared to largely account for the higher capacity of redcedar to maintain photosynthetic induction state during the longer 15 and 30 minute shading intervals.

The slow induction component (the requirement for Rubisco activation and stomatal opening) normally dominates limitations to photosynthesis but when the slow induction component does not decay, limitations to photosynthesis can shift to the fast induction component (RuBP regeneration) (Sassenrath-Cole and Pearcy 1992). Because the slow induction component of both western redcedar and coastal Douglas-fir underwent only minimal decay during the 2 minute shading interval (Table 4.7), the role of the fast induction component in limiting photosynthesis was of some interest at this time. Inspection of the initial stages of the absolute photosynthetic response of both species (Figure 4.8) revealed that the fast induction component had not completely decayed in either species during the 2 minute shading interval (residual activity of the fast induction component accounts for the
initial linear increase in photosynthesis), and that it imposed similar limitations on both species. Limitations due to the fast induction component also dominated following the 5 minute shading interval, but the slow induction component was most important after longer shading intervals of 15 and 30 minutes (the fast inducing component, although still present, contributes relatively little further limitation when the slow induction component is present).

Table 4.7 The decay of photosynthetic induction in western redcedar and coastal Douglas-fir. Values are mean activities measured 60 s after removal of shading expressed relative to steady-state, light-saturated rates prior to shading (induction state, IS60 values). Standard errors are in parentheses.

<table>
<thead>
<tr>
<th>Relative activity 60 s after removal of shading</th>
<th>Shading interval, minutes</th>
<th>IS60 values after shading removed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Western redcedar</td>
</tr>
<tr>
<td>Net CO2 assimilation (A-IS60), relative units</td>
<td>2</td>
<td>0.971 (0.007)</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.925 (0.008)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>0.730 (0.015)</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>0.474 (0.020)</td>
</tr>
<tr>
<td></td>
<td>prolonged shade, ≥1 h</td>
<td>0.307 (0.016)</td>
</tr>
<tr>
<td>Photosynthetic CO2 use efficiency (A/Cr-IS60), relative units</td>
<td>2</td>
<td>0.966 (0.010)</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.909 (0.012)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>0.707 (0.023)</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>0.488 (0.027)</td>
</tr>
<tr>
<td></td>
<td>prolonged shade, ≥1 h</td>
<td>0.355 (0.015)</td>
</tr>
<tr>
<td>Stomatal conductance (gs-IS60), relative units</td>
<td>2</td>
<td>0.974 (0.023)</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.937 (0.012)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>0.684 (0.015)</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>0.249 (0.030)</td>
</tr>
<tr>
<td></td>
<td>prolonged shade, ≥1 h</td>
<td>0.012 (0.008)</td>
</tr>
</tbody>
</table>

4.2.2.3 Effect of shading intervals on absolute photosynthetic rates

Species rankings for photosynthetic performance following shading differed when comparisons were drawn on the basis of absolute photosynthetic rates (A) instead of on the basis of photosynthetic induction state (A-IS60). In particular, whereas A-IS60 values were similar for redcedar and Douglas-fir following 2 and 5 minutes of shading (Table 4.7), corresponding absolute photosynthetic rates measured 60 s after the light increase were in both cases significantly greater for redcedar than for Douglas-fir (Table 4.8; see also Figure 4.8). In contrast, species rankings based on absolute photosynthetic rates (Table 4.8) were consistent with those based on photosynthetic induction state (A-IS60, Table 4.7) after 15 and 30 minutes of shading (redcedar > Douglas-fir) and after prolonged shading (redcedar = Douglas-fir).
Figure 4.8 Representative plots of the first 2 minutes of the absolute photosynthetic response of A) western redcedar and B) coastal Douglas-fir following exposure of fully induced foliage to various intervals of shading. The solid line highlighting the initial linear photosynthetic response after the 2 minute shading interval is taken to represent the initial increase in photosynthetic rate due to that portion of the fast component of photosynthetic induction (RuBP regeneration) which did not decay during the 2 minute interval at low light. Because for both species there was little decay of the slow induction component (Rubisco activation, stomatal opening) during the 2 minute shading interval (see Table 4.7), the extent to which the fast induction component limited carbon gain is roughly represented by the shaded area between the maximum expected steady-state photosynthetic rate at high light ($A_{HL}$) and the plot of transient photosynthetic rate following the 2 minute shading interval. The stippled vertical line at 60 s indicates the time at which photosynthetic induction state ($A-IS_{60}$) values were calculated. Data represent predicted values derived from the curve-fit responses of individual saplings.
Table 4.8 Mean absolute net CO₂ assimilation rates of western redcedar and coastal Douglas-fir measured 60 s after the return to high light following various shading intervals. Foliage was fully induced prior to the imposition of each shading treatment. Values are means with standard errors in parentheses.

<table>
<thead>
<tr>
<th>Shading treatment</th>
<th>Western redcedar</th>
<th>Coastal Douglas-fir</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 minutes shading</td>
<td>5.72 (0.31)</td>
<td>4.36 (0.41)</td>
<td>0.024</td>
</tr>
<tr>
<td>5 minutes shading</td>
<td>5.56 (0.31)</td>
<td>4.14 (0.38)</td>
<td>0.015</td>
</tr>
<tr>
<td>15 minutes shading</td>
<td>4.58 (0.27)</td>
<td>3.16 (0.31)</td>
<td>0.006</td>
</tr>
<tr>
<td>30 minutes shading</td>
<td>3.39 (0.24)</td>
<td>2.43 (0.18)</td>
<td>0.010</td>
</tr>
<tr>
<td>prolonged shading (≥1 h)</td>
<td>2.68 (0.26)</td>
<td>2.29 (0.18)</td>
<td>0.235</td>
</tr>
</tbody>
</table>

4.2.2.4 Intrinsic water use efficiency during shade periods

For both species, intrinsic water use efficiency (A/gs) in shade varied with the length of time since the light decrease (Table 4.9). Water use efficiency was highest given long periods in low light and lowest at the end of the briefest (2 min) shading interval when photosynthetic rates had been rapidly reduced but stomata were still fully or near fully open. Water use efficiency did not differ between species after any length of shading interval (Table 4.9).

Table 4.9 Intrinsic water use efficiency of western redcedar and coastal Douglas-fir at the end of various shading intervals. Shading intervals were applied to fully induced foliage and water use efficiency was measured at the end of each interval. Values are means with standard errors in parentheses.

<table>
<thead>
<tr>
<th>Shading treatment</th>
<th>Intrinsic water use efficiency (A/gs), μmol CO₂·mol H₂O⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Western redcedar</td>
</tr>
<tr>
<td>2 minutes shading</td>
<td>8.48 (1.24)</td>
</tr>
<tr>
<td>5 minutes shading</td>
<td>11.28 (1.63)</td>
</tr>
<tr>
<td>15 minutes shading</td>
<td>14.73 (1.38)</td>
</tr>
<tr>
<td>30 minutes shading</td>
<td>24.16 (1.97)</td>
</tr>
<tr>
<td>prolonged shading (≥1 h) (non-induced foliage under steady-state at low light)</td>
<td>27.42 (2.89)</td>
</tr>
</tbody>
</table>
4.2.3 Photosynthetic induction and carbon gain in fluctuating light

4.2.3.1 General observations

Western redcedar and coastal Douglas-fir exhibited qualitatively similar responses to the simulated sunfleck (lightfleck) series, insofar as photosynthesis closely tracked changes in light whereas stomatal conductance did not (Figure 4.9, Figure 4.10). However, the pattern of stomatal opening was somewhat different for the two species. In redcedar, a distinct lag phase was again evident before stomatal opening commenced but, once initiated, stomatal opening increased continuously throughout both lightflecks and intervening shade periods (Figure 4.9b). In contrast, a lag phase for stomatal opening was less well defined in Douglas-fir (Figure 4.10b). However, although the initiation of stomatal opening took longer in redcedar than in Douglas-fir, redcedar exhibited a stronger increase in conductance once stomatal opening began. In contrast to what was observed for foliage after exposure to two or more minutes in saturating light (see earlier, Figure 4.7), photorespiratory bursts were not evident for either species following exposure to lightflecks of short duration. Rather, positive net post-illumination CO₂ fixation was evident as residual carbon gain after the high light was switched off (Figure 4.9a, Figure 4.10a).

4.2.3.2 Photosynthetic induction state

The light-dependency of photosynthetic induction was demonstrated for both western redcedar and coastal Douglas-fir by observations that photosynthetic induction state (A-ISₜ) was considerably lower at the end of the fifth lightfleck than after an equivalent total elapsed time under continuous high light (630 s, time equivalent to reach the end of the fifth lightfleck; Table 4.10). Nonetheless, photosynthetic induction state approximately doubled in both species between the first and the fifth lightfleck and was as high or higher at the end of the lightfleck series than after an equivalent photon exposure to continuous high light (150 s continuous high light, equivalent to five lightflecks of 30 s duration; Table 4.10). In both species, photosynthetic induction in fluctuating light was associated with increases in both Rubisco activation (A/Cᵢ-ISₜ₀) and stomatal conductance (gs-ISₜ₀) (Table 4.10). However, as during photosynthetic induction in continuous high light, changes in net CO₂ assimilation (A) again lagged behind those in A/Cᵢ in redcedar but not Douglas-fir (Table 4.10).

Species rankings for photosynthetic induction state (A-ISₜ) were different in fluctuating light than under continuous illumination with high light. Given continuous exposure to high light, photosynthetic induction state was significantly lower for redcedar than for Douglas-fir (A-IS₁₅₀ and A-IS₆₃₀, Table 4.10), but in the fluctuating light regime induction states were similar for the two species (A-IS₃₀ values for lightflecks 1–5, Table 4.10). The change in species rankings in fluctuating light was related to an improvement in the rate of photosynthetic induction in redcedar rather than a depression in the rate of induction in Douglas-fir because the induction state of redcedar was greater after the fifth lightfleck than after an equivalent photon exposure to continuous high light (150 s) whereas no difference was evident for Douglas-fir.
Figure 4.9  Representative A) photosynthetic and B) stomatal responses of understory western redcedar to a series of five 30 s lightflecks. The first lightfleck was given following a prolonged period in shade, and subsequent lightflecks were separated by 2 minute intervals of low light. Upward arrows indicate the beginning of a lightfleck, downward arrows indicate the start of a post-lightfleck shading interval. Post-illumination CO$_2$ fixation is evident in A) as continued carbon gain after the high light was switched off.
Figure 4.10 Representative A) photosynthetic and B) stomatal responses of understory coastal Douglas-fir to a series of five 30 s lightflecks. Explanation as in Figure 4.9.
Table 4.10 Photosynthetic induction in western redcedar and coastal Douglas-fir in response to a simulated sunfleck ('lightfleck') series. Relative activities (IS\textsubscript{n} induction states at time t after a light increase) of net CO\textsubscript{2} assimilation, photosynthetic CO\textsubscript{2} use efficiency, and stomatal conductance were measured at the end of each of five sequential 30 s lightflecks separated by 2 minute intervals of low light. Also shown (below the stippled horizontal line) are the relative activities of these parameters after an equivalent photon exposure to continuous high light (150 s, equivalent to five lightflecks of 30 s duration) and after an equivalent total elapsed time under continuous high light (630 s, time equivalent to the end of the fifth lightfleck). Values are means with standard errors in parentheses.

<table>
<thead>
<tr>
<th>High light treatment</th>
<th>Induction state of net CO\textsubscript{2} assimilation (A-IS\textsubscript{n}), relative units</th>
<th>Induction state of photosynthetic CO\textsubscript{2} efficiency (A/C\textsubscript{n-IS\textsubscript{n}}, relative units</th>
<th>Induction state of stomatal conductance (gs-IS\textsubscript{n}), relative units</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Western redcedar</td>
<td>Coastal Douglas-fir</td>
<td>p-value</td>
</tr>
<tr>
<td>Lightfleck series</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lightfleck #1 (t=30 s)</td>
<td>0.249 (0.020)</td>
<td>0.267 (0.028)</td>
<td>0.623</td>
</tr>
<tr>
<td>Lightfleck #2 (t=30 s)</td>
<td>0.353 (0.019)</td>
<td>0.396 (0.027)</td>
<td>0.220</td>
</tr>
<tr>
<td>Lightfleck #3 (t=30 s)</td>
<td>0.415 (0.019)</td>
<td>0.465 (0.035)</td>
<td>0.240</td>
</tr>
<tr>
<td>Lightfleck #4 (t=30 s)</td>
<td>0.486 (0.011)</td>
<td>0.506 (0.027)</td>
<td>0.517</td>
</tr>
<tr>
<td>Lightfleck #5 (t=30 s)</td>
<td>0.528 (0.011)</td>
<td>0.593 (0.053)</td>
<td>0.265</td>
</tr>
<tr>
<td>Equivalent photon exposure to continuous high light (t=150 s)</td>
<td>0.456 (0.022)</td>
<td>0.562 (0.013)</td>
<td>0.002</td>
</tr>
<tr>
<td>Equivalent total elapsed time under continuous high light (t=630 s)</td>
<td>0.762 (0.023)</td>
<td>0.935 (0.017)</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

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The enhanced rate of photosynthetic induction in redcedar in fluctuating versus continuous high light appeared to be related to enhanced stomatal opening rather than, or in addition to, an improvement in the rate of Rubisco activation (limitations due to the fast induction component were considered of negligible importance because non-induced foliage was used for the test). This is because for this species the induction state of stomatal conductance (gs-IS,) was 538% greater at the end of the fifth lightfleck than after the same photon exposure to continuous high light (150 s), whereas the induction state of photosynthetic CO$_2$ use efficiency (A/C$_{IS}$) was similar given the same comparison (Table 4.10). Thus, although some stomatal opening was observed for both species during low light periods between lightfleck events, the overall improvement in conductance in fluctuating versus continuous high light was much greater for redcedar (538%) than for Douglas-fir (92%). In consequence, the greater initial lag time for stomatal opening in redcedar than Douglas-fir (compare Figure 4.9b and Figure 4.10b, and see also Figure 4.5) was largely compensated for by the end of the lightfleck series (Table 4.10, Figure 4.11). In contrast, under continuous illumination with high light species differences in relative stomatal conductance remained large (Table 4.10, Figure 4.11). Species differences in stomatal dynamics could not be attributed to differences in initial (starting) conductance, as steady-state values of conductance at low light did not differ between species prior to induction testing in either fluctuating or continuous high light (not shown).

![Stomatal opening in western redcedar and coastal Douglas-fir](image)

**Figure 4.11** Stomatal opening in western redcedar and coastal Douglas-fir during a series of five 30 s lightflecks separated by 2 minute intervals of low light (bars) and during continuous illumination with high light (circles). Species differences in the induction state of stomatal conductance (gs-IS,) were much smaller at the end of the fifth lightfleck (LF#5, bars at 630 s) than under continuous illumination with high light for either a similar total elapsed time (circles at 630 s) or for a comparable photon exposure (circles at 150 s). ‘End of test’ (750 s) represents the end of the 2 minute shading interval following the last lightfleck in the series.
4.2.3.3 Lightfleck use efficiency

Mirroring the results for photosynthetic induction state, exposure to previous lightflecks increased the efficiency of use of subsequent lightflecks to the extent that lightfleck use efficiency (LUE) underwent an approximate doubling in both species, from 35–38% on the first lightfleck to 65–73% on the fifth lightfleck (Table 4.11). Lightfleck use efficiency did not differ between redcedar and Douglas-fir at any point in the lightfleck series.

Table 4.11 Lightfleck use efficiency (LUE) and post-lightfleck contribution (PLF-contribution) to the overall carbon gain attributable to lightflecks (contribution of post-illumination CO₂ fixation minus any photorespiratory bursts) for non-induced foliage of western redcedar and coastal Douglas-fir during exposure to a series of five 30 s lightflecks separated by 2 minute intervals of low light. Values are means with standard errors in parentheses.

<table>
<thead>
<tr>
<th>Sequential lightfleck in series</th>
<th>LUE, %</th>
<th>PLF-contribution, %&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Western redcedar</td>
<td>Coastal Douglas-fir</td>
</tr>
<tr>
<td>Lightfleck #1</td>
<td>37.56 (3.74)</td>
<td>35.18 (5.85)</td>
</tr>
<tr>
<td>Lightfleck #2</td>
<td>47.50 (3.84)</td>
<td>46.69 (11.17)</td>
</tr>
<tr>
<td>Lightfleck #3</td>
<td>49.98 (8.49)</td>
<td>58.08 (9.39)</td>
</tr>
<tr>
<td>Lightfleck #4</td>
<td>60.25 (7.15)</td>
<td>64.82 (11.79)</td>
</tr>
<tr>
<td>Lightfleck #5</td>
<td>64.55 (9.60)</td>
<td>73.12 (10.61)</td>
</tr>
</tbody>
</table>

<sup>a</sup> The percent contribution of CO₂ fixation during the lightfleck-proper is 100 – PLF-contribution (not shown).

For both species, net post-lightfleck CO₂ fixation made a considerable contribution to the carbon gain attributable to individual lightflecks, accounting for, on average, 38–62% of the CO₂ fixed (Table 4.11). Although variation was fairly high, post-illumination CO₂ fixation tended to contribute proportionately more to carbon gain on the first lightfleck than for other lightflecks in the series.

4.2.3.4 Absolute carbon gain in fluctuating light

Although variation was high and the result somewhat marginal, western redcedar and coastal Douglas-fir did not differ significantly when compared on the basis of the absolute amount of carbon gained during the lightfleck series (Table 4.12). This was true regardless of whether comparisons were made based on total carbon gain attributable to lightflecks, or the component carbon gain achieved during lightflecks and that achieved during post-lightfleck responses. Maximum absolute rates of photosynthesis achieved during the lightfleck series also did not differ significantly between species, albeit the result was again somewhat marginal; mean maximum rates at the end of lightfleck #5 were 3.65 ± 0.26 µmol CO₂ m<sup>-2</sup> s<sup>-1</sup> for redcedar and 3.07 ± 0.17 µmol CO₂ m<sup>-2</sup> s<sup>-1</sup> for Douglas-fir (p=0.095).
**Table 4.12** Absolute carbon gain of non-induced foliage of western redcedar and coastal Douglas-fir during exposure to five 30 s lightflecks separated by 2 minute intervals of low light. Shown is the total carbon gain attributable to the five lightflecks and the component carbon gain during lightflecks and during post-lightfleck responses. Values are means with standard errors in parentheses.

<table>
<thead>
<tr>
<th>Computation</th>
<th>Total integrated absolute carbon gain due to treatment with high light, µmol CO$_2$ m$^{-2}$</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Western redcedar</td>
<td>Coastal Douglas-fir</td>
</tr>
<tr>
<td>Total carbon gain attributable to all five lightflecks *</td>
<td>351.60 (33.15)</td>
<td>259.33 (45.73)</td>
</tr>
<tr>
<td>Total carbon gain during lightflecks</td>
<td>164.95 (13.97)</td>
<td>130.66 (18.02)</td>
</tr>
<tr>
<td>Total carbon gain during post-lightfleck responses</td>
<td>186.66 (23.48)</td>
<td>128.67 (32.55)</td>
</tr>
</tbody>
</table>

*a. The carbon gain shown is incremental to that observed under steady-state conditions at low light, i.e., is attributable only to exposure to high light (470 µmol photons m$^{-2}$ s$^{-1}$) in the form of lightflecks.

*b. Species differences were likewise not significant for any individual lightfleck in the series (not shown).

To better illustrate the effects that photosynthetic induction state and net post-illumination CO$_2$ fixation can have on the absolute carbon gain of western redcedar and coastal Douglas-fir under dynamic light conditions, comparisons are shown in Table 4.13 for the absolute carbon gain attributable to a 70.5 mmol photons m$^{-2}$ dose of high light, given i) to non-induced foliage as five 30 s lightflecks of 470 µmol photons m$^{-2}$ s$^{-1}$; ii) to non-induced foliage as 150 s continuous illumination at 470 µmol photons m$^{-2}$ s$^{-1}$; and iii) hypothetically to fully induced foliage (with no induction requirement) as 150 s continuous illumination at 470 µmol photons m$^{-2}$ s$^{-1}$. For both species, absolute carbon gain of non-induced foliage (cases i and ii) differed dramatically from steady-state expectations (case iii), being about 2–3-fold lower than expected (Table 4.13). However, for non-induced foliage carbon gain in fluctuating light (case i) was about 50–60% higher than that during continuous illumination with the same high light dose (case ii), presumably owing to the combination of a considerable amount of net post-lightfleck CO$_2$ fixation (Table 4.12) and a low rate of induction loss during 2 minute shading intervals (see earlier, Table 4.7).
Table 4.13 The effects of photosynthetic induction state and the temporal distribution of high light on the absolute carbon gain attributable to treatment with a 70.5 mmol photons·m⁻²·s⁻¹ dose of high light administered at 470 μmol photons·m⁻²·s⁻¹. Shown is the absolute carbon gain of western redcedar and coastal Douglas-fir for i) non-induced foliage exposed to five 30 s lightflecks separated by 2 minute intervals of low light (carbon gain is integrated and summed over the lightfleck series); ii) non-induced foliage exposed to a comparable photon exposure to continuous high light (150 s at 470 μmol photons·m⁻²·s⁻¹); and iii) the hypothetical situation where foliage responds instantaneously to the same photon exposure to high light (as for fully induced foliage having no induction requirement). Values are means with standard errors in parentheses.

<table>
<thead>
<tr>
<th>High light treatment (470 μmol photons·m⁻²·s⁻¹)</th>
<th>Total integrated absolute carbon gain due to treatment with high light a, μmol CO₂·m⁻²</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>five 30 s lightflecks given to non-induced foliage</td>
<td>Western redcedar: 351.60 (33.15)</td>
<td>Coastal Douglas-fir: 259.33 (45.73)</td>
</tr>
<tr>
<td>150 s continuous illumination of non-induced foliage</td>
<td>216.99 (15.64)</td>
<td>176.71 (26.21)</td>
</tr>
<tr>
<td>150 s continuous illumination assuming a hypothetical instantaneous photosynthetic response (as for foliage with no induction requirement)</td>
<td>686.81 (30.69)</td>
<td>491.43 (61.64)</td>
</tr>
</tbody>
</table>

a. The carbon gain shown is incremental to that observed under steady-state conditions at low light, i.e., is attributable only to the 150 s exposure to high light (470 μmol·m⁻²·s⁻¹) in the manner specified.

4.2.3.5 Intrinsic water use efficiency in fluctuating light

Intrinsic water use efficiency (A/gs) did not differ between western redcedar and coastal Douglas-fir in fluctuating light, either at the end of lightflecks or at the end of the shading intervals between lightfleck events (Table 4.14). Water use efficiency was more similar for the two species at the end of lightfleck #5 (Table 4.14) than when given the same photon exposure to continuous high light (in Figure 4.6, the data along the stippled vertical line at 150 s) because stomatal opening in redcedar but not Douglas-fir was enhanced in fluctuating light (in Table 4.10 compare for each species the gs-ISv value for lightfleck #5 and that for 150 s continuous illumination). The marginally nonsignificant differences between species for water use efficiency at the end of lightfleck #2 and lightfleck #3 presumably reflected in part the longer lag phase for stomatal opening in redcedar than Douglas-fir (compare Figures 4.9b and 4.10b, and see Figure 4.5).
Table 4.14 Intrinsic water use efficiency of western redcedar and coastal Douglas-fir during the simulated sunfleck (lightfleck) series. Each of the five lightflecks (470 μmol·m⁻²·s⁻¹) was 30 s in duration and individual lightflecks were separated by 2 minute intervals of low light (30 μmol·m⁻²·s⁻¹). Water use efficiency (A/gs) was computed from assimilation (A) and conductance (gs) rates measured at the end of each lightfleck or at the end of each post-lightfleck shading interval, at times during the lightfleck sequence as indicated. Values are means with standard errors in parentheses.

<table>
<thead>
<tr>
<th>Point in the lightfleck series</th>
<th>Western redcedar</th>
<th>Coastal Douglas-fir</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Starting value (low light mean)</td>
<td>28.49 (1.30)</td>
<td>27.62 (3.70)</td>
<td>0.830</td>
</tr>
<tr>
<td>End of lightfleck #1, @30 s</td>
<td>53.41 (4.44)</td>
<td>44.38 (5.91)</td>
<td>0.257</td>
</tr>
<tr>
<td>End of shade interval #1, @150 s</td>
<td>27.72 (1.49)</td>
<td>24.45 (2.84)</td>
<td>0.338</td>
</tr>
<tr>
<td>End of lightfleck #2, @180 s</td>
<td>61.37 (4.21)</td>
<td>47.16 (5.15)</td>
<td>0.065</td>
</tr>
<tr>
<td>End of shade interval #2, @300 s</td>
<td>25.86 (1.90)</td>
<td>22.86 (2.46)</td>
<td>0.362</td>
</tr>
<tr>
<td>End of lightfleck #3, @330 s</td>
<td>62.60 (5.10)</td>
<td>48.59 (5.64)</td>
<td>0.103</td>
</tr>
<tr>
<td>End of shade interval #3, @450 s</td>
<td>23.71 (2.05)</td>
<td>22.18 (2.30)</td>
<td>0.633</td>
</tr>
<tr>
<td>End of lightfleck #4, @480 s</td>
<td>63.10 (5.90)</td>
<td>50.23 (5.58)</td>
<td>0.152</td>
</tr>
<tr>
<td>End of shade interval #4, @600 s</td>
<td>21.91 (1.98)</td>
<td>21.79 (2.22)</td>
<td>0.969</td>
</tr>
<tr>
<td>End of lightfleck #5, @630 s</td>
<td>62.33 (6.18)</td>
<td>52.06 (4.99)</td>
<td>0.232</td>
</tr>
<tr>
<td>End of shade interval #5, @750 s</td>
<td>20.68 (1.89)</td>
<td>21.53 (2.17)</td>
<td>0.777</td>
</tr>
</tbody>
</table>

4.3 STEADY-STATE PHOTOSYNTHESIS AND DARK RESPIRATION

4.3.1 Response to photosynthetic photon flux density

Photosynthetic light-response curves are shown for western redcedar and coastal Douglas-fir in Figure 4.12. Maximum light-saturated rates of CO₂ assimilation (A<sub>max</sub>), apparent convexity (θ), and apparent quantum yield (Φ<sub>i</sub>) did not differ significantly between species (Table 4.15), suggesting similar photosynthetic potential of the two species at high and intermediate light levels. Results for A<sub>max</sub> and convexity were however marginal. In contrast, photosynthetic light compensation points (LCP) and dark respiration rates (R<sub>d</sub>) were approximately two-fold lower for redcedar than for Douglas-fir (Table 4.15, Figure 4.12).
Figure 4.12 Steady-state area-based foliar photosynthetic light-response curves for western redcedar and coastal Douglas-fir from the understory of red alder. Complete light-response curves are shown for each species in A), whereas species responses to low light and darkness are highlighted in B). Arrows in B) indicate the corresponding photosynthetic light compensation point for each species. Data represent predicted values derived from curve-fitting the combined data of all individuals of each species. Equations are $y = \frac{0.0547x + 5.941 - \sqrt{(0.0547x + 5.941)^2 - 4 \times 0.0547 \times 5.941 \times 0.6048x}}{2 \times 0.6048} - 0.3427$ for redcedar ($r^2 = 0.97$); and $y = \frac{0.0602x + 5.020 - \sqrt{(0.0602x + 5.020)^2 - 4 \times 0.0602 \times 5.020 \times 0.7071x}}{2 \times 0.7071} - 0.6011$ for Douglas-fir ($r^2 = 0.89$).
Table 4.15 Steady-state area-based foliar photosynthetic light-response parameters for western redcedar and coastal Douglas-fir from the understory of red alder. Values are means with standard errors in parentheses.

<table>
<thead>
<tr>
<th>Light-response curve parameter</th>
<th>Western redcedar</th>
<th>Coastal Douglas-fir</th>
<th>p-value&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light saturated rate of net CO&lt;sub&gt;2&lt;/sub&gt; assimilation, A&lt;sub&gt;max&lt;/sub&gt; (µmol CO&lt;sub&gt;2&lt;/sub&gt; m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>5.37 (0.22)</td>
<td>4.48 (0.47)</td>
<td>0.100</td>
</tr>
<tr>
<td>Convexity, θ&lt;sup&gt;c&lt;/sup&gt; (unitless)</td>
<td>0.47 (0.09)</td>
<td>0.74 (0.10)</td>
<td>0.071</td>
</tr>
<tr>
<td>Apparent quantum yield, Φ&lt;sub&gt;i&lt;/sub&gt; (µmol CO&lt;sub&gt;2&lt;/sub&gt; µmol incident photons&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>0.056 (0.003)</td>
<td>0.057 (0.009)</td>
<td>0.902</td>
</tr>
<tr>
<td>Light compensation point, LCP (µmol photons m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>6.42 (1.73)</td>
<td>12.62 (1.68)</td>
<td>0.032</td>
</tr>
<tr>
<td>Dark respiration rate, R&lt;sub&gt;d&lt;/sub&gt; (µmol CO&lt;sub&gt;2&lt;/sub&gt; m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>0.31 (0.10)</td>
<td>0.63 (0.04)</td>
<td>0.023</td>
</tr>
</tbody>
</table>

<sup>a</sup> An electronic file for the light-response data of one Douglas-fir sapling was corrupted and not retrievable. Thus, sample size was six for redcedar and five for Douglas-fir.

<sup>b</sup> A<sub>max</sub> is reported as 90% of the curve-fit maximum.

<sup>c</sup> Convexity determines photosynthetic efficiency in the intermediate light range and varies from 0.0 when the response is a smooth rectangular hyperbola (lowest possible efficiency), to 1.0 when the response is of the Blackman type (highest possible efficiency).

Species rankings for photosynthetic light-response parameters and dark respiration were maintained when the data were alternatively expressed on a leaf mass rather than on a leaf area basis (Figure 4.13). Based on the analysis of light-response parameters obtained for individual saplings, mean A<sub>max/mass</sub> (as 90% of fitted maximum) was 60.83 ± 4.43 nmol CO<sub>2</sub> g<sup>-1</sup> s<sup>-1</sup> and 64.01 ± 6.43 nmol CO<sub>2</sub> g<sup>-1</sup> s<sup>-1</sup> (p=0.685) and mean R<sub>d/mass</sub> was 4.05 ± 1.09 nmol CO<sub>2</sub> g<sup>-1</sup> s<sup>-1</sup> and 8.27 ± 0.97 nmol CO<sub>2</sub> g<sup>-1</sup> s<sup>-1</sup> (p=0.020), for redcedar and Douglas-fir respectively. The nonsignificant tendency for a higher A<sub>max</sub> for redcedar evident on a leaf area basis (A<sub>max/area</sub>) was not evident on a leaf mass basis (A<sub>max/mass</sub>) (compare Figures 4.12a and 4.13), probably because specific leaf area (SLA, cm<sup>2</sup> g<sup>-1</sup>) was significantly lower for redcedar (112.6 ± 4.9 cm<sup>2</sup> g<sup>-1</sup>) than for Douglas-fir (143.7 ± 5.0 cm<sup>2</sup> g<sup>-1</sup>) (p=0.002).
4.3.2 Response to intercellular carbon dioxide concentration

The line plots in Figure 4.14 depict the steady-state photosynthetic responses of western redcedar and coastal Douglas-fir to intercellular CO$_2$ concentration under saturating light conditions, and thus the biochemical capacity for CO$_2$ fixation (von Caemmerer and Farquhar 1981). There was no clear difference between species in the slope of the initial linear portion of the response where carboxylation capacity is limiting (in Figure 4.14, initial slopes were 0.028 for redcedar and 0.026 for Douglas-fir). However, beyond the linear portion of A/Q response, at which point the limitation shifts to RuBP regeneration and therefore electron transport capacity, redcedar tended to have higher photosynthetic rates than Douglas-fir. Thus, because under ambient atmospheric CO$_2$ concentrations (reference 360 μmol CO$_2$ mol$^{-1}$) and saturating light the ‘operating’ C$_i$ of both redcedar (249.5 ± 8.5 μmol CO$_2$ mol$^{-1}$) and Douglas-fir (255.8 ± 7.6 μmol CO$_2$ mol$^{-1}$) fell within or beyond this transition zone, redcedar tended to have higher maximum photosynthetic rates ($A_{max}$) than Douglas-fir. The similar operating C$_i$ of the two species reflected the covariance observed between the biochemical capacity for CO$_2$ fixation and stomatal conductance. Under ambient CO$_2$ concentrations and saturating light, redcedar tended to have both a higher biochemical capacity for CO$_2$ fixation (Figure 4.14) and higher stomatal conductance ($g_{SIL}$, Table 4.4) than Douglas-fir.
Intercellular CO₂ concentration (C_i), μmol CO₂ mol⁻¹

Figure 4.14 Steady-state and transient responses of net CO₂ assimilation to intercellular CO₂ concentration for western redcedar and coastal Douglas-fir. Steady-state A/C_i responses at saturating light (solid and broken lines) are shown as predicted values derived from the fitted response of data pooled from three individuals per species. Equations describing these responses were:

For redcedar (r² = 0.99):
\[ y = \frac{(0.0281 \times x + 12.14) - \left[ (0.0281 \times x + 12.14)^2 - 4 \times 0.0281 \times 12.14 \times 0.9691 \times x \right]^{0.5}}{2 \times 0.9691} - 2.1481 \]

For Douglas-fir (r² = 0.97):
\[ y = \frac{(0.0259 \times x + 9.57) - \left[ (0.0259 \times x + 9.57)^2 - 4 \times 0.0259 \times 9.57 \times 0.9209 \times x \right]^{0.5}}{2 \times 0.9209} - 1.8257 \]

Representative transient A/C_i responses during photosynthetic induction (shaded and open dot-symbols) are superimposed on steady-state A/C_i response curves to show the relationship between the two. Transient data are shown by way of example for one representative sapling per species for a complete transition from steady-state conditions at low light (30 μmol m⁻² s⁻¹) to steady-state conditions at high light (470 μmol m⁻² s⁻¹), in the direction indicated. The dashed vertical line at 250 μmol intercellular CO₂ mol⁻¹ indicates the approximate observed ‘operating’ C_i for both species under steady-state conditions at high light at the ambient reference CO₂ concentration of 360 μmol CO₂ mol⁻¹ (second dashed vertical line).

Superimposing representative non-steady-state (transient) A/C_i responses during photosynthetic induction in continuous high light on steady-state A/C_i responses at high light demonstrates the relationship between the two (Figure 4.14) and serves to support the interpretation of the relative importance of biochemical and stomatal limitations to photosynthesis made earlier (Pearcy 1994; Pearcy et al. 1994). Both biochemical and stomatal limitations are evident during photosynthetic induction. In both species the transient A/C_i plot does not initially fall along the steady-state A/C_i curve, as it would if only stomatal conductance were responsible for the changes in assimilation. Instead, the transient A/C_i plot begins to the lower right of the steady-state A/C_i curve and then gradually moves towards it as photosynthetic induction proceeds, as indicative of biochemical activation (Kirschbaum and Pearcy 1989b). That biochemical activation is important at this time is also exemplified by the observation that transient photosynthetic rates at ≥250 μmol intercellular CO₂ mol⁻¹ are initially only a fraction of the steady-state rates at the 250 μmol mol⁻¹ ‘operating’ C_i of both species. When during photosynthetic induction the transient A/C_i data reaches the steady-state A/C_i curve, activation of Rubisco is complete. Where after this point
photosynthetic rates then increase in step with increasing $C_i$ along the steady-state $A/C_i$ curve, a stomatal limitation to photosynthesis is suggested (Farquhar and Sharkey 1982). Therefore, the observation that the transient $A/C_i$ response follows the steady-state $A/C_i$ line much longer in redcedar than in Douglas-fir supports the earlier interpretation of greater stomatal limitations in redcedar (Section 4.2.1.1). When no further increases in $A$ or $C_i$ are evident in the transient data (data points cluster), the steady-state rate of photosynthesis has been reached at under ambient atmospheric $CO_2$ and saturating light. That is, $A_{\text{max}}$ has been attained at the operating $C_i$.

### 4.4 OTHER MEASUREMENTS (SUPPORTING DATA)

Mean mid-day xylem water potential ($\psi_{x_{\text{md}}}$) of redcedar was approximately 2.4-fold less negative than that of Douglas-fir, a difference which was highly significant (Table 4.16). Although the range in $\psi_{x_{\text{md}}}$ was small, regression of xylem water potential on various photosynthetic induction parameters, maximum conductance ($gs_{\text{max}}$), and maximum photosynthetic rate ($A_{\text{max}}$) gave no indication that the gas exchange of Douglas-fir was dependent on xylem water potential.

With reference to chlorophyll fluorescence characteristics, the photochemical efficiency of PSII ($F_v/F_m$) was similarly high for both species (Table 4.16). In contrast, the fluorescence half-rise time from $F_0$ to $F_m$ ($T/2$) was significantly longer for redcedar than for Douglas-fir (Table 4.16).

<table>
<thead>
<tr>
<th>Physiological parameter</th>
<th>Western redcedar</th>
<th>Coastal Douglas-fir</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\psi_{x_{\text{md}}}$, MPa</td>
<td>-0.48 (0.06)</td>
<td>-1.17 (0.08)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$F_v/F_m$, relative units</td>
<td>0.847 (0.006)</td>
<td>0.838 (0.003)</td>
<td>0.315</td>
</tr>
<tr>
<td>$T/2$, seconds</td>
<td>179 (2)</td>
<td>173 (1)</td>
<td>0.046</td>
</tr>
</tbody>
</table>
CHAPTER 5
DISCUSSION

Tree species from mid- to high-latitudes lie somewhere along a continuum or gradient of shade tolerance (e.g., Pacala et al. 1994; Kobe et al. 1995; Kobe and Coates 1997). As such, the most marked physiological differences among these species with regard to light use efficiency might be expected between those species which occupy opposing ends of this gradient. However, because species of strongly contrasting shade tolerance are frequently not found together naturally in the forest understory, to comparatively study these combinations of species at low light often requires either growth chamber and nursery studies with artificial shading or the out-planting of seedlings under forest canopies. The former can be fraught with difficulties related to ecological relevance, while the latter may require long time-frames before the effects of light can be reliably distinguished from those of planted seedling establishment (Literature Review, Section 2.2.3).

In this study, the coexistence, 13 years after planting, of well-established saplings of very shade tolerant western redcedar and shade intolerant coastal Douglas-fir under a closed canopy of red alder provided a unique opportunity to study physiological mechanisms of shade tolerance in forest tree species, out-doors under a natural canopy. The hypothesis tested was whether the relatively greater shade tolerance of western redcedar than coastal Douglas-fir (as verified by interspecific differences in survival and growth at low light; Section 2.3.3) may be related to a superior capacity of redcedar for photosynthetic utilization of sunflecks (transient photosynthesis under dynamic light conditions), in accordance with conventional ideas of shade tolerance. Species differences in steady-state photosynthesis and dark respiration were also examined and used as factors against which to gauge the relative importance of species differences in transient photosynthesis. More generally then, the overall goal was to determine the extent to which gas exchange characteristics (transient and steady-state photosynthesis and dark respiration) differed between redcedar and Douglas-fir, and the extent to which any differences reflected the contrasting shade tolerances of these species.

5.1 UNDERSTORY ENVIRONMENT

Although the relative performance of western redcedar and coastal Douglas-fir are discussed in this work in reference to the extent to which their gas exchange characteristics might enhance or limit their survival and growth in a low light environment, it should be pointed-out that in this and other field studies, relative measures of light availability (e.g., % canopy transmittance) actually represent integrative indices of canopy influence, i.e., light and all factors that co-vary with light (Horn 1971). Thus, survival and growth in the forest understory may not only involve tolerance to low light, but tolerance to other environmental conditions which may also differ from those in open environments. In general, maximum summer daytime air and soil temperatures and vapour pressure deficits tend be lower under canopy cover than in the open, whereas effects on edaphic factors tend to be more variable
Nevertheless, low light availability was considered the primary if not the only constraint to the performance of the understory conifers examined in this study. Air temperatures and vapour pressure deficits in the understory (Table 4.1) and those during physiological measurements (22 °C and 1.0 kPa, Materials and Methods) were generally moderate and non-limiting to the photosynthesis of both western redcedar (Major 1990; Grossnickle 1993; Weger et al. 1993; Pepin and Livingston 1997) and coastal Douglas-fir (Krueger and Ferrell 1965; Brix 1967, Sørensen and Ferrell 1973; Waring and Franklin 1979; Leverenz 1981; Lassoie 1982; Meinzer 1982; Johnson and Ferrell 1983; see also Running 1976; Livingston and Black 1987). Although the availability of soil water and nutrients was not directly measured, it is improbable that either of these factors was limiting. The site was classified as very moist and nutrient rich (i.e., as typically having growing-season water surplus and relatively large amounts of available nitrogen and rapid turnover of organic matter) within a climatic area (CWHdm subzone) in which growing-season water deficits are unlikely (Meidinger and Pojar 1991). In August when physiological measurements were made, precipitation was above average for this location (Table 3.1). That nitrogen availability may have been relatively high might also be inferred from the well known association of red alder root nodules with a nitrogen-fixing actinomycete and the expected high inputs of nitrogen from deciduous leaf litter (Tarrant and Trappe 1971). Furthermore, regardless of the actual availability of soil water or nitrogen, soil water and nitrogen deficiencies, unless severe, are unlikely to have an important impact on tree performance in deep shade (ca. ≤5% full light; e.g., Reed et al. 1983; Lehto and Grace 1994; Canham et al. 1996; Walters and Reich 1996; see also substrate studies of Kayahara 2000 and field studies of Pacala et al. 1994, 1996; but see Walters and Reich 1997).\[11\]

The foliage of both western redcedar and coastal Douglas-fir was judged to be healthy because measured $F_v/F_m$ values (Table 4.16) were optimally high for C$_3$ species in the absence of stress (Björkman and Demmig 1987; Adams et al. 1990)\[12\]. Xylem water potential was slightly depressed in Douglas-fir (but not redcedar; Table 4.16), but as will be discussed in detail in Section 5.2.5 this was not considered to result from soil water deficits.

### 5.1.1 Canopy transmittance

Closed canopy conditions 13 years after clear-cutting and burning resulted in deeply shaded conditions in the understory of red alder. Canopy transmittance was only 3–4%, which is much lower than the 11% canopy transmittance reported beneath naturally established red alder on slightly dry sites 6–8 years after clear-cutting and burning elsewhere in the Dry Maritime Coastal Western Hemlock (CWHdm) subzone of British Columbia (Burton Direct measurements of soil moisture and nutrients usually validate site classifications of this type (e.g., Walters and Reich 1997).

Low water and nutrient supplies can reduce growth along most of the light gradient (light and soil resources can co-limit growth, but the effect becomes increasingly small as light availability decreases.

Because $F_v/F_m$ is proportional to the quantum yield of absorbed light (Björkman and Demmig 1987), it may decline from optimum in response to such factors as water and nutrient stress, unfavourable temperatures, diseases, and anthropogenic air pollutants (e.g., see Lichtenthaler 1988).
However, it was not clear whether closed canopy conditions existed in the cited study, and no other measurements of light availability under closed canopy red alder appear to be available for further comparison.

Comparatively, the 3–4% canopy transmittance reported here for red alder was broadly within the range reported (ca. <1%–20% full light) for closed canopy conditions in other mid-latitude forest stands comprised of a single predominant deciduous angiosperm tree species (Canham et al. 1994; Lieffers and Stadt 1994; Constabel and Lieffers 1996; Carlson and Groot 1997; Comeau et al. 1998; Pinno et al. 2001; see also Canham 1988; Canham et al. 1990; Beaudet and Messier 1998; Beaudet et al. 2000). However, canopy transmittance tends to be inversely related to the shade tolerance of the dominant tree species (Vézina and Péch 1964; Horn 1971; Canham et al. 1994; Messier et al. 1998), and the measured levels of light availability under red alder may therefore have been somewhat lower than what is typically reported for shade intolerant tree species in particular. For example, in a study that examined light availability beneath five hardwood canopy types, canopy transmittance ranged from 0.95% for very shade tolerant *Fagus grandifolia* Ehrh. to 6.2% for intermediately shade intolerant *Fraxinus americana* L. (Canham et al. 1994). In contrast, higher understory light levels (ca. 10–20% full light) have been reported for some more shade intolerant hardwood species at mid-latitudes (Horn 1971), and likewise for hardwood forests dominated by very shade intolerant *Populus tremuloides* Michx. in the colder climate boreal forests of eastern and western Canada (Lieffers and Stadt 1994; Constabel and Lieffers 1996; Carlson and Groot 1997). If not otherwise inherent, the lower than expected values of canopy transmittance observed here for red alder might be related to the relatively young age (13 years) of the stand (15 years may be the minimum age at which light availability initially increases under alder; Peterson et al. 1996) and/or the relatively more favourable climate and/or edaphic quality of the site in comparison with other studies (the maximum leaf area supported by a forested site is a function of climate, site water balance, and soil nutrition; Grier and Running 1977; Waring et al. 1978; see also Gholz et al. 1976). Indeed, it was recently shown that light transmittance through *Populus tremuloides* can be as low as 4% for young stands on good sites (Pinno et al. 2001).

Canopy transmittance did not differ above western redcedar and coastal Douglas-fir, suggesting that both species were persisting at similarly low light levels (3–4% full light). The result was marginal (p=0.073), but if there was a difference between the light environments of redcedar (2.8 ± 0.3 % full light) and Douglas-fir (3.6 ± 0.2 % full light) it was probably unimportant to survival at this stage of stand development. If Douglas-fir was in fact restricted to microsites with slightly higher light levels than redcedar, then dead Douglas-fir saplings would presumably have been evident on the site at marginally lower light levels. This was not the case.

It is not known how long or to what size redcedar and Douglas-fir may survive at such low light levels. Live western redcedar and coastal Douglas-fir saplings have also been observed at ≤5 % full light under coniferous forest canopies in the Coastal Western Hemlock (CWH) zone of B.C. (Carter and Klinka 1992). Conversely, elsewhere in the CWH zone seedlings of both redcedar (Wang et al. 1994) and Douglas-fir (Mailly and Kimmins 1997; Kayahara 2000) have been reported to die within 2–3 years after being planted under coniferous canopies at equivalent or higher light levels. Although these observations might suggest that saplings can be more tolerant of shade than seedlings, it is possible that planted seedlings might respond differently given a longer period for
acclimation to the site. It must also be acknowledged that past light conditions were not measured for any of the saplings studied (this study and Carter and Klinka 1992) and may have been higher at one time. Certainly, it is quite probable that the saplings examined here experienced higher light levels during the early stages of stand development following clear-cutting and burning. Notwithstanding, growing-season light levels at this site must have been low for quite some time, because red alder will normally dominate recently disturbed sites within about 4 years (Peterson et al. 1996).

5.1.2 Sunfleck activity

No published reports appear to exist which describe sunfleck activity under red alder. Data obtained in this study demonstrate that light conditions under red alder can be highly dynamic. In this closed canopy stand, the overwhelming majority of all measured sunflecks were \( \leq 30 \text{ s} \) in duration (Figure 4.1) and the time interval between sunflecks was also typically short (Figure 4.2). Sunflecks occasionally persisted for as long as 5.5–6 min, but only rarely lasted longer than 2–2.5 min. The peak PPFD of the majority of sunflecks (ca. 68\%) was low, just above the threshold value (40 \( \mu\text{mol photons m}^{-2}\text{s}^{-1} \)) in the 40–90 \( \mu\text{mol m}^{-2}\text{s}^{-1} \) category (Figure 4.3). That most sunflecks were short and of low peak PPFD was not surprising given the closed nature of this tall canopy and the associated likelihood of strong penumbral effects (Holbo et al. 1985; Smith et al. 1989; Baldocchi and Collineau 1994). However rare, peak sunfleck PPFD nonetheless reached values as high as 1291–1340 \( \mu\text{mol m}^{-2}\text{s}^{-1} \), some 32–34-fold greater than the background diffuse light (10–30 \( \mu\text{mol m}^{-2}\text{s}^{-1} \)). Although not known, these high intensity sunflecks were likely caused by transient parting of the canopy as a result of canopy movement (stem sway and/or leaf flutter) (Pearcy 1994).

It is difficult to make meaningful comparisons of sunfleck activity between forest types owing to the different methodologies used to measure sunfleck activity and probable differences among stands with respect to site quality and crown closure. Nonetheless, it may be noteworthy in a general sense that, for both pure and mixed evergreen conifer and broad-leaved deciduous forests of mid- to high-latitudes, the available data suggest that most sunflecks, when measured directly by sensors and not estimated from analysis of hemispherical canopy photographs, tend to be relatively short (ca. \( \leq 60 \text{ s} \)), frequent (ca. \( \leq 120 \text{ s} \) duration between sunflecks), and of low maximum PPFD (ca. \( \leq 200 \mu\text{mol m}^{-2}\text{s}^{-1} \)) (Washitani and Tang 1991; Gildner and Larson 1992; Pfitsch and Pearcy 1992; Roden and Pearcy 1993a; Naumburg and Ellsworth 2000). Whether these forest types differ with respect to finer-scale variation in sunfleck activity remains to be determined.

5.2 TRANSIENT PHOTOSYNTHETIC RESPONSES TO DYNAMIC LIGHT CONDITIONS

Given the dynamic nature of the light environment under red alder (as above), the carbon gain of any associated understory conifers could conceivably be dependent on their capacity for efficient transient photosynthetic responses to fluctuating light conditions. Here it was shown that the requirement for photosynthetic induction did strongly limit the carbon gain of understory saplings of both western redcedar and coastal Douglas-fir and that differences in the efficiency of photosynthetic response to dynamic light conditions do exist between the two species. Species differences in photosynthetic induction potential (induction in continuous high light),
maintenance of induction state in shade, and induction in fluctuating light are discussed below. Simultaneously, the results from these analyses are contrasted to species comparisons based more simply on an analysis of absolute carbon gain or rates of carbon gain. Associated implications for water use efficiency are then considered towards the end of this section.

5.2.1 Photosynthetic induction and carbon gain in continuous high light

Rapid photosynthetic induction has been considered a trait associated with efficient photosynthetic utilization of sunflecks, and one which is differentially associated with shade tolerant versus shade intolerant species (Chazdon and Pearcy 1991). However, contrary to this expectation, times required to reach 50% (A-T$_{50}$) and 90% (A-T$_{90}$) of full photosynthetic induction were markedly longer for very shade tolerant western redcedar than for shade intolerant coastal Douglas-fir (Table 4.3).

Examination of the kinetics of photosynthetic CO$_2$ efficiency (A/C) and stomatal conductance (gs) during photosynthetic induction revealed that species differences in induction times were unrelated to Rubisco activation and driven instead by interspecific differences in stomatal response$^{13}$, with stomatal opening requiring about twice as long in redcedar as in Douglas-fir (Table 4.3, Figure 4.4). Thus, although shade tolerance in woody species has been suggested to be associated specifically with short stomatal opening times in response to high light (Woods and Turner 1971; Davies and Kozlowski 1975; Tinoco-Ojanguren and Pearcy 1992), this was clearly not the case in this study. Comparisons of stomatal opening times from darkness (cf. low light) in sun-grown (cf. shade-grown) ecotypes of redcedar and Douglas-fir reportedly yielded the same result (Pepin and Livingston 1997). Although long times for stomatal opening and photosynthetic induction can frequently be attributed to lower values of initial (starting) conductance (Ögren and Sundin 1996; Valladares et al. 1997; Han et al. 1999; Allen and Pearcy 2000; Naumburg and Ellsworth 2000), this was not the case here because redcedar maintained similar conductance in shade as Douglas-fir. Rather, redcedar exhibited a significantly longer lag period before stomatal opening commenced (80.7 ± 5.7 s in redcedar versus 35.8 ± 3.8 s in Douglas-fir; Figure 4.5), and a tendency for a greater overall change in conductance (Table 4.4).

A lag period prior to stomatal opening has sometimes been observed for other species (e.g., Pearcy et al. 1985; Greenway and Lieffers 1997; Valladares et al. 1997; Naumburg and Ellsworth 2000), but there appears to be no clear relationship between the presence or absence and duration of a lag period and the shade tolerance of a species. Rather, it seems likely that the lag period for stomatal opening is not a fixed characteristic of a species, but may vary with at least some factors which can affect initial conductance. For example, lag times have been reported to vary both with soil moisture stress (Davies and Kozlowski 1975) and atmospheric moisture stress (Tinoco-Ojanguren and Pearcy 1993$b$), and may be evident where induction is measured from darkness rather than from some low level of background light (e.g., Zipperlen and Press 1997). Nonetheless, irrespective of how the lag phase for stomatal opening in redcedar and Douglas-fir might (or might not) vary with environmental conditions, it can be concluded that redcedar is likely to exhibit a longer lag phase for stomatal opening than Douglas-fir in

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$^{13}$ The fast induction component was not of interest here because non-induced foliage was used for the test.
...understory of red alder on sunny days in summer when sunflecks would be important. This is because measurement conditions which could potentially affect initial conductance, such as the initial low light level, VPD, temperature, and CO₂ concentration, were selected to be closely representative of understory conditions.

The expectation that in deeply shaded environments shade tolerant species are likely to exhibit higher capacities to become rapidly photosynthetically induced than more shade intolerant species (Chazdon and Pearcy 1991) has not always been met. Exceptions have been reported among various tree and herbaceous species from low-latitude forests (e.g., Chazdon and Pearcy 1986a; Zipperlen and Press 1997⁴⁴; see also Poorter and Oberbauer 1993) and broad-leaved deciduous angiosperm tree species from mid-latitude forests (e.g., Han et al. 1999; Naumburg and Ellsworth 2000). The same now appears true for conifer species from mid- to high-latitude forests (this study and Ögren and Sundin 1996). Values of T₉₀ reported to date include: 31.8 ± 2.7 min for very shade tolerant western redcedar and 19.8 ± 1.8 minutes for shade intolerant Douglas-fir (this study); and 27.7 min (one sample) for very shade tolerant *Tsuga heterophylla* (Raf.) Sarg., 21.5 ± 4.0 min for moderately shade tolerant *Picea sitchensis* (Bong.) Carr., and 30.7 ± 0.7 min. for shade intolerant *Pinus sylvestris* L. (growth chamber study of Ögren and Sundin 1996). There is no obvious relationship between T₉₀ values and the shade tolerance of these conifers.

If the capacity to become rapidly photosynthetically induced is a trait which confers shade tolerance, then presumably the corollary of this would be that species which become rapidly induced will exhibit more favourable carbon gain than species which are slower to become induced. However, despite the fact that coastal Douglas-fir became photosynthetically induced much quicker than western redcedar, when these species were compared instead on the basis of absolute photosynthetic rates at common points along the same induction time-course, redcedar either performed comparably (up to ca. 15 min) or better (after ca. 15 min) than Douglas-fir (Table 4.5, based on p ≤0.100). This raises concerns about the relevance of induction potential parameters as a basis for gauging the relative competitive abilities of species in shade.

Lei and Lechowicz (1997) noted that among species with similar absolute photosynthetic rates prior to and during the initial stages of induction (as for redcedar and Douglas-fir in this study; Table 4.5), those with highest maximum photosynthetic rates (*A*ₘₐₓ) would necessarily have the lowest induction states at similar points along the induction time-course simply because *A*ₘₐₓ is the divisor for the computed induction state values (see Equ. 5, Materials and Methods). They questioned whether in such cases one could infer from the low induction state of a species a lack of adaptation to sunflecks simply because it had a high *A*ₘₐₓ. In a similar vein, in this study absolute rates of carbon gain during photosynthetic induction were either similar or greater in redcedar than in Douglas-fir, yet redcedar was observed to have a longer induction time because it tended towards higher *A*ₘₐₓ (see also Naumburg and Ellsworth 2000)⁵⁰. Can one infer from its longer induction time a lesser adaptation of redcedar for photosynthetic use of sunflecks just because it had a higher *A*ₘₐₓ? The answer is probably ‘no’. However, it is

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⁴⁴ Induction potential was measured from darkness in Zipperlen and Press (1997).

⁵⁰ This probably also explains observations of longer induction times for leaves under higher versus lower, non-saturating light intensities (Chen and Klinka 1997). For leaves tested under both light levels, initial photosynthetic rates would be similar prior to induction, but the maximum achievable photosynthetic rate would be higher at higher light intensities.
probably also not appropriate to conclude that redcedar is better adapted to use sunflecks because it achieved higher absolute photosynthetic rates during induction in continuous high light. Absolute photosynthetic rates were greater for redcedar, but only when $A_{\text{max}}$ was approached (Table 4.5). Such a situation may be unlikely in the understory where saturating light conditions ($\geq 470 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), which are necessary for the expression of $A_{\text{max}}$, are relatively rare (Figure 4.3).

Overall it might be concluded that: i) induction potential parameters ($T_{50}, T_{90}$) are poorly related to shade tolerance; and ii) where interspecific comparisons of ecological fitness are of interest, analysis of absolute carbon exchange rates probably provides a more meaningful basis on which to compare species than times to reach species-specific values of maximum photosynthesis (induction potential). Although very shade tolerant western redcedar required more time to become fully induced than shade intolerant coastal Douglas-fir, the requirement for photosynthetic induction limited photosynthetic rates similarly in both species during the initial stages following exposure of non-induced foliage to continuous high light.

5.2.2 Maintenance of photosynthetic induction during shade periods

As shown above, the requirement for photosynthetic induction has the potential to strongly limit the carbon gain of both western redcedar and coastal Douglas-fir in an understory environment. For the non-induced foliage of both species, this limitation can initially be as high as 70% (based on $A_{\text{IS}_{60}}$ values after prolonged shading, Table 4.7). Therefore, any difference in the capacity of these species to maintain photosynthetic induction state in low light intervals between sunfleck events could be important. Shade tolerant species have been observed to maintain photosynthetic induction longer than shade intolerant species when both are grown under similarly low light levels (Tinoco-Ojanguren and Pearcy 1993b; Küppers et al. 1996; see also Poorter and Oberbauer 1993), although this is not always the case (Naumburg and Ellsworth 2000; see also Rijkers et al. 2000).

Western redcedar was better able to maintain photosynthetic induction state ($A_{\text{IS}_{60}}$) than Douglas-fir, but only during the longer shading intervals examined (Table 4.7). There was $\leq 10\%$ reduction in $A_{\text{IS}_{60}}$ in either species during shading periods of 2 or 5 minutes, but $A_{\text{IS}_{60}}$ decayed considerably more during longer shading intervals of 15 and 30 minutes (Table 4.7, Figure 4.7). Redcedar maintained induction state better than Douglas-fir during these longer shading intervals due primarily to a superior capacity for maintaining Rubisco activation rather than stomatal conductance (Table 4.7). Although the fast induction component (RuBP regeneration) was potentially important after 2 and 5 minute shading intervals when loss of the slow induction component (Rubisco activation, stomatal opening) was minimal (Kirschbaum and Pearcy 1988c; Pons et al. 1992; Sassenrath-Cole and Pearcy 1992), it appeared to impose similar limitations on both species at this time (Figure 4.8).

The above comparisons of the photosynthetic induction state ($A_{\text{IS}_{60}}$) of western redcedar and coastal Douglas-fir after various periods of shading (Table 4.7) might suggest that the two species will perform similarly after 2 and 5 minutes of shade (when induction states are similar), but that redcedar will perform better than Douglas-fir after longer 15 and 30 minute shading intervals (when induction state is greater for redcedar than for Douglas-fir). However, an alternative comparison of the two species on the basis of absolute photosynthetic rates
again yielded contrasting results, in-as-much as redcedar exhibited higher rates of carbon gain than Douglas-fir following all four experimental shading intervals of 2, 5, 15, and 30 minutes (Table 4.8, Figure 4.8) (carbon exchange rates were again similar for the two species after prolonged shading because the foliage of both species was non-induced). The higher photosynthetic rates of redcedar after 2 and 5 minutes of shading were clearly not attributable to a higher photosynthetic induction state, but rather again to its tendency to have a higher maximum photosynthetic capacity ($A_{\text{max}}$). In contrast, the higher photosynthetic rates in redcedar after 15 and 30 minutes of shade were due, at least in part, to the higher capacity of this species for maintaining photosynthetic induction state.

What might these differences in response to shading mean to the comparative performance of redcedar and Douglas-fir under light regimes characteristic of the understory of red alder? On sunny days in summer when sunflecks would be important, recorded times between sunfleck events were only rarely in excess of 5 minutes (>300 s, Figure 4.2). Under such conditions, little induction is likely to be lost in either species between successive sunfleck events (Table 4.7). Thus, whether or not carbon gain would be greater for redcedar than for Douglas-fir would presumably then be dependent on whether or not redcedar could achieve in fluctuating light an induction state high enough to permit rates of photosynthesis which approach its maximum photosynthetic capacity ($A_{\text{max}}$), which tends to be higher than that of Douglas-fir (Tables 4.5, 4.15 and Figures 4.12, 4.14). Given that both species attained similar photosynthetic induction states and carbon gain during an experimental sunfleck regime (see later) this may not be the case, especially when it is considered that saturating light conditions ($\geq 470 \mu\text{mol m}^{-2}\text{s}^{-1}$), which are necessary for the expression of $A_{\text{max}}$ are infrequent under the red alder canopy studied here (Figure 4.3). At the low and intermediate light levels representative of most sunflecks (ca. $\leq 140 \mu\text{mol m}^{-2}\text{s}^{-1}$, Figure 4.3), maximum achievable photosynthetic rates are expected to be similar for the two species (compare predicted steady-state photosynthetic rates at $\leq 140 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ from the light-response curves in Figure 4.12).

Although the higher capacity of redcedar for maintaining photosynthetic induction state during longer 15 and 30 minute intervals of shading may not generally be important on sunny days when intervals between sunflecks are typically $<5$ minutes, this difference might become more important on intermittently cloudy days when the duration between sunfleck events increases (Pearcy 1983). However, although cloudiness, which is frequent in the Pacific coastal region (Table 3.2; Waring and Franklin 1979; Klinka and Krajina 1986), could conceivably disadvantage Douglas-fir in this manner, it must also be considered that species differences in induction states and absolute photosynthetic rates were not different after prolonged shading (Tables 4.7 and 4.8). Thus, the manner of sky conditions which might result in a good number of shade periods $>15$ minutes but less than those which would cause complete loss of induction in both species could conceivably be quite limited. Still, however infrequent, shading periods within this range might possibly be important over the long-term.

Comparatively, the loss of photosynthetic induction in conifers, which appears to require 30–60 minutes or more (this study and Ögren and Sundin 1996), tends to occur much slower (i.e., induction state is maintained much better) than in hardwood species such Salix sp. ($\leq 20$ min; Ögren and Sundin 1996) and some understory associates of the conifers such as Calamagrostis canadensis (Michx.) Beauv. (approx. 5 min based on stomatal response; Greenway and Lieffers 1997). Adenocaulon bicolor Hook., another understory associate, has been shown to exhibit
an induction state of only 0.56 after 5 minutes of shading, which is much lower than the 0.89–0.93 induction state values observed here for redcedar and Douglas-fir after the same interval of shading.

Also notable is that the rate of induction loss was slower than the rate of induction gain for both of the conifers examined in this study (compare Table 4.7 with Table 4.3 and Figure 4.4). This is consistent with what has been observed for other conifers (Ögren and Sundin 1996) and hardwood species (Küppers and Schneider 1993; Poorter and Oberbauer 1993; Roden and Pearcy 1993b) and contrasts to the more symmetrical rates of induction gain and loss observed for some fast-growing herbaceous species (Ögren and Sundin 1996). In western redcedar and coastal Douglas-fir, the faster gain than loss of photosynthetic induction was associated with faster increases than decreases in both the activation state of Rubisco and stomatal conductance. Faster activation than deactivation of Rubisco has previously been reported for some tree species (Roden and Pearcy 1993b; Ögren and Sundin 1996) and faster opening than closing of stomata may be a particularly common feature of woody species (e.g., Woods and Turner 1971; Davies and Kozlowski 1975; Pereira and Kozlowski 1977; Ceulemans et al. 1989; Tinoco-Ojanguren and Pearcy 1992; Roden and Pearcy 1993b), at least in the absence of soil or atmospheric water stress. The loss of photosynthetic induction in woody species may be more closely related to the deactivation of Rubisco than to the closing of stomata (Roden and Pearcy 1993b; Ögren and Sundin 1996) as was observed here (Table 4.7), whereas other times both factors appear to be important (Naumburg and Ellsworth 2000).

With regard to the decay of photosynthetic induction state in shade, it might be concluded that i) western redcedar and coastal Douglas-fir exhibit responses qualitatively similar to other woody species, most especially the few other conifers examined to date; and ii) western redcedar was better able to maintain photosynthetic induction than Douglas-fir, but only during long shading intervals generally atypical of the understory on sunny days in summer. Thus, although the higher capacity of redcedar for maintaining photosynthetic induction was in a general sense consistent with what is expected for shade tolerant species, it is probably of little overall importance to the comparative capacities of the two species for photosynthetic utilization of sunflecks, except perhaps on cloudy days.

5.2.3 Photosynthetic induction and carbon gain in fluctuating light

The analysis of photosynthetic induction potential demonstrated the extent to which photosynthetic induction of both western redcedar and coastal Douglas-fir could proceed in continuous high light. Extended periods of continuous high light are however rare or nonexistent in the understory of red alder (Figure 4.1), where the overwhelming majority of sunflecks recorded were ≤30 s in duration and only rarely exceeded 2.5 minutes (150 s). The potential of western redcedar and coastal Douglas-fir to become photosynthetically induced by a series of sunflecks was therefore assessed by exposing foliage to a simulated sunfleck (lightfleck) regime consisting of five 30 s lightflecks each separated by 2 minute intervals of low light.

Both western redcedar and coastal Douglas-fir were capable of becoming photosynthetically induced in fluctuating light, similar to what has been observed for other species (e.g., Pearcy et al. 1985; Chazdon and Pearcy 1986a; Pfitsch and Pearcy 1989; Poorter and Oberbauer 1993; Roden and Pearcy 1993b; Sims and Pearcy 1993). Prior to imposition of the experimental sunfleck regime, low induction state initially limited the photosynthetic rates
of both species by about 75% (based on A-IS$_{30}$ values on the first lightfleck, Table 4.10). Then, from the first to the fifth lightfleck induction state approximately doubled in both species as limitations to photosynthesis were gradually removed, and by the end of the fifth lightfleck photosynthetic rates were 50–60% of steady-state light saturated rates. The two-fold increase in the foliar photosynthetic induction state of redcedar and Douglas-fir was similar to that observed for the non-induced foliage of herbaceous and woody species of rainforest understories when exposed to a lightfleck series identical to that used here (Chazdon and Pearcy 1986a; Poorter and Oberbauer 1993). Although this might suggest a degree of commonality among diverse species in the rate of photosynthetic induction in fluctuating light, no other studies have tested the same lightfleck regime and further interspecific comparisons cannot be made.

In contrast to the slower rate of photosynthetic induction observed for western redcedar than for coastal Douglas-fir under continuous illumination with high light, in the fluctuating light regime photosynthetic induction proceeded as rapidly in redcedar as it did in Douglas-fir (Table 4.10). This change in species rankings was due to an improvement in the rate of induction of redcedar in fluctuating light rather than a depression in the rate of induction in Douglas-fir and was related to stomatal dynamics. Specifically, in redcedar a continued high rate of stomatal opening in the low light periods between lightflecks compensated for its longer initial lag period for stomatal opening and led to the attainment of a similar photosynthetic induction state (A-IS$_{30}$) as Douglas-fir by the end of the fifth lightfleck (Table 4.10). Whether or not the two species would have exhibited similar induction states after longer periods in fluctuating light is, however, not known. Although the initial stomatal opening response was strong in Douglas-fir, it appeared to weaken as the lightfleck series progressed (compare the stomatal response of redcedar in Figure 4.9b with that of Douglas-fir in Figure 4.10b), similar to what has been reported for some other shade intolerant species when grown in heavy shade (Tinoco-Ojanguren and Pearcy 1992, 1993a). Nonetheless, Douglas-fir still achieved a similar level of stomatal opening in fluctuating light (gs-IS$_{30}$ on lightfleck #5 = 0.243) as when given a similar photon exposure to continuous high light (IS$_{I50}$ = 0.264) (Table 4.10).

As with photosynthetic induction state, lightfleck use efficiency (LUE) approximately doubled in both western redcedar and coastal Douglas-fir from the beginning (LUE 35–38%) to the end (LUE 65–73%) of the lightfleck series (Table 4.11). Neither the proportional contribution (Table 4.11) nor the absolute amount (Table 4.12) of net post-illumination CO$_2$ fixation (post-illumination CO$_2$ fixation minus any losses to photorespiratory bursts) differed significantly between species, despite the higher electron transport capacity of redcedar (T'/i results in Table 4.16, A/C$_i$ curves in Figure 4.14) (an overshoot in electron transport is required to build-up photosynthetic intermediates for post-illumination CO$_2$ fixation; Laisk et al. 1984; Sharkey et al. 1986; Kirschbaum and Pearcy 1988a). Consequently, LUE also did not differ significantly between the two species for any lightfleck in the series.

The observation that lightfleck use efficiency (LUE) was similar for redcedar and Douglas-fir is contrary to the expectation that more shade tolerant species should exhibit higher LUE than more shade intolerant species (e.g., Pearcy 1990; Chazdon and Pearcy 1991)$^{16}$, although other exceptions have previously been reported (e.g., Pearcy et

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$^{16}$ Although Chazdon and Pearcy (1986b) is widely cited as an example of this, the shade tolerant and shade intolerant species examined in that study were grown in different light environments (tolerant under low light, intolerant under high light).
al. 1985; Tinoco-Ojanguren and Pearcy 1992; Küppers et al. 1996). Granted, it cannot be ruled out that differences in post-illumination CO$_2$ fixation and lightfleck use efficiency might have been found if very short sunflecks ($\leq 10$ s) had been examined. Sunflecks of such short duration could not be tested owing to data logging constraints and because errors introduced by manual control of light transitions increased unacceptably with shorter lightfleck duration; computerized shutter control of light transitions would be required (Chazdon and Pearcy 1986a). Regardless, it should also be considered that post-illumination CO$_2$ fixation is most important in saturating sunflecks (it depends on an overshoot in electron transport during a sunfleck) and makes an increasingly smaller contribution with decreasing sunfleck (or lightfleck) PPFD (Kirschbaum and Pearcy 1988a). In the understory of red alder where most sunflecks were short, most sunflecks were also of low maximum PPFD, much lower than what was saturating to both species ($\ll 470$ μmol·m$^{-2}$·s$^{-1}$, Figure 4.3).

Because both photosynthetic induction state (A-IS$_3$) and lightfleck use efficiency (LUE) are relative parameters and as such do not necessarily equate with absolute photosynthetic performance, western redcedar and coastal Douglas-fir were also compared on the basis of the absolute amount of carbon gained during lightflecks. This was done in two ways, firstly by comparing between species the total integrated net carbon gain attributable to lightflecks and secondly by comparing maximum photosynthetic rates achieved during lightflecks. Given that in both species post-illumination CO$_2$ fixation made a considerable contribution to the total carbon fixed in response to lightflecks (38–62%), comparison of the former may be equally or more important than the latter.

Total integrated carbon gain attributable to the lightfleck series (net carbon gain during lightflecks and during post-lightfleck responses) tended to be higher for western redcedar than for coastal Douglas-fir, but variation was high and the result was not statistically significant (Table 4.12). Absolute photosynthetic rates achieved during lightflecks also did not differ significantly between redcedar and Douglas-fir, albeit rates did again tend to be higher for redcedar by the end of the last lightfleck ($3.65 \pm 0.26$ μmol·m$^{-2}$·s$^{-1}$ for redcedar versus $3.07 \pm 0.17$ μmol·m$^{-2}$·s$^{-1}$ for Douglas-fir). It is notable that the photosynthetic rates achieved by both species on the last lightfleck were nearly equivalent to the maximum attainable photosynthetic rates of these species at PPFD’s characteristic of most sunflecks measured under red alder (ca. 85% of sunflecks were $\leq 140$ μmol photons·m$^{-2}$·s$^{-1}$, Figure 4.3). From steady-state light response curves (equations, Figure 4.12 caption), maximum achievable photosynthetic rates at 140 μmol photons·m$^{-2}$·s$^{-1}$ were approximately 3.75 μmol CO$_2$·m$^{-2}$·s$^{-1}$ for redcedar and 3.38 μmol CO$_2$·m$^{-2}$·s$^{-1}$ for Douglas-fir. This might suggest that as long as foliage was previously exposed to as few as five 30 s lightflecks of $\leq 140$ μmol photons·m$^{-2}$·s$^{-1}$ and with as long as 2 minutes of low light in between (during which time Rubisco activation and stomatal conductance undergo only minimal decay), both species would realize near-maximum achievable photosynthetic rates during most sunflecks received under red alder. As Chazdon and Pearcy (1991) pointed out, the more numerous and frequent sunflecks of lower PPFD may in some cases be more important to total daily carbon gain than the less frequent higher intensity ones.

Despite the general lack of significant differences between redcedar and Douglas-fir in regard to most aspects of transient photosynthetic responses to light, it is important not to lose sight of the fact that low induction state did impose a considerable limitation on the photosynthesis of both species, and that in fluctuating light this
effect was partially offset by post-illumination CO2 fixation which benefited both species substantially. This was explicitly demonstrated by comparing for both species total integrated carbon gain during a 150 s (2.5 minute) exposure to high light, given to fully induced and non-induced foliage, and to non-induced foliage in different temporal patterns. During the first 150 s of exposure of non-induced foliage to constant high light, low induction state limited carbon gain by 68% and 64% in redcedar and Douglas-fir, respectively (compare second and third entries, Table 4.13). This limitation was 47% (Douglas-fir) to 62% (redcedar) lower in non-induced foliage when the 150 s high light dose was given instead as a series of five lightflecks, because of the contribution of net post-lightfleck CO2 fixation and, for redcedar, the attainment of a higher induction state. Despite this, however, the restriction on carbon gain due to the requirement for photosynthetic induction was still substantial for both species, nearly 50% in the 150 s test (compare first and third entries, Table 4.13). This supports the earlier assertion that some temporal aspect of the growth light regime is important to the biomass growth of Douglas-fir (Brix 197017), and suggests that the same is true for western redcedar.

5.2.4 Intrinsic water use efficiency under transient conditions

Stomatal dynamics have implications not only for carbon gain, but also for water loss. Notable in this regard is that, at least in relatively mesic habitats18, conifers (e.g., Knapp and Smith 1989; see also Ng and Jarvis 1980) and other woody species (e.g., Pearcy and Calkin 1983; Knapp and Smith 1989; Tinoco-Ojanguren and Pearcy 1992) tend to exhibit a ‘nontracker’ stomatal response to changes in light (sensu Knapp and Smith 1990). In this study western redcedar and coastal Douglas-fir were shown to be no exceptions (see also Livingston 1994 regarding redcedar response to fluctuations in light at high light). Instead of stomatal conductance rapidly increasing and decreasing as light intensity increased and decreased (i.e., ‘tracking’ changes in light, as photosynthesis does), once initiated stomatal opening continued slowly during both lightflecks and short intervening low light periods (Figure 4.9b, 4.10b) and decayed only slowly during longer periods in low light (Table 4.7).

Any ecological benefit to redcedar and Douglas-fir, or other woody species, of a nontracker stomatal response to fluctuating light appears to be related to the enhancement of carbon gain, with a tradeoff of greater water loss (Knapp and Smith 1989, 1990). In such species the stomatal response to a sunfleck may be too slow to allow for increased photosynthetic use of that sunfleck, but it does allow for improved photosynthetic use of subsequent sunflecks because stomata either continue to open or close only slowly in low light intervals between sunfleck events (e.g., Tinoco-Ojanguren and Pearcy 1992). However, because during intervening shade periods photosynthetic rates decline rapidly but stomatal conductance does not, the result is also usually lower water use efficiency in shade (e.g., Weber et al. 1985; Knapp and Smith 1989). Such a reduction in water use efficiency in shade was evident for both redcedar and Douglas-fir, particularly when fully induced foliage was exposed to only 2 minutes of shading. In that case, water use efficiency was reduced in both species by about 80% in comparison to steady-state conditions at high light (compare water use efficiencies at the end of the 2 min shading interval in Table 4.9 with those at steady-state conditions at high light in Table 4.6). Where minimizing water loss, or water loss per

17 The treatments in this study did not appear to be replicated.
18 In water-limited ecosystems, woody species may instead exhibit tracker responses (Knapp 1992).
unit carbon gain, is more important, a 'tracker' stomatal response (where stomata respond rapidly to changes in light) may be more suitable. Perhaps not surprisingly, a tracker stomatal response is more characteristic of herbaceous species, particularly those common to open or relatively open-understory habitats (Knapp and Smith 1989, 1990; Greenway and Liffers 1997).

Although redcedar and Douglas-fir both exhibited nontracker stomatal responses to light, the stomatal dynamics of these two species did differ in other respects (length of lag phase, opening time), and in some cases differences in water use efficiency resulted. Both species tended towards optimizing carbon gain per unit water loss in a similar manner, as indicated by similar intrinsic water use efficiency (A/gs) and C/Co ratios under steady-state conditions at low light and under steady-state conditions at high light (Table 4.6). However, under non-steady-state conditions water use efficiency was not always similar. Redcedar exhibited markedly higher water use efficiency than Douglas-fir during the initial stages of photosynthetic induction in continuous high light (Figure 4.6), albeit during induction in fluctuating light this initial difference was reduced to a non-significant trend (values for end of lightflecks, Table 4.14). Water use efficiency was also similar for both species during both short and long shading intervals (Table 4.9, Table 4.14).

If redcedar in some cases has higher water use efficiency than Douglas-fir during exposure to high light under transient conditions, is this likely to be important? Where water use efficiency differed between the two species, absolute photosynthetic rates were similar but conductance was lower in redcedar. Therefore, any apparent advantage to redcedar of a higher water use efficiency would be achieved by virtue of its lower conductance, and thus lower potential water loss. However, as Sheriff et al. (1995) emphasize, a higher resource use efficiency has the potential to increase productivity only if the supply of the resource (in this case water) is limiting in the particular environment in question. Moisture was unlikely to be limiting in this study, and any interspecific difference in intrinsic water use efficiency would therefore be expected to be relatively inconsequential to the comparative performance of these species. Xylem water potential of Douglas-fir was consistently lower than that of redcedar, but this was not considered to be directly related to either atmospheric or soil water deficits, as discussed below.

5.2.5 Xylem water potential: implications for transient photosynthetic responses to light?

In this study mid-day xylem water potential ($\Psi_{x_{md}}$) was measured on each conifer sapling on the same day that it was being assessed, in situ in the forest understory, for transient photosynthetic responses to light. Results from this analysis showed that mid-day xylem water potentials ($\Psi_{x_{md}}$) of western redcedar and coastal Douglas-fir were never low enough to reduce the photochemical efficiency of photosystem II ($F_v/F_m$) below optimum, but that the mean value for redcedar ($-0.48 \pm 0.06$ MPa) was significantly less negative than that for Douglas-fir ($-1.17 \pm 0.08$ MPa) (Table 4.16). Given that even mild water stress can in some cases limit maximum conductance and photosynthesis, the more negative $\Psi_{x_{md}}$ of Douglas-fir may be of interest. In reference to transient photosynthetic responses to light, water stressed plants may require more time for stomatal opening and less time for stomatal
closing than non-water stressed plants (Willis and Balasubramaniam 1968; Davies and Kozlowski 1975), although faster stomatal opening times have also been reported (Barradas et al. 1994). Effects on photosynthetic induction can likewise be variable (Allen and Pearcy 2000; Tang and Liang 2000).

Mid-day water potential ($\Psi_{x_{md}}$) is a function of pre-dawn water potential and any imbalances between water uptake and loss that develop during the day as a result of transpirational water loss (the latter resulting from the interaction between stomatal conductance and leaf-to-air vapour pressure deficits) (Ritchie and Hinckley 1975). Evaporative demand (VPD) was low in this stand (Table 4.1) and in the range to be normally non-limiting to Douglas-fir (Running 1976; Waring and Franklin 1979; Lassoie 1982; Meinzer 1982; Johnson and Ferrell 1983; Livingston and Black 1987). Pre-dawn water potential, on the other hand, was not measured.

Pre-dawn water potential can reflect soil water potential, but in some cases it can also reflect plant hydraulic architecture and any night-time transpiration when present (Tyree 1988; Donovan et al. 2001). Thus, neither the possibility that soil water deficits occurred during the study period nor the possibility that there were important interspecific differences in hydraulic architecture and/or night-time transpiration can be excluded (none of these factors was directly measured). However, soil water deficits seem particularly unlikely as an explanation for the more negative mid-day xylem water potential of Douglas-fir, because during the study period this very moist and nutrient rich lower slope received sufficient rain (Table 3.1) that soil water deficits were improbable. That predawn water potential of Douglas-fir may not always reflect soil water potential has been demonstrated (Kelliher et al. 1984).

Night-time transpiration might have occurred, but its importance in reducing plant water potential in the forest understory is questionable. It is not known whether redcedar will exhibit night-time transpiration, but the stomata of Douglas-fir have sometimes been reported to remain open at night (e.g., Hodges 1967; Running 1976; Leverenz 1981). However, although maintaining stomata open at night would theoretically allow for night-time transpiration in Douglas-fir, given the high humidity in the understory even at mid-day (Table 4.1) the driving force for night-time transpiration must have been small. Furthermore, even where night-time transpiration is experimentally eliminated by bagging, the disequilibrium between soil and plant water potential is not always alleviated (Donovan et al. 2001).

Given presumably similar atmospheric and soil moisture deficits for the two species, there are at least two alternative explanations for lower mid-day xylem water potentials in Douglas-fir than in redcedar. Both explanations are related to the development of an unfavourable growth form of Douglas-fir in shade. That growth in shade acts to depress the xylem water potential of Douglas-fir is suggested by the study of Drew and Ferrell (1979), where it was shown that Douglas-fir seedlings grown under low light intensity had lower xylem water potential for any given level of leaf conductance than those grown under full light, regardless of soil moisture status (for a given soil water potential, xylem water potential was lower in shaded seedlings). Two possible explanations for this are: i) the development of an unfavourable shoot:root biomass ratio in shade (as proposed by Drew and Ferrell 1979); and ii) the development of an unfavourable internal hydraulic architecture in shade.
As in many other species, acclimation to shade in Douglas-fir often involves a shift in carbon allocation from root growth to shoot growth, resulting in an increase in the shoot:root biomass ratio of the plant (e.g., Brix 1970; Krueger and Ruth 1969; Chan et al. 1988; Minore 1988; but see Mailly and Kimmins 1997). If there were a stronger shift in the shoot:root ratio of Douglas-fir than in redcedar, Douglas-fir might have exhibited a lower capacity than redcedar to keep the transpirational demands of its crown in balance with the water available from its roots. Similarly, an unfavourable shoot:root ratio might also result if the production of new roots in Douglas-fir were limited by carbohydrate supply. Given a high shoot:root ratio, vapour pressure deficits which are normally non-limiting to Douglas-fir (i.e., those encountered in this study) could conceivably lead to mild plant water deficits.

The second possible explanation for the more negative water potential of Douglas-fir is related to potentially stronger shade-dependent changes in hydraulic conductance of the xylem in Douglas-fir than in redcedar. Although Douglas-fir in particular has not been studied in this capacity, some other woody species have been shown to develop an unfavourable hydraulic architecture when grown in shade (Sellin 1993; Protz et al. 2000; see also Ryan and Yoder 1997). This situation develops because under conditions of suppression, very slow growth results in the production of very narrow tracheids with low permeability to water and this, coupled with the low sapwood (conducting) area of shade-grown trees, leads to higher resistance to water transport in the xylem (Sellin 1993). Indeed, although virtually unexplored, the development of unfavourable hydraulic architecture might be an additional or alternative explanation (Ryan and Yoder 1997) to carbon starvation by light limitation per se (Givnish 1988) for control of the theoretical maximum sustainable height of tree species in shade.

Regardless of the cause, the issue arises as to what, if any, effect the lower xylem water potentials of Douglas-fir (−1.17 ± 0.08 MPa) might have had on the gas exchange responses observed for this species, and thus on the comparisons drawn with redcedar. Although this cannot be known with certainty, several factors would suggest that there was probably no important effect. First, stomatal conductance in Douglas-fir tends to show a threshold response to xylem water potential, i.e., conductance remains relatively unaffected by xylem water potential until a threshold water potential is reached. For the saplings of this species, this threshold typically does not occur until about −2.0 MPa (Running 1976; Tan et al. 1977). Although little studied, growth in shade would appear to lower the threshold water potential for stomatal closure to even more negative values (Drew and Ferrell 1979). Second, regression of xylem water potential on gas exchange parameters measured in situ in the field gave no indication that the gas exchange of Douglas-fir was in any way dependent on xylem water potential within the range explored. Third, during the construction of light-response curves, it was noted that the maximum stomatal conductance of Douglas-fir measured on excised shoots in the laboratory (0.093 ± 0.016 mol H₂O m⁻² s⁻¹), for which any water stress may be in large part removed, was not different from that measured in situ on attached shoots in the field (0.096 ± 0.009 mol H₂O m⁻² s⁻¹). For these reasons, the somewhat lower water potentials observed for

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19 It is likely that the anomalous results for shoot:root ratio in Douglas-fir observed in this short-term analysis of planted seedling performance (Mailly and Kimmins 1997) resulted from a failure to take into account initial seedling size.

20 More negative values tend to be observed for mature or old growth Douglas-fir (e.g., Running 1976) and less negative values for seedlings of Douglas-fir (e.g., Running 1976; Drew and Ferrell 1979; Johnson and Ferrell 1983; see also Brix 1979).
Douglas-fir (−1.17 ± 0.08 MPa) in comparison with redcedar (−0.48 ± 0.06 MPa) were considered to have had little, if any, effect on the comparative gas exchange kinetics of these species.

### 5.2.6 Summary and conclusions: transient photosynthetic responses to dynamic light conditions

The requirement for photosynthetic induction was shown to impose a considerable limitation on the efficiency with which very shade tolerant western redcedar and shade intolerant coastal Douglas-fir could use light for photosynthetic carbon gain, whether high light was administered continuously or intermittently in the form of lightflecks. For both species, differences between photosynthesis under transient conditions and that based on steady-state expectations were substantial. However, species did not clearly separate on the basis of photosynthetic efficiency in fluctuating light. Moreover, even where significant differences in photosynthetic induction characteristics were observed between species, these were generally judged to be relatively inconsequential when interpreted either in context of absolute carbon gain (the relevance of some induction parameters was questioned) and/or the measured sunfleck regime under red alder.

To summarize the major points, under non-steady-state conditions, redcedar was able to maintain induction state in shade longer than Douglas-fir (albeit not within a range generally relevant on days in which sunflecks would be important), but its induction times were either similar (in fluctuating light) or longer (in continuous high light) and its photosynthetic rates and absolute carbon gain were generally equivalent to Douglas-fir during induction under both constant and fluctuating light conditions (or slightly better as its \( A_{\text{max}} \) was approached). Given that redcedar and coastal Douglas-fir occupy opposing ends of the shade tolerance gradient in coastal British Columbia, the conclusion that species differences in transient photosynthetic responses to dynamic light conditions provide a strong mechanistic basis for explaining their opposing light ecologies is probably not warranted. Some of the observed differences might contribute the differential success or failure of these species in shade, but they do not appear strongly causal.

Multi-species studies, although sparsely available, suggest that the greatest differences in transient photosynthetic responses to light may occur between species differing in leaf lifespan (Kursar and Coley 1993) or habitat of origin (Ögren and Sundin 1996). Thus, the so-called stress tolerant conifers (with generally long-lived leaves) may respond with relatively minor variation as a group, which has in one case been described as long-lived, "slow-growing ‘sun’ plants" (Ögren and Sundin 1996). In a study in which perhaps the greatest diversity of species have been examined, three conifers of differing successional status tended to exhibit longer induction times than a variety of faster-growing deciduous angiosperm tree species and herbaceous shade plants, the slower induction response of the conifers being associated both with longer times for both Rubisco activation and stomatal opening (Ögren and Sundin 1996). Based on the response of the one conifer species examined with respect to lightfleck use efficiency (\textit{Pinus sylvestris} L.), it was further suggested that conifers might exhibit higher photosynthetic efficiency in rapidly fluctuating light than faster-growing sun plants and, if so, this may occur because the generally lower photosynthetic capacity (\( A_{\text{max}} \)) of the conifers tends to be compensated in part by proportionately greater electron transport capacity and thus higher post-illumination \( \text{CO}_2 \) fixation.
Patterns of transient photosynthetic responses to light similar to those suggested by Ögren and Sundin (1996) do appear to be evident across studies, despite the wide variety of growth and measurement conditions employed. For example, the relatively long induction times of conifers from mid- to high-latitudes ($T_{90}$ approx. 20–32 min; this study and Ögren and Sundin 1996) contrasts with the shorter induction times ($T_{90}$ approx. 5–14 min) of their understory associates such as herbs, ferns, and grasses (Pfistsch and Pearey 1989; Gildner and Larson 1992; Greenway and Lieffers 1997) and the typically shorter induction times ($T_{90}$ <20 min and often ≤10 min) of the shade tolerant and shade intolerant hardwoods that occur within their range (Küppers and Schneider 1993; Roden and Pearcy 1993c; Yehong et al. 1994; Han et al. 1999; Naumburg and Ellsworth 2000; Tang and Liang 2000). If relatively little variation in transient photosynthetic responses to light has evolved among the conifers then, presumably, some other factor(s) must exert a stronger selection pressure on the differential survival and growth of these species in shade.

5.3 STEADY-STATE PHOTOSYNTHESIS AND DARK RESPIRATION

Given that differences in transient photosynthesis between western redcedar and coastal Douglas-fir were generally not marked (as above), the question arises as to which other aspects of leaf-level gas exchange, if any, better differentiate these species, e.g., are differences in steady-state photosynthesis more or less marked for these species than those in transient photosynthesis? To address this issue, interspecific differences in photosynthetic parameters were explored from steady-state photosynthetic light-response ($A/PPFD$) curves and intercellular carbon dioxide-response ($A/C_i$) curves. Dark respiration rates were also examined to determine the relative importance of rates of foliar carbon loss versus rates of carbon gain through photosynthesis. Both species exhibited gas exchange responses typical of shade plants, such as relatively low maximum photosynthetic capacity ($A_{\text{max}}$), high apparent quantum yield ($\Phi_i$), low photosynthetic light compensation points (LCP), and low dark respiration rates ($R_d$).

Although species differences were observed, species were not well differentiated on the basis of parameters related to carbon gain ($A_{\text{max}}, \theta, \Phi_i$), but rather on the basis of carbon loss ($R_d$, and associated effects on LCP).

5.3.1 Photosynthetic capacity

It is generally expected that shade tolerant species will show lower maximum photosynthetic capacity ($A_{\text{max}}$) than more shade intolerant species when both are grown at similar light levels (e.g., Bazzaz 1979; Bazzaz and Carlson 1982) (shade tolerant species are expected to perform better given low light, and shade intolerant species better given high light). This pattern was not evident in this study, as $A_{\text{max}}$ of very shade tolerant western redcedar did not differ significantly from that of shade intolerant coastal Douglas-fir on either a leaf area ($A_{\text{max/area}}$) or leaf mass ($A_{\text{max/mass}}$) basis (Results, Section 4.3.1). In fact, there was a tendency in photosynthetic light-response ($A/PPFD$) curves for redcedar to have a higher $A_{\text{max/area}}$ than Douglas-fir. Although a poor correspondence between shade tolerance and $A_{\text{max/area}}$ might be expected wherever species differ in specific leaf area (see Reich et al. 1998b), a poor correspondence between shade tolerance and $A_{\text{max/mass}}$ has also previously been reported, both for other conifers (Reich et al. 1998b) and angiosperm tree species (Field 1988; Kitajima 1994; Zipperlen and Press 1996).

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21 Induction times from darkness are either similar or even longer (Pharis et al. 1967; Pepin and Livingston 1997).
That the tendency for higher $A_{\text{max/area}}$ in redcedar was real was suggested by statistical significance when $A_{\text{max/area}}$ was alternatively derived from the asymptote of photosynthetic induction curves (Results, Section 4.2.1.2), rather than from steady-state light-response curves (perhaps because sample size was balanced for the former, but not for the latter). However, the tendency for higher $A_{\text{max}}$ in redcedar was not evident when $A_{\text{max}}$ was expressed on a leaf mass basis ($A_{\text{max/mass}}$), thereby suggesting that both species had similar potentials for carbon gain per unit carbon invested in leaves (although this potential should also be amortized over leaf lifespan). Only area-based $A_{\text{max}}$ results, which are of primary interest where light use efficiency is of concern, are discussed further here (light is received on a unit leaf area basis).

Inspection of steady-state $A/C_i$ responses (Figure 4.14) indicated that the tendency towards higher $A_{\text{max/area}}$ in redcedar was not simply associated with the tendency for this species to have higher stomatal conductance ($g_{sH} \rightarrow$ Table 4.4; Wong et al. 1979). When stomatal limitations to photosynthesis were removed (i.e., when $C_i$ was made equivalent to the ambient reference CO$_2$ concentration of 360 μmol·mol$^{-1}$) the tendency for higher $A_{\text{max}}$ in redcedar remained (Figure 4.14). Thus, biochemically based differences in $A_{\text{max}}$ were involved. Redcedar did not however appear to have a higher maximum amount (activity) of Rubisco, but rather a higher electron transport capacity (von Caemmerer and Farquhar 1981), a result supported by the significantly higher $T'/i$ values observed for redcedar from fluorescence analysis (Table 4.16) (Krause and Weis 1991). Although potentially important, this difference in electron transport capacity was, however, insufficient to result in significant differences between species in the relative or absolute amount of net post-illumination CO$_2$ fixation in response to lightflecks (Tables 4.11 and 4.12).

The generality of the $A_{\text{max}}$ results for redcedar and Douglas-fir are somewhat uncertain, as these species have not been compared together under common conditions in other studies. Individually, few $A_{\text{max}}$ reports exist for redcedar, while more are available for Douglas-fir. The lowest growth light environment examined for redcedar appears to be 400 μmol·m$^{-2}$·s$^{-1}$ or approximately 20% full light for seedlings reared in a growth chamber (Weger et al. 1993). In that study, $A_{\text{max}}$ values were roughly similar to those observed here (6.0 μmol CO$_2$·m$^{-2}$·s$^{-1}$). The $A_{\text{max}}$ values for Douglas-fir in this study (5.0 μmol CO$_2$·m$^{-2}$·s$^{-1}$) were also roughly similar to those reported for this species in field studies under natural shade within a crown (Leverenz 1981) and under relatively low growth light conditions in controlled environment studies (e.g., Zavitkovski and Ferrell 1970; Sørensen and Ferrell 1973). The values of $A_{\text{max}}$ observed may therefore be generally representative of these species when grown in shade.

### 5.3.2 Convexity and quantum yield

Between the light saturated region and the photosynthetic light compensation point on the steady-state photosynthetic light-response ($A/PPFD$) curve, two often overlooked parameters can in some cases contribute to interspecific differences in carbon gain and be useful in distinguishing between species. The first is apparent convexity and the second is the apparent quantum yield.

At intermediate light levels occurring below light saturation but above the quantum yield (linear) region of the photosynthetic light-response, photosynthetic efficiency of intact shoots is determined by apparent convexity ($\theta$),
the rate of bending of the photosynthetic light-response curve towards light saturation (Leverenz 1987). The higher the convexity, the more efficient photosynthesis is in the intermediate light range. Shade leaves tend to show higher convexity than sun leaves of the same species (Ogren 1993), and thus it might also be expected that under similar conditions shade tolerant species would show higher convexity than shade intolerant species. Comparisons of the convexity of shade tolerant and shade intolerant species are however sparsely available and, at least for shade acclimated foliage of tropical rainforest tree species (Riddoch et al. 1991) and needle-leaved conifer species (Leverenz 1988, 1995), no clear relationship between shade tolerance and convexity is evident. In this study, convexity did not differ significantly between western redcedar and coastal Douglas-fir but the result was marginal (p=0.071), with mean apparent convexity tending to be lower for redcedar (0.47 ± 0.09) than for Douglas-fir (0.74 ± 0.10). Although not known, it may be that the tightly overlapping leaf arrangement of redcedar (Parker and Johnson 1987) increases the gradient of light within individual leaves and leads to a more gradual pattern of saturation of all photosynthetic units (Leverenz and Hinckley 1990).

At lower light levels still, photosynthetic efficiency under steady-state conditions is characterized by the apparent quantum yield (Φa), the slope of the linear region of the photosynthetic light response curve for intact leaves or shoots. Unlike the quantum yield based on absorbed light (Φa) which is invariant between species in the absence of photoinhibition (Ehleringer and Björkman 1977), the quantum yield based on incident light (apparent quantum yield, Φj) can vary among species. For conifer shoots, Φj is a function not only of Φa, but also leaf absorptance and shoot structure (Leverenz 1996). Where species differ, it is generally expected that shade tolerant species will have higher apparent quantum yields than shade intolerant species (Bazzaz 1979).

Interspecific differences in apparent quantum yield were potentially important in this study, because diffuse light in the understory (10–30 μmol·m⁻²·s⁻¹ on clear days) was within the quantum yield region of the photosynthetic response of both species (Figure 4.12). However, apparent quantum yields were very similar for redcedar (0.056 ± 0.003 μmol CO₂·μmol incident photons⁻¹) and Douglas-fir (0.057 ± 0.009 μmol CO₂·μmol incident photons⁻¹). Other studies with forest tree species have likewise not found the expected relationship between shade tolerance and apparent quantum yield (e.g., Loach 1967; Jurik 1986; Ramos and Grace 1990; Riddoch et al. 1991; Leverenz 1995; Zipperlen and Press 1996).

5.3.3 Light compensation point and dark respiration

In contrast to the general lack of expected differences between western redcedar and coastal Douglas-fir on the basis of steady-state gas exchange parameters related to carbon gain (Amax, apparent convexity, apparent quantum yield), marked and significant differences were observed between species in both light compensation point (light level at which net CO₂ exchange is zero) and dark respiration rate. These differences remained irrespective of whether net CO₂ exchange rates were computed on a leaf area or a leaf mass basis. Species differences in light compensation points resulted from differences in dark respiration rates because apparent quantum yields did not differ.
In agreement with the generalization that in shaded environments shade tolerant species exhibit lower light compensation points than more shade intolerant species (Daniel et al. 1979; Björkman 1981), the light compensation point of redcedar (6.4 μmol photons m\(^{-2}\) s\(^{-1}\)) was approximately half that of Douglas-fir (12.6 μmol photons m\(^{-2}\) s\(^{-1}\)). On clear days, diffuse light in the understory (ca. 10–30 μmol photons m\(^{-2}\) s\(^{-1}\)) was generally above the foliar light compensation point of both species, and thus sunflecks were not required for the foliage of either species to maintain a positive carbon balance. However, this was not the case on overcast days when absolute light levels dropped to as low as 3–5 μmol photons m\(^{-2}\) s\(^{-1}\). On cloudy days, which are not uncommon to the area (Table 3.2; Waring and Franklin 1979; Klinka and Krajina 1986), the lower foliar light compensation point of redcedar would put it at an increasing advantage over Douglas-fir. No other literature reports of foliar light compensation points are available for shade phenotypes of redcedar, but in general agreement these results, light compensation points of 12–16 μmol photons m\(^{-2}\) s\(^{-1}\) have been reported for Douglas-fir grown at 4.5–8% full light (Krueger and Ferrell 1965; Leverenz 1995).

Given that conifer leaves that cease to be self-supporting may be shed (Reich et al. 1995), foliage retention in shade might be poorer for species with higher light compensation points. Consistent with previous observations (Cole and Newton 1986), in this study it did appear that Douglas-fir was not able to retain foliage well in shade (see Materials and Methods). If leaf lifespan in shade were shorter in Douglas-fir than in redcedar, then if leaf-level photosynthetic rates of Douglas-fir (roughly similar to those for redcedar, on both a leaf area and mass basis) were amortized over a shorter leaf lifespan, Douglas-fir would exhibit lower overall return in absolute carbon gain per unit carbon invested in leaves. Interspecific differences in leaf lifespan could conceivably lead to large differences in whole-plant carbon balance even where leaf-level photosynthetic rates are similar and, as such, should be fully investigated in future studies.

Dark respiration rates (base 22 °C) were also two-fold lower for western redcedar than for coastal Douglas-fir, regardless of whether expressed on a leaf area (R\(_{d,area}\)) or leaf mass (R\(_{d,mass}\)) basis. This supports the assertion that in shaded environments shade tolerant species have lower dark respiration rates than more shade intolerant species (Björkman 1981; Givnish 1988), and furthermore suggests that for tree species of mid-latitude forests these differences may in some cases be relatively large. Other reports of foliar respiration rates were not located for shade grown western redcedar (cf. 0.31 μmol CO\(_2\) m\(^{-2}\) s\(^{-1}\) in this study). However, the respiration rate observed here for mature coastal Douglas-fir foliage (0.63 μmol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) was similar to the 0.6–0.8 μmol CO\(_2\) m\(^{-2}\) s\(^{-1}\) range reported in other studies with shade-grown Douglas-fir (Leverenz 1981; Leverenz 1995).

Because dark respiration contributes proportionately more to total daily leaf carbon balance as light intensity decreases (e.g., Hodges and Scott 1968; Field 1988; Lehto and Grace 1994), the observed difference in dark respiration rate between redcedar and Douglas-fir would become increasingly important as light intensity decreases. This can be demonstrated by comparing between species the ratio of dark respiration to maximum achievable steady-state rates of assimilation as light intensity decreases. For example, as light intensity decreased from saturating (470 μmol m\(^{-2}\) s\(^{-1}\)) to the background diffuse level of 30 μmol m\(^{-2}\) s\(^{-1}\), this ratio increased from 0.06 to 0.24 in redcedar and from 0.14 to 0.53 in Douglas-fir. Indeed, dark respiration had a strong effect on the
photosynthetic light compensation point of both species, and the resulting interspecific differences in light compensation point were shown to be in the range to be ecologically important on cloudy days.

5.3.4 Summary and conclusions: steady-state photosynthesis and dark respiration

Steady-state photosynthetic responses to light did not clearly characterize western redcedar and coastal Douglas-fir as shade tolerant and shade intolerant species, respectively. In comparison with Douglas-fir, redcedar exhibited tendencies towards higher maximum photosynthetic capacity (leaf area basis) and lower apparent convexity, and did not differ significantly from Douglas-fir on the basis of apparent quantum yield. Conversely, a 'typical' shade tolerant species would be expected to show lower $A_{\text{max}}$, higher apparent convexity, and higher apparent quantum yield than more shade intolerant species (Bazzaz 1979; Björkman 1981; Bazzaz and Carlson 1982). However, species differed in attributes of steady-state gas exchange more closely related to carbon loss than to carbon gain (dark respiration, light compensation point), and these differences were consistent with the contrasting shade tolerance of these species.

Overall then, foliar dark respiration rates (and associated effects on light compensation points) appeared to be much more important in characterizing the differing shade tolerance of western redcedar and coastal Douglas-fir than any measure of photosynthetic performance under either transient or steady-state conditions in either dynamic or constant light. The potential importance of foliar dark respiration rates in distinguishing between species of contrasting shade tolerance is considered as part of the discussion below (Section 5.4).

5.4 RELATIONSHIP OF RESULTS TO ECOLOGICAL THEORY

Ultimately, the goal of physiological ecology is to reveal the mechanisms that underlie species differences in distribution and habitat-specific competitive ability (Givnish 1988). Thus, as emphasized by Pearcy et al. (1989), regardless of the space- or time-scale at which ecophysiology or physiological ecology studies are carried out, researchers "must be cognizant both of the underlying mechanisms as well as the consequences to ecological and evolutionary processes". In this final section, the results from this study are interpreted in this context. Three issues are addressed: i) the extent to which the physiological characteristics observed for western redcedar and coastal Douglas-fir are consistent with their shade tolerance and light ecologies; ii) possible explanations for the presence and presumed persistence, 13-years after planting, of the putative shade intolerant Douglas-fir under closed canopy of red alder; and iii) the likely course of future stand development.

5.4.1 Integration of results with ecological theory

When evaluated on the basis of absolute carbon gain, the capacity for efficient transient photosynthesis under dynamic light conditions was shown to be somewhat greater for western redcedar than for coastal Douglas-fir. However, these differences were not marked and appeared generally insufficient for providing a mechanistic basis for explaining the contrasting shade tolerance of these species. Further, when these differences were considered in the ecological context of the measured sunfleck regime under alder on sunny days in summer, species differences in
performance were expected to be even less. Although some minor differences in both transient and steady-state photosynthesis were noted, by far the most dramatic difference between species was in terms of dark respiration rate and its associated effect on the light compensation point. It therefore appears that, relative to low respiration rates (minimization of carbon loss), high photosynthetic light use efficiency (maximization of carbon gain) may have little overall impact on the success or failure of these species in shade. A poor or weak relationship between the successional status of tree species and their photosynthetic efficiencies in shade has also been demonstrated by others (Krueger and Ruth 1969; Bazzaz and Carlson 1982; Ramos and Grace 1990; Lehto and Grace 1994; Zipperlen and Press 1996).

A better correspondence between shade tolerance and dark respiration (carbon loss) than between shade tolerance and net photosynthesis (carbon gain) may be better understood if it is considered that among different species (cf. individuals within a given species) shade tolerance may really only be closely linked to survival and that it invokes no requirement for fast low light growth. Although this hypothesis was put forward years ago (Baker 1945; Shirley 1945; Grime and Jeffrey 1965) evidence one way or the other has only recently come to light. The tradeoff between forest tree species of contrasting successional status, if there is one, appears to be one between fast high light growth and good low light survivorship, rather than one between fast high light growth and fast low light growth as has generally been assumed (Pacala et al. 1994, 1996; Kobe et al. 1995; and compare Kobe and Coates 1997 with Wright et al. 1998). Such a tradeoff implies that irrespective of any plasticity in the physiological and morphological traits of individual species in relation to light, there are inherent (genotypic) trait(s) favouring either rapid high light growth or good low light survivorship, and that these traits are not compatible with the converse condition. Furthermore, not only is shade tolerance not closely associated with fast growth at low light, but perhaps most frequently it is observed that shade tolerant species actually grow slower at low light than more shade intolerant species (on the basis of whole-plant biomass growth, examples include Loach 1970; Ramos and Grace 1990; Latham 1992; Walters et al. 1993a; Kitajima 1994; Watling et al. 1997; Reich et al. 1998b; Poorter 1999; Walters and Reich 1999). In other words, shade intolerant species tend to maintain higher growth potential than shade tolerant species in both sun and shade.

Dark respiration rate may provide a mechanistic basis for these reported successional patterns, viz, both the tradeoff between fast high light growth and good low light survivorship and the tendency for shade tolerant species to exhibit slower growth rates at low light than more shade intolerant species. This is because there may be an inherent evolutionary constraint that links fast growth with high dark respiration rates needed for high metabolic activity (e.g., Poorter et al. 1990; Reich et al. 1998b; Walters and Reich 1999). Thus, high respiration rates would permit the observed fast growth of shade intolerant species in both sun and shade, but restrict their survival in deep shade. Conversely, low respiration rates may restrict the growth of shade tolerant species in both sun and shade, but with the tradeoff of higher survivorship at low light. This does often appear to be the case. Under favourable conditions in the open (at full sun, or near full sun irradiance), shade intolerant tree species exhibit fast growth in association with high dark respiration rates, whereas shade tolerant tree species exhibit slower growth in association with lower dark respiration rates (e.g., Grime 1965; Reich et al. 1998a). As indicated, it now also appears that the higher growth rates of shade intolerant species in sun also tend to be carried over into deeply shaded environments,
where interspecific differences in growth persist even on a total biomass (whole-plant) basis (e.g., Loach 1970; Latham 1992; Ramos and Grace 1990; Walters et al. 1993a; Kitajima 1994; Watling et al. 1997; Reich et al. 1998b; Poorter 1999; Walters and Reich 1999). This fast growth of shade intolerant species at low light is, however, also accompanied by high mortality, such that shade intolerant species which grow fast in shade also tend to die fast in shade (e.g., Shirley 1945; Bourdeau and Laverick 1958; Kitajima 1994; Pacala et al. 1996; see also Zipperlen and Press 1996). Although little studied, high dark respiration rates appear to accompany the fast growth and high rate of mortality of shade intolerant species in shade (Loach 1967; Reich et al. 1998b; see also Walters and Reich 1999). That inherent differences between species in dark respiration rate may be much more important than any acclimation in this trait to light has recently been shown for a variety of tree species (Lusk and Reich 2000).

In further support of the hypothesis that dark respiration rates may exert strong control over the sun-shade performance of species of contrasting successional status, some evidence has also been accumulating that physiological plasticity in relation to light is frequently greater in shade intolerant species than in more shade tolerant species (e.g., Bazzaz 1979; Bazzaz and Carlson 198222; Chazdon 1992; Tinoco-Ojanguren and Pearcy 1992; see also Langenheim et al. 1984), except perhaps in very low light environments where low light together with higher respiration rates limit its expression in intolerant species (see Walters and Reich 1999). If generally true, this has similarly been suggested to have arisen because high maintenance respiration rates are compatible with the high enzyme turnover rates (high metabolic cost) prerequisite for physiological acclimation (Penning de Vries 1975), whereas low respiration rates (typical of shade tolerant species as necessary for persistence at low light) are not.

Thus, the literature when synthesized appears to i) support the early suggestion of Baker (1945), Shirley (1945), and Grime and Jeffrey (1965) that shade tolerance should be considered only as the capacity of a species to persist (survive) for long periods under low light, and should invoke no requirement for fast low light growth; ii) physiological plasticity tends to be lower for shade tolerant than shade intolerant species; and iii) evolutionary constraints on dark respiration may underlie the explanations for both i) and ii).

Notwithstanding the above discussion, the literature also shows that interspecific differences in shade tolerance (in the post-establishment stage) are clearly not so simple as to be explained solely on the basis of dark respiration rates. Although there is a clear tendency for more shade tolerant tree species to exhibit lower foliar dark respiration rates than more shade intolerant tree species when grown under similar levels of shade (e.g., Loach 1967; Szaniawski and Wierzbicki 1978; Jurik 1986; Riddoch et al. 1991; Letho and Grace 1994; Leverenz 1995; Reich et al. 1998b; Walters and Reich 1999; Lusk and Reich 2000), some exceptions have nonetheless been reported for tree species specifically of mid- and high-latitude forests (e.g., Hodges and Scott 1968; Krueger and Ruth 1969; Bazzaz and Carlson 1982; Leverenz 1995; Han et al. 1999; Lusk and Reich 2000). Although species rankings for dark respiration rate can sometimes differ depending on whether rates are expressed on an area or mass basis (e.g., Reich et al. 1998b), as shown in this study this is not always the case. Thus, factors other than foliar dark respiration rates may also be important. Owing to the multiplicity of factors which scale with increasing plant size (e.g., Givnish 1988), this is probably particularly so for tree species.

22 It should be cautioned that the early successional group considered by Bazzaz and Carlson (1982) included no tree species, which is in contrast to the mid- and late-successional groups with which comparisons were made.
Dark respiration rates measured in this study presumably represent only maintenance respiration of leaves (Sprugel et al. 1995). However, whole-plant carbon balance will be dependent on all sources of respiration collectively, and thus species differences in maintenance respiration of non-photosynthetic tissue may also be important, as may differences in growth respiration (Givnish 1988, e.g., Lehto and Grace 1994). Other factors that might also be important to whole-plant carbon balance (although not necessarily independent of respiration rates) may include carbon allocation patterns (particularly the proportional amount allocated to leaves, storage, and to defensive compounds and structures); the arrangement of leaf area into an effective crown (for light interception); leaf lifespan (leaf longevity and turnover); developmental and reproductive processes; and seasonal aspects of performance (Horn 1971; Björkman 1981; Coley 1988; Givnish 1988; Körner 1991).

Overall then, it seems increasingly evident that individual morphological and/or physiological characters are probably not useful as surrogate measures of shade tolerance. No single attribute appears consistently related to shade tolerance given the data available. Even though patterns may be obscured to some extent by different light level(s), environment(s), or plant size(s) selected for comparison(s), the evidence in sum nonetheless suggests that commonality of traits traditionally associated with shade tolerant species (those conventionally considered as adaptive to low light conditions) have been overemphasized, and that the relative success or failure of species in shade may be better described using species-specific suites of traits or histograms of plant characteristics (sensu Körner 1991). Data from the present study support this suggestion. However, of all the physiological traits measured for western redcedar and coastal Douglas-fir, dark respiration rate (and thus also LCP) provided by far the most striking and consistent contrast between the two species.

In a recent comprehensive analysis of a diversity of tree species, Walters and Reich (1999) confirmed that there is little support for the common assumption that shade tolerant species have traits which maximize their net rate of carbon capture in shade. Rather, instead of maximizing photosynthesis and growth rates in low light, shade tolerant evergreen species minimized biomass loss through low respiration rates and long leaf lifespans. Thus, although fast growth at low light does not appear prerequisite to shade tolerance, what is probably important in terms of growth is net growth, in which biomass losses to all agents are taken into account (Poorter 1999; Walters and Reich 1999). Because high growth rates are usually associated with high respiration rates, high tissue turnover rates, decreased carbohydrate storage, and in some cases lower allocation to leaves and/or greater herbivory and/or mechanical damage, in light-limited environments shade intolerant species with typically high growth rates tend to exhibit lower overall net growth (Walters and Reich 1999; also King 1991, 1994) and survival (Shirley 1945; Bourdeau and Laverick 1958; Kitajima 1994; Pacala et al. 1996; see also Zipperlen and Press 1996).

5.4.2 The persistence of Douglas-fir saplings under closed canopy red alder

The presence and presumed persistence of saplings of coastal Douglas-fir at very low light levels (3–4% full light) under closed canopy red alder some 13 years after stand establishment gives rise to the question as to what has allowed this putative shade intolerant species to survive to such a size and age under highly suppressed conditions. Although it must be acknowledged that in this study past light conditions are not known and at one time
were probably much higher (following planting), light conditions must nonetheless have been very low for quite some time. The presence of suppressed Douglas-fir saplings under red alder in this study is not an anomalous occurrence, because Newton (1978) also observed some suppressed Douglas-fir on a coastal site dominated by red alder, and in that case the site was even older (25 years) than that examined here (13 years).

Although not known, it seems likely that the persistence of Douglas-fir under red alder (despite relatively poor form and vigour) may be attributed to a relatively high amount of photosynthetic carbon gain outside of the normal growing-season. Understory light availability increases markedly in the leafless period of deciduous canopies (Lassoie et al. 1983; Oberhuber and Bauer 1991; Constabel and Lieffers 1996; Skillman et al. 1996; Man and Lieffers 1997), and this may provide Douglas-fir with a photosynthetic 'window-of-opportunity' for carbon gain which is asynchronous with that of red alder. Although higher light levels can only be used for photosynthesis if temperatures remain favourable, in the mild coastal environment of the Pacific Northwest this is likely to be so.

It has been well demonstrated that in winter-mild climates open-grown or dominant/co-dominant conifers may achieve positive net photosynthesis and dry weight increase in seasons other than summer (e.g., Hagem 1962; Pollard and Waring 1968; van den Driessche 1968; Neilson et al. 1972; Fry and Phillips 1977; Bradbury and Malcolm 1978). In the Pacific coastal region, western redcedar (Hawkins et al. 1995; see also Weger et al. 1993) and coastal Douglas-fir (Helms 1964, 1965; van den Driessche 1968; Brix 1971; Hawkins et al. 1995) are no exceptions. In fact, from simulations it has been estimated that on moist coastal sites in the Pacific Northwest, 37% the annual photosynthesis of exposed coastal Douglas-fir foliage occurs outside of the normal growing-season, between October and May (Emmingham and Waring 1977). In contrast, in the same climatic region suppressed Douglas-fir in the understory of coniferous canopy (under continuous shade) tends to exhibit zero or negative net CO₂ assimilation during this time (Helms 1965).

However, although open-grown conifers may carry-out considerable photosynthesis in winter, the situation might be somewhat different for conifers under deciduous canopies which undergo only seasonal exposure to high light. For these individuals, the potential to use seasonally high light levels is dependent to some degree on the extent to which shade acclimated foliage expanded under closed canopy conditions can undergo post-expansion (physiological) acclimation in response to higher light levels and lower temperatures when the overstory is leafless (e.g., Oberhuber and Bauer 1991; Skillman et al. 1996; Landhäusser et al. 1997). For the conifers examined in this study, seasonal measurements of leaf pigments and chlorophyll fluorescence ($F_{v}/F_{m}$) revealed marked physiological acclimation in the xanthophyll cycle pigment pool size (which has an important role in protection from light stress), and indicated that Douglas-fir was better able than redcedar to maintain its photosynthetic potential (as assayed by $F_{v}/F_{m}$) under the higher light and lower temperature conditions during winter (unpublished data). For Douglas-fir it would therefore appear that a substantial amount of photosynthesis may be possible during the leafless period of red alder. Appreciable rates of carbon gain in the leafless period of deciduous overstories (so long as temperatures are not too low) have been demonstrated for some understory evergreen conifers (Lassoie et al. 1983; Man and Lieffers 1997) and evergreen herbs (e.g., Skillman et al. 1996).
Irrespective of the type of canopy cover under which Douglas-fir may be grown, mild summer temperatures probably also contribute to the survival of coastal Douglas-fir in the understory. This is because cooler versus warmer temperatures reduce dark respiration rates much more than photosynthesis (for Douglas-fir, see Krueger and Ferrell 1965; Brix 1967), resulting in a demonstrated increase in the shade tolerance of this species as assayed by both survival and growth (Minore 1988\(^{23}\); see also Sørensen and Ferrell 1973). Thus, in reference to temperature, what is probably important for Douglas-fir is the “special balance of temperatures” (sensu Gholz et al. 1976) characteristic of the mild coastal climate, i.e., mild summer temperatures which limit (to a moderate level) respiration rates and light compensation points in summer, and mild winter temperatures which permit considerable net photosynthesis outside of the normal growing-season. Such temperature-control of physiological processes was previously proposed to explain trends in maximum community leaf area as related to forest site productivity (Gholz et al. 1976; Waring et al. 1978).

### 5.4.3 Future stand development

Although live saplings of both redcedar and Douglas-fir can be observed at relatively low levels of current light availability (ca. \(\leq 5\%\) full light) in the understory (this study and Carter and Klinka 1992; Wright et al. 1998), the light histories of these individuals are not known and, consequently, it is unclear how long or to what size these individuals may survive under continuously low light conditions. Relatively long-term (5–15 year) observations from permanent sample plots do however suggest that in the Pacific Northwest, Douglas-fir will exhibit markedly higher annual mortality rates under closed canopy coniferous forest than western redcedar (Spies et al. 1990). Likewise, retrospective studies suggest that similar interspecific differences in mortality can be expected beneath red alder (Stubblefield and Oliver 1978). Other reports for only Douglas-fir (without comparison to redcedar) suggest that mortality of Douglas-fir is also likely to be very high when grown with high initial densities of alder, and that adequate stocking of Douglas-fir can only be expected given low initial densities of alder or where the alder component is for the most part removed at an early stage (Miller and Murray 1978).

Thus, despite an apparently high potential for coastal Douglas-fir saplings to exhibit compensatory carbon gain during the leafless period of red alder (as above, Section 5.4.2), it is nonetheless likely that the Douglas-fir saplings examined in this study are destined to die. Although Douglas-fir may increase its potential for light interception in shade by sharply increasing specific leaf area (Mailly and Kimmins 1997) and adopting a planar shoot form (Leverenz and Hinckley 1990), such morphological adjustments are likely to be insufficient for survival given the physiological constraint of a high foliar dark respiration rate. In contrast to redcedar, when grown in deep shade Douglas-fir exhibits poor overall vigour (Carter and Klinka 1992) and maintains only a short, sparse crown of low apparent leaf area (whole-plant photosynthetic potential) (Cole and Newton 1986, 1987; Hermann and Lavender 1990) which in this study appeared to be caused in part by poor foliage retention in shade (see the vigour criteria described for shade-grown coastal Douglas-fir in Carter and Klinka 1992)\(^{24}\) presumably as a result of high foliar

\^{23} \text{The light x temperature treatments were not replicated in the study of Minore (1988).}

\^{24} \text{Low whole-plant leaf area may also be related to a proportionately low allocation of carbon to leaves (King 1991). The analysis of plant proportions in newly planted seedlings suggests that coastal Douglas-fir has relatively lower allocation to leaves and/or shorter leaf lifespan than other more shade tolerant conifers (Mailly and Kimmins 1997).}
dark respiration rates. Leaf area duration is in general very important to the annual CO₂ uptake for evergreen conifers (Schulze et al. 1977), and interspecific differences in the ability to maintain leaf area in shade may be a major distinguishing factor among shade tolerant and shade intolerant tree species (King 1991, 1994; Walters and Reich 1999). Poor foliage retention in shade might be a particularly critical factor to the persistence of Douglas-fir under red alder, because it limits not only carbon gain in summer, but also the amount of compensatory carbon gain achievable in the leafless period of the canopy. Douglas-fir also requires current photosynthate for new root growth (van den Driessche 1987), and in spring this must be provided by older needle age classes because current-year foliage does not expand until later. Given that the negative effects of poor foliage retention (and/or low leaf allocation) in saplings is likely to increase with time, and that whole-plant light requirements may also increase in a time-dependent manner with increasing plant size, Douglas-fir may soon reach its maximum sustainable height in shade (Givnish 1988).
CHAPTER 6
SUMMARY AND CONCLUSIONS

Under dynamic light conditions, the requirement for photosynthetic induction was shown to impose a considerable limitation on the carbon gain of both very shade tolerant western redcedar and shade intolerant coastal Douglas-fir. Species differences in transient photosynthetic responses to light were observed, but were not always consistent with expectations for species of contrasting shade tolerance. Moreover, those differences which were observed were generally less important when considered either on the basis of absolute carbon gain rather than in terms of various relative parameters conventionally used to gauge the photosynthetic efficiency of sunfleck utilization and/or in context of the actual (measured) sunfleck regime under red alder. Measurements of photosynthesis under steady-state conditions (maximum photosynthetic capacity, apparent convexity, apparent quantum yield) likewise did not reveal differences between species consistent with their contrasting shade tolerance. Differences in dark respiration rates and thus also light compensation were, however, marked and in the direction expected, approximately two-fold lower for western redcedar than for coastal Douglas-fir.

The study suggests that the commonality of physiological traits associated with shade tolerant species has been overemphasized, and that the suite of traits conferring tolerance or intolerance to shade may need to be defined on a species-specific basis and possibly also in context of the light environment within the particular forest type in question. Notwithstanding, the literature suggests that phylogenetic constraints on dark respiration rates may have been a particularly important determinant in the development of interspecific differences in shade tolerance among forest tree species. In agreement, differences in carbon loss through dark respiration were far more useful in explaining the contrasting shade tolerance of western redcedar and coastal Douglas-fir than were differences in either the efficiency of sunfleck utilization or steady-state photosynthesis at high and intermediate light levels.

To more fully understand the physiological ecology of these species in the context of alder-conifer mixedwood systems, more detailed examinations of light conditions under red alder and the photosynthetic performance of redcedar and Douglas-fir should be conducted throughout the year. Some further characterization of the light regime under red alder in summer may be warranted, such as a further partitioning of the distribution of sunflecks with the ≤ 30 s category and characterization of light conditions under variable weather conditions. Likewise, some further assessment of the photosynthetic efficiency of western redcedar and Douglas-fir in fluctuating light may be needed, in particular the response to sunflecks of very short duration (<<30 s) and a comparison of the photosynthesis and induction states of the two species after extended exposures to fluctuating light (longer lightfleck series). Given such further characterization of light environment and sapling physiology, the effects of light regime on the daily carbon gain of understory saplings could be modelled. Models of dynamic photosynthesis have greatly improved in recent years (Kirschbaum et al. 1998; Stegemann et al. 1999) and may...
represent the best means of studying complex interactions between the dynamics of the light environment and those of enzyme activation and stomatal opening which determine photosynthetic induction state and carbon gain in an understory environment (Naumburg et al. 2001). Finally, an assessment of conifer performance in response to the seasonal changes in light environment under red alder would be useful, as it may be that coastal Douglas-fir has survived under alder for as long as it has owing in part to compensatory photosynthetic carbon gain during the leafless period of the deciduous canopy.

The principle limitation of this study may be that only one site and one seed-source each of western redcedar and coastal Douglas-fir was examined. As Chazdon (1988) points out, although detailed studies carried out in the field with plants growing under natural light conditions are the most ideal for studying transient photosynthetic responses to light of understory plants, such studies are by nature frequently limited by the inability to generalize the results to other situations. Site quality generally has little impact on tree performance in deep shade (Reed et al. 1983; Lehto and Grace 1994; Pacala et al. 1994; Canham et al. 1996; Pacala et al. 1996; Walters and Reich 1996; Kayahara 2000), but if either seed source in this study was an anomalous representation of the species, then the conclusions drawn with respect to the comparative physiology of the two species may not be widely applicable. However, the use of local seed sources of both species was considered to reduce the potential for such error. The greatest variation in redcedar appears to be associated with elevation and other aspects of climate (Cherry 1995), and genetic variation in Douglas-fir is likewise largely associated with topographical and geographical variation (Hermann and Lavender 1990). Given that red alder occupies only a relatively narrow belt at low elevations along the Pacific coast (elevations <750 m and within 200 km of the coast; Harrington 1990), the local conifer seed sources studied were likely representative of those that would be found naturally in association with red alder.
LITERATURE CITED


APPENDICES
APPENDIX I

CR-10 PROGRAM FOR SUNFLECK MAXIMUM PPFD AND FREQUENCY DISTRIBUTIONS

* 1 Table 1 Programs
  01: 2 Sec. Execution Interval

  01: P2 Volt (DIFF)
  01: 06 Reps
  02: 24 250 mV 60 Hz rejection range
  03: 01 IN Chan
  04: 1 Loc [:"PPFD" #1]
  05: 1 Mult
  06: 0 Offset

  02: P53 Scaling Array (A*loc +B)
  01: 01 Start Loc [:"PPFD" #1]
  02: 15.43 A1 (Multiplier #1)
  03: 0 B1 (Offset #1)
  04: 15.88 A2 (Multiplier #2)
  05: 0 B2 (Offset #2)
  06: 16.24 A3 (Multiplier #3)
  07: 0 B3 (Offset #3)
  08: 16.97 A4 (Multiplier #4)
  09: 0 B4 (Offset #4)

  03: P53 Scaling Array (A*loc +B)
  01: 05 Start Loc [:"PPFD" #5]
  02: 15.77 A1 (Multiplier #5)
  03: 0 B1 (Offset #5)
  04: 16.23 A2 (Multiplier #6)
  05: 0 B2 (Offset #6)
  06: 1 A3
  07: 0 B3
  08: 1 A4
  09: 0 B4

The value one must be entered in the following Location 57 to weight the input data of the histogram.

  04: P30 Z=F
  01: 01 F
  02: 00 Exponent of 10
  03: 57 Z Loc : [W_Value]

  05: P10 Battery Voltage
  01: 55 Loc [:BatVolt ]

  06: P87 Beginning of Loop
  01: 0 Delay

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25 The assistance of Y. Cardinal (Campbell Scientific, Edmonton, Alta.) in the writing of this program is gratefully acknowledged.

113
02: 6    Loop Count

07: P89  If X<=>F
01: 1--  X Loc "PPFD" #1
02: 03   >=
03: 40   F
04: 30   Then Do

08: P89  If X<=>F
01: 25--  X Loc Flag#1
02: 01   =
03: 0    F
04: 30   Then Do

09: P30  Z=F
01: 1    F
02: 0    Exponent of 10
03: 25--  Z Loc [:Flag#1 ]

10: P30  Z=F
01: 0    F
02: 0    Exponent of 10
03: 7--   Z Loc [:OnCount#1]

11: P30  Z=F
01: 0    F
02: 0    Exponent of 10
03: 19--  Z Loc [:MaxPPFD#1]

12: P91  If Flag/Port
01: 18   Do if flag 8 is high
02: 30   Then Do

13: P30  Z=F
01: 01   F
02: 0    Exponent of 10
03: 37--  Z Loc [:OfOutput#1]

14: P86  Do
01: 04   Call Subroutine 4

15: P95  End

16: P95  End

17: P32  Z=Z+1
01: 7--   Z Loc [:OnCount#1]

18: P86  Do
01: 01   Call Subroutine 1

19: P94  Else

20: P89  If X<=>F
01: 25--  X Loc Flag#1
02: 01   =
03: 01   F
04: 30   Then Do
21: P30 Z=F
   01: 0 F
   02: 0 Exponent of 10
   03: 25-- Z Loc [:Flag#1 ]

22: P30 Z=F
   01: 0 F
   02: 0 Exponent of 10
   03: 13-- Z Loc [:OffCount#]

23: P30 Z=F
   01: 01 F
   02: 0 Exponent of 10
   03: 31-- Z Loc [:OnOutpu#1]

24: P86 Do
   01: 01 Call Subroutine 1

25: P86 Do
   01: 02 Call Subroutine 2

26: P86 Do
   01: 03 Call Subroutine 3

27: P95 End

28: P32 Z=Z+1
   01: 13-- Z Loc [:OffCount#]

29: P95 End

30: P95 End

31: P91 If Flag/Port
   01: 28 Do if flag 8 is low
   02: 30 Then Do

32: P86 Do
   01: 18 Set high Flag 8

33: P19 Signature
   01: 56 Loc [:PgmSig ]

34: P95 End

35: P92 If time is
   01: 00 minutes into a (seconds--)
   02: 180 minute interval (same units as above)
   03: 30 Then Do

36: P86 Do
   01: 10 Set high Flag 0 (output)

37: P80 Set Active Storage Area
   01: 01 Final Storage Area 1
   02: 240 Array ID or location [_______]

38: P77 Real Time
   01: 0221 Day,Hour-Minute,Seconds (prev day & 2400 h @ midnight)
39: P86  Do
01: 19  Set high Flag 9

40: P86  Do
01: 02  Call Subroutine 2

41: P86  Do
01: 03  Call Subroutine 3

42: P86  Do
01: 04  Call Subroutine 4

43: P86  Do
01: 29  Set low Flag 9

44: P87  Beginning of Loop
01: 0  Delay
02: 6  Loop Count

45: P30  Z=F
01: 0  F
02: 0  Exponent of 10
03: 25-- Z Loc [:Flag#1 ]

46: P95  End
47: P95  End
48: P  End Table 1

* 2  Table 2 Programs
01: 0.0000  Sec. Execution Interval
01: P  End Table 2

* 3  Table 3 Subroutines
01: P85  Beginning of Subroutine
01: 01  Subroutine Number (#1)

02: P88  If X <=> Y
01: 1--  X Loc "PPFD" #1
02: 03  >=
03: 19--  Y Loc MaxPPFD#1
04: 30  Then Do

03: P31  Z=X
01: 1--  X Loc "PPFD" #1
02: 19--  Z Loc [:MaxPPFD#1]
04: P95  End
05: P95  End

06: P85  Beginning of Subroutine
01: 02  Subroutine Number (#2)
07: P36    Z=X*Y
01: 7--    X Loc OnCount#1
02: 31--   Y Loc OnOutput#1
03: 43--   Z Loc [:Histo#1 ]

08: P75    Histogram
01: 06     Reps
02: 60     No. of Bins
03: 01     Closed form
04: 43     Bin Select Value Loc Histo#1
05: 57     Weighted value loc
06: 01     Low Limit
07: 1800   High Limit

09: P30    Z=F
01: 0      F
02: 0      Exponent of 10
03: 43--   Z Loc [:Histo#1 ]

10: P36    Z=X*Y
01: 57     X Loc W-Value
02: 31--   Y Loc OnOutput#1
03: 49--   Z Loc [:Total#1 ]

11: P72    Totalize
01: 06     Reps
02: 49     Loc Total#1

12: P30    Z=F
01: 0      F
02: 0      Exponent of 10
03: 49--   Z Loc [:Total#1 ]

13: P95    End

14: P85    Beginning of Subroutine
01: 03     Subroutine Number (#3)

15: P36    Z=X*Y
01: 19--   X Loc MaxPPFD#1
02: 31--   Y Loc OnOutput#1
03: 43--   Z Loc [:Histo#1 ]

16: P30    Z=F
01: 0      F
02: 0      Exponent of 10
03: 31--   Z Loc [:Output#1]

17: P75    Histogram
01: 06     Reps
02: 39     No. of Bins
03: 01     Closed form
04: 43     Bin Select Value Loc Histo#1
05: 57     Weighted value loc
06: 40     Low Limit
07: 1990   High Limit

18: P30    Z=F
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<td>F</td>
</tr>
<tr>
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<td>Exponent of 10</td>
</tr>
<tr>
<td>03: 43--</td>
<td>Z Loc [:Histo#1 ]</td>
</tr>
<tr>
<td>19:</td>
<td>P95 End</td>
</tr>
<tr>
<td>20:</td>
<td>P85 Beginning of Subroutine</td>
</tr>
<tr>
<td>01: 04</td>
<td>Subroutine Number (#4)</td>
</tr>
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<td>21:</td>
<td>P36 Z=X*Y</td>
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<tr>
<td>01: 13--</td>
<td>X Loc OffCount#</td>
</tr>
<tr>
<td>02: 37--</td>
<td>Y Loc OfOutpu#1</td>
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<tr>
<td>03: 43--</td>
<td>Z Loc [:Histo#1 ]</td>
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<td>22:</td>
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