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Factors Influencing Net Primary Production in Red Spruce

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FACTORS INFLUENCING NET PRIMARY PRODUCTION IN RED SPRUCE

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An Abstract of the Thesis Presented
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Management of forest resources, even when practiced at the scale of ecosystems, is implicitly based on managing photosynthetic acquisition of carbon by trees. This thesis examines several aspects of carbon balance at the scale of individual trees, using red spruce ***(Picea rubens*** Sarg.**)** as a model species.

Age-related declines in net primary productivity have been described for many species, including red spruce. A potential explanation is that ontogenetic changes in meristems lead to lower photosynthetic rates, which was confirmed here for red spruce. A grafting study used scions from juvenile, 60y, and 120y trees to demonstrate that age-related morphological and physiological trends were retained in the grafts after 3 growing seasons, providing evidence that those age-related trends are inherent in meristems. In contrast with the stomatal limitations to gas exchange indicated by research on conifers in western North America, gas exchange results from both field populations and grafted scions suggested that age-related declines in photosynthetic rates are caused by other factors in red spruce. Indirect evidence hints at feedback limitations to photosynthesis from reduced sink strength for carbohydrates in old trees.

A further study evaluated the effects of temperature (T) and leaf-to-air vapor pressure deficit (VFD) on net photosynthesis in sapling red spruce. VPD responses were investigated in a field population and were found to have significant influence on stomatal conductance and photosynthesis above a threshold of 2 kPa. As VPD and T are highly correlated, a subsequent study employed growth chambers to separate their influences. Those results demonstrated that red spruce has a substantially broader T range for maximum photosynthetic rates than has been previously reported, and the effects of T and VPD are additive. These findings have implications for understanding the response of red spruce to silvicultural treatments and climate change.

The relative importance of potential environmental stresses and their influence on ***in situ*** photosynthesis were tested using data collected from micrometeorological stations in three contrasting silvicultural systems and a seasonally integrative carbon gain model, VPD proved to be the most significant limiting factor, followed by T. Integrated photosynthethic carbon gain was roughly equal in clearcut and shelterwood systems, but was light-limited in selection stands.

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Chapter 1: Literature Review

Introduction

Carbon budgets of green plants, at individual, community and ecosystem levels, are the foundation of food webs and, thus, influence most ecological processes. To a large extent, autogenic mechanisms control the structure and function of ecosystems, and these are, in turn, based on capture and retention of solar energy through photosynthesis and subsequent carbon dynamics. The dominant influence of carbon dynamics has been recognized in such diverse processes as intra and interspecific competition (Kimmins 1987) and global climate change (Lugo and Brown 1986).

Consequently, effective natural resource management paradigms must be founded in an understanding of carbon processes. Manipulation of carbon assimilation and allocation at individual tree and stand levels forms the basis for silvicultural practices (Nyland 1996, Oliver and Larson 1990, Smith 1986). However, as forest managers have embraced new silvicultural paradigms, such as multicohort stands, mixed-species approaches, and extended rotations, it has become apparent that there are large deficiencies in our knowledge of those essential processes (O'Hara et al. 1994). In addition, recent national policy shifts toward ecosystem and landscape management strategies (SAF 1992, Kessler et. al. 1992) have placed distinct emphasis on refining knowledge of the interaction between tree physiology and ecological mechanisms.

Process models are valuable tools in our understanding of ecophysiology, but their effectiveness as predictive instruments is impaired by lack of empirical data for calibration,

validation, and refinement (Running and Milner 1993). This is particularly true in multiage, multispecies forest ecosystems (Lavigne 1992). Present theories of forest carbon dynamics largely rely on logical hypotheses that explain observations in nature, but have not been subjected to rigorous examination through field studies. Potential dissimilarities among carbon process attributes in forests of different physiographic regions may further obscure validation of general hypotheses.

An enormous body of literature has developed concerning factors that directly or indirectly control photosynthetic carbon gain (net primary production). This review covers only selected factors that have significant influences on photosynthetic carbon gain associated with sapling growth or tree age. Specific mechanisms can operate at foliar or canopy levels. An example of a leaf-level impediment to photosynthetic carbon gain would be diminishing stomatal conductance with decreasing waterpotential (Conroy et al. 1988). Increased mutual leaf shading is a canopy-level constraint (Roberts and Long 1992, Assmann 1970). Stand and leaf level mechanisms may interact to cause decreases in assimilation; thus, net primary production is the result of the interaction of extrinsic (environmental) and intrinsic (physiological) factors. Extrinsic factors are associated with the physical environment, but may be highly modified by structure or competitive processes associated with biotic communities. For trees, light is perhaps the most significant resource. However, temperature, water availability, nutrient resources, and other factors will determine a plant's ability to utilize incident light. Intrinsic factors are related to inherent abilities of tree species or individuals to use available resources for growth. The following subsections explore the influence of age-related factors,

micrometeorological parameters, and microenvironments created by stand structure on photosynthetic carbon gain.

The influence of tree age on net primary production

Observations have established that aboveground net primary productivity negatively correlates with tree age for both individual trees and single cohort stands (Whittaker and Woodwell 1968, Assmann 1970, Whittaker 1975, Bormann and Likens 1979, Harcombe et al. 1990). Long-term studies on even-aged forests showed that maximum bole increment rate, at the stand level, occurs shortly after crown closure and declines as trees reach maturity (Assmann 1970). Although less common, studies considering both aboveground net primary production (ANPP) and belowground primary production (BNPP) have found similar regressions (e.g., Crier et al. 1981). Carbon budget theories advanced to explain this observed trend can be generally divided into two categories: assimilation rate and allocation hypotheses. The former stress the significance of photosynthate source, and the latter carbohydrate sinks.

Allocation-based hypotheses

Allocation hypotheses are based on relative importance of various photosynthate sinks and observed declines in the ratio of photosynthetic to nonphotosynthetic tissue as trees and stands age. Theories in this category have traditionally received the widest acceptance and prominence (Jarvis and Leverenz 1983, Waring and Schlesinger 1985, Oliver and Larson 1990). The trend of increasing quantity of nonphotosynthetic tissue mass per unit leaf area with tree age has been commonly advanced as the predominant factor explaining reduced ANPP with tree age (Whittaker and Woodwell 1968, Waring

and Schlesinger 1985). At the stand-level, allocation theory has been supported by numerous studies that provide indirect evidence.

Developmental patterns of even-aged stands result in the redistribution of leaf area (LA) among fewer individuals of larger size (Oliver and Larson 1990). Although the total LA a monoculture growing on a specific site type can support is more plastic for shade tolerant than intolerant species (Jack and Long 1991), a general pattern emerges. As developing stands reach their maximum potential leaf area, autogenic thinning of less competitive individuals frees growing space which is captured by more competitive trees (Long and Smith 1984). Leaf area index (LAI, m^2 leaf surface per m^2 ground) increases rapidly until the time of crown closure, often experiences a transient maximum (graphic "hump") as LAI slightly overshoots site-potential LA, then stabilizes or declines slowly as the stand matures (Assmann 1970, Waring and Schlesinger 1985, Oliver and Larson 1990).

Although stand LAI remains relatively constant, the foliage biomass supported by individual trees increases. This has several potential effects on productivity. As leaf area is concentrated on fewer large trees, individual tree crowns expand in both horizontal and vertical dimensions, and density (LA per unit volume) may increase (Oliver and Larson 1990, Margolis et al. 1995). Smith and Long (1989) found that growth efficiency (defined as stemwood production per unit LAI) for *Pinus contorta* stands was inversely related to canopy depth. They attributed this loss in efficiency to increased carbon allocation to branches.

Although overall utilization of solar irradiance increases with canopy depth

(Larcher 1983), light intensity exponentially decreases with depth according to Beer's law of light extinction (Jarvis and Leverenz 1983). Thus, foliage at lower crown levels may be photosynthesizing at rates near the compensation point, contributing little to a tree's net carbon balance (c.f. Leverenz 1996). Kaufmann and Ryan (1986) and Oliver and Larson (1990) have suggested that a greater percent of foliage in lower canopy positions and increased mutual shading contributes to declining overall photosynthetic efficiency in older stands.

Roberts and Long (1992) evaluated the influence of canopy architecture on ***Abies lasiocarpa*** and concluded that tree-level efficiency was inversely related to canopy depth and positively correlated to the ratio of photosynthetic to nonphotosynthetic tissue. They generalized that individuals of codominant and dominant canopy classes with moderately sized crowns achieve maximum efficiency. Lower efficiencies are typical of both smaller and larger trees. As irradiance decreases with canopy depth, shorter individuals with a greater proportion of their foliage in lower canopy positions exhibit decreased relative productivity. Although the largest trees support most of their foliage in high h-radiance environments, they have a greater woody infrastructure associated with each unit of leaf area; thus their foliar efficiency is decreased by a lower assimilation-to-respiration ratio (A:R).

Long and Smith (1990) added support to A:R explanations for the inverse relationship between foliar efficiency and crown size by reporting that the ratio of foliage to total crown biomass decreased with increasing crown size for ***Pinus contorta.*** A study conducted with a lodgepole pine chronosequence by the same authors (Long and Smith

1992) indicated that declining growth efficiency with age is due to both a decrease in LAI and a reduction in NPP per unit leaf area. The former was attributed to abrasive crown interactions or “crown shyness”. They suggested that LA efficiency decreases were due to an increasing ratio of nonphotosynthetic to photosynthetic tissue.

Ryan and Waring (1992) evaluated the relative importance of assimilation rate and allocation hypotheses in *Pinus contorta* forests. Using a carbon budget model, they found that relative increases in the maintenance respiration to photosynthesis ratio (R_m:A) account for only 15% of the measured difference in ANPP between young and old stands. Murty et al. (1996) evaluated the data from Ryan and Waring (1992) using a stand-level process model and came to the same conclusion. However, Hunt et al. (1999) used process modeling to show that allocation to respiration explained age-related decline in productivity observed in balsam fir stands in Newfoundland, Canada. From this disparity of results, they suggested that different mechanisms may dominate age-related productivity changes in different climates and stand-types.

Assimilation-based hypotheses

Yoder et al. (1994) suggested that age-related declines in photosynthetic rates for lodgepole and ponderosa pine may be a significant cause of net production decreases in old trees. This is supported by studies of age-related differences in photosynthetic rates in scots pine (Kull and Koppel 1987), bristlecone (Schoettle 1994), and hybrid Englemann x white x Sitka spruce (Richardson et al. 2000). However, photosynthetic rates in eastern larch have been reported to be higher in older trees (Hutchison et al. 1990). Several

explanations for these age-related differences in photosynthetic rates have been advanced (Ryan et al. 1996): nutrient limitations may be greater in older trees (nutrient limitation hypothesis), hydraulic constraints may limit gas exchange in older (larger) trees (hydraulic limitation hypothesis), or these difference may be due to ontogenetic changes (maturation hypothesis).

Nutrient limitation hypothesis

Photosynthetic rates are strongly correlated with leaf nitrogen content in a wide range of plant species (Field and Mooney 1986, Pearcy et al. 1987, Lambers et al. 1990). However, this relationship may be complicated by partitioning between various photosynthetic system and nonphotosynthetic components (Evans 1989, 1990), and the occurrence of nitrogenous osmoregulatory and storage substances (Sarjala et al. 1987, Margolis and Vezina 1988, Lavoie et al. 1992, Billow et al. 1994). Reich and Schoettle (1988) suggested that photosynthetic response is more strongly linked to the interaction of nitrogen and phosphorus content than the former element alone.

However, Ryan and Waring (1992) and Yoder et al. (1994) found no significant tree age-related differences in total foliar nitrogen content for chronosequences of *Pinus contorta* and *P. ponderosa.* However, their analyses were limited to first year foliage. Numerous investigations have shown that foliar nitrogen content is inversely related to leaf age (Lehto and Grace 1994, Field 1983, Field and Mooney 1983, Matyssek 1986, Lang et al. 1987). If older trees have an increased proportion of foliage in older age classes, an overall lower nitrogen content per unit leaf mass may contribute to decreased photosynthetic rates. No direct evaluations of this hypothesis have been reported.

Hydraulic limitation hypothesis

Yoder et al. (1994) and Ryan and Yoder (1996) proposed the hydraulic limitation hypothesis to explain the results of their study on ponderosa pine, which indicated that photosynthesis was limited in older trees relative to younger individuals by reductions in midday stomatal conductance. This hypothesis is based on older trees having lower hydraulic conductivity in water pathways between roots and foliage due to longer or more complex hydraulic pathways. Due to this lower conductivity, stomata of older trees show greater sensitivity to evaporative demand and more tightly regulate transpiration to minimize the potential for xylem embolism (Ryan and Yoder 1996).

The rate of xylem water flow is determined by Darcy's law (Tyree and Ewers 199 1, Margolis et al. 1995), in which flow rate is directly proportional to cross-sectional area of the transmitting structure (sapwood xylem), its permeability, and the water potential gradient. As conductivity is equivalent to the combination of area and permeability terms, a decrease in this combined parameter will require an increase in water potential gradient to maintain constant flow. If xylem conductance is lower in older (larger) trees, a critical water potential for stomatal closure will be reached more rapidly than in younger (smaller) trees as evaporative demand increases.

Studies of tree hydraulic architecture provide evidence that potential xylem flux decreases with tree size. Darcy's law further states that flow is inversely related to pathway length. Thus, maintaining an equal flow to leaves at greater distance from a root absorption point, as in larger trees, requires either an increase in conductivity or water potential gradient. Leaf specific conductivity (LSC) is commonly used as a measure of the

ability of a particular section of stem or branch to supply water to more distal leaves, and values for this parameter have been found to be relatively constant along the length of tree stems (Tyree and Ewers 1991). However, Ewers and Zimmerman (1984a,b) have found LSC values to be much lower in branches, strongly influenced by branch diameter and order, and subject to significant restriction at branch-stem junctions. Although stem LSC values, if strictly height-determined, would not be expected to differ greatly between younger and older trees of the same height, the longer branches typical of older crowns may provide significantly reduced LSC values.

Several studies indicate that larger trees are capable of altering their hydraulic architecture to compensate for the longer, more complex pathways between roots and foliage. These are summarized in a critique of the hydraulic limitation hypothesis by Becker et al. (2000). For example, Pothier et al. (1989) have reported that sapwood permeability, and thus conductance for trees of equal sapwood cross-sectional area, is positively related to tree age in *Pinus banksiana*. They viewed this relationship as an adaptive response that provides foliage with a constant water supply as trees increase in height and crowns expand. In addition, several attempts to provide direct evidence in support of the hydraulic limitation hypothesis by experimental manipulation have been unsuccessful. Hubbard et al. (1999) girdled young lodgepole pine trees to reduce LSC and removed foliage from older trees to increase it, but found that neither manipulation significantly changed stomatal conductance or photosynthetic rates. A similar study in which foliage of old Douglas-fir was enclosed in plastic bags to reduce transpiration, and

thus LSC, was also unsuccessful at increasing gas exchange rates of uncovered foliage on the same branches (Brooks et al. 2000).

Although a physiological cause-and-effect pathway to link lower LSC and stomatal behavior has not been established (Becker et al. 2000), some recent studies may provide insight into the physiological mechanisms involved. Sperry et al. (1993) have suggested that a feedback mechanism between xylem pressure potential and stomatal conductance may protect trees from xylem cavitation during periods of water stress. Such a mechanism may be related to pH changes in the mesophyll under mild water stress caused by high transpirational demand, and their activation of ABA bound to cell walls (Wilkinson and Davies 1996).

Maturation hypothesis

The possible relationship between ontogenetic changes and declining productivity with tree age is poorly understood, with only circumstantial evidence either for or against this potential explanation (Ryan et al. 1996). Dramatic changes in morphological and physiological attributes of foliage, including photosynthetic capacity, have been described for numerous species during their early development and have been attributed to different challenges to growth and survival at various life-stages (Greenwood and Hutchison 1993, Rebeck et al. 1992, Hackett 1985, Greenwood 1984). Although little is known about age-related trends in foliar attributes beyond reproductive maturity or mid-age, there is some evidence that supports a concept of continuing change. Richardson et al. (2000) reported that changes in foliar morphology and gas exchange attributes continue past mid-age in hybrid Englemann x white x Sitka spruce. Similar trends in foliar attributes have been

described for Norway spruce (Ku11 and Koppel 1987), and in needle morphology of Sitka spruce (Steele et al. 1989). However, none of these studies have directly addressed the potential for ontogenetic changes in meristematic tissue as a contributing mechanism to age-related declines in productivity.

Common rootstock studies, in which scions donated by juvenile and mature trees are grafted onto rootstock of common age, hint at the possibility that differences in morphological and physiological traits associated with those life-stages are inherent in meristems. Such studies have been carried out on loblolly pine (Greenwood 1985), eastern larch (Greenwood and Hutchison 1989), and red spruce (Rebbeck et al. 1992). Emebiri et al, (1998) and Hutchison et al. (1990) have implicated a genetic basis for ontogenetic changes by identifying differential patterns of gene expression related to life-stages. However, pathways by which genetic changes in meristems and/or the foliage they produce affect photosynthetic rates have not been described.

A possible pathway by which ontogenetic changes in meristems may effect photosynthetic rates is by producing tissue in older trees that has an inherently lower growth rate. Shoots resulting from grafts of meristems from older trees have lower growth rates than scions from young trees. This has been shown for loblolly pine (Greenwood 1985), eastern larch (Greenwood et al. 1989, Takemoto and Greenwood 1992) and red spruce (Rebbeck et al. 1992). Takemoto and Greenwood speculated that the older meristems may be weak sinks for resources compared to shoots arising from scions taken from younger trees. Weak sinks for carbohydrate, due to reduced growth, can result in feedback limitations to photosynthesis (Stitt 1990). Leverenz (198 1) suggested that sink

strength limitations may explain differential photosythetic capacity among branches in the crowns of mature Douglas-fir. Removal of strong carbon sinks has been shown to reduce maximum leaf photosynthetic rates in herbaceous plants (Gifford and Evans 198 1). Maier and Teskey (1992) provided evidence that sink strength enhanced by increased growth stimulates increases in photosynthetic rates in white pine.

Micrometeorological factors influencing net photosynthetic carbon gain

Light intensity

Solar n-radiance is the most apparent control on photosynthetic rates. Assimilation is directly, nonlinearly related to photosynthetic photon flux density (PPFD): the quantum flux of photosynthetically active radiation (PAR, wavelength 400-700 nm) (Salisbury and Ross 1992). The response curve of photosynthesis to PPFD passes through the x-axis at a compensation point where assimiltion equals respiration, rises through a nearly linear initial phase, then becomes asymptotically nonlinear as PPFD approaches the saturation point (Larcher 1983, Teskey et al. 1995). At saturation, further increases in assimilation rate are prevented by substrate (CO_2) limitations, carboxylation reactions, electron transport limitations, photosynthate sink-source relationships, and the influence of environmental factors (Leverenz 1988, Farquhar et al. 1980). At the needle-level saturation PPFD levels for most temperate conifers occur near 1000 $\mu mol\ m^{-2}\ s^{-1}$ (Kozlowski 1991, Teskey et al. 1995). Mutual shading in shoots and tree crowns results in higher saturation points at those levels (Terashima and Hikosaka 1995). However, due to the rapid linear rise in assimilation at lower PPFD levels, rates of 50% of light-saturated

rates commonly occur at PPFD levels of less than 10% of saturation flux (Teskey et al. 1995, Bazzaz and Carlson 1982). The convexity of photosynthesis response curves is highly correlated with both species shade tolerance and needle position in the shade-sun foliar adaptation continuum (Leverenz 1988).

Individual needles develop morphological and physiological adaptations to their light environment which are reflected in their photosynthetic response curves (Leverenz and Jarvis 1980). Shade-leaves allocate a greater percentage of resources (carbon and nutrients) to the light harvesting complexes of photosystems I and II, while sunleaf resource partitioning favors carboxylation and photosystem electron transport infrastructures (Evans 1990). Shade-leaves are characterized by lower compensation and saturation points than sun-leaves providing decreased maximum photosynthesis rates when fully illuminated (Givinish 1988). Five-fold differences in photosynthetic capacity can exist between sun and shade-leaves on the same plant (Pearcy et al. 1987). The overall maximum assimilation rate for a tree crown is thus a function of not only total foliage but of the relative proportions of shade- and sun-foliage (Givinish 1988, Pearcy et al. 1987).

While morphological attributes of shade- and sun-leaves are determined during development, Lieffers et al. (1993) found a high degree of physiological plasticity in shade-foliage of ***Picea glauca*** saplings exposed to higher light regimes by thinning. However, Pothier and Margolis (199 1) reported that the determinate shoots of ***Abies balsamea*** saplings (with preformed buds and leaf characteristics) were unable to significantly respond to increased light levels in the growing season following thinning. Kull and Koppel(l987) found that ***Picea abies*** shade needles from lower crown positions

showed significantly lower assimilation rates, which, they suggested, were principally due to morphological factors. Additionally, foliage from older trees have a greatly reduced plasticity in response to changing light regimes (Richardson et al. 2000, Kull and Koppel 1987).

Leaf-to-air vapor pressure deficit

Stomata regulate gas exchange rates between leaves and the environment; thus, stomata1 resistance to gas exchange influences both rates of water efflux through transpiration and CO, uptake. This provides the basis for a significant physiological tradeoff: plants must continually compromise between water loss and supply of CO,, the substrate for photosynthetic carboxylation (Kramer and Koslowski 1987). Plant water relations have a powerful influence on assimilation rates, primarily through control of stomatal conductance, thus gas exchange. Control of internal water status is necessary to prevent air embolisms from blocking xylem water flux (Sperry et al. 1993). Resistance to cavitation is variable among species, with critical xylem water potentials for red spruce reported to be between -2.5 and -3.0 MPa (Sperry and Tyree 1990).

Leaf-to-air vapor pressure deficit is the driving force for transpiration (Grantz 1990), and therefore the movement of water through the soil-plant-air continuum. As water flux is limited by a series of resistances between soil and leaf (Pallardy et al 1994), high rates of transpiration can result in internal plant water stress. Plants minimize harmful effects of water stress by controlling transpiration rate through stomatal closure (Mansfield 1985). Plants appear to have developed several pathways by which stomata1 aperture is regulated to prevent internal water stress. Evidence indicates that stomata1

response to water stress is mediated by abscisic acid (ABA), which promotes stomatal closure by altering ion transport across the membranes of guard cells (Squire et al. 1988). Leaf-level ABA concentrations may increase when mesophyll water potential drops below a threshold (Cowan et al. 1982). Soil water stress may also induce stomatal closure independently of leaf water status (Blackman and Davis 1985). This response has been linked to root-produced ABA intermediation (Zhang and Davis 1990), and other hormonal control processes (Munns and Ring 1988). In some species, root-produced ABA, transported in the transpiration stream, may accumulate in leaves and mediate stomatal closure after a certain volume of water has transpired (Loveys 1984). Zhang and Davies (1989) have demonstrated that decreasing water potential in roots can induce production of ABA. Alternatively, transpiration rate appears to be an initiating factor in inducing stomatal closure, even in the absence of significant plant water stress (Grantz 1990). Although the physiological details of this cause-and-effect pathway have not been fully described, Wilkinson and Davies (1996) provided evidence that this process may be mediated by changes in apoplastic pH in the leafmesophyll, which convert ABA from an inactive form bound to cell walls to a free, active form. The latter pathway is consistent with rapid responses of stomata to increasing VPD_{leaf} in tree foliage, which have been described for numerous tree species (e.g., Day 2000, Weibel et al. 1993, Warkentin et al. 1992, Sanford and Jarvis 1986, Running 1976). Day (2000) has proposed that interspecific differences in stomatal sensitivity to leaf-to-air vapor pressure deficit may be the result of adaptation to the microclimates of different regions or stand-types of varying structural characteristics.

Matyssek (1986) and Squire et al. (1988) have reported that photosynthesis and stomata1 conductance show strong, approximately linear, relationships. Many studies have established a strong correlation between lowered photosynthetic rates and decreased xylem and mesophyll pressure potential for coniferous species (summarized in Margolis et al. 1995). Kaufmann and Ryan (1986), Ryan and Waring (1992), Yoder et al.(1994), and Ryan and Yoder (1997) have suggested, but provided no empirical evidence for, a link between water stress-induced stomatal closure and declining net primary production with tree age.

Temperature

Temperature can influence carbon gain through several pathways. High temperatures can result in denaturation of enzymes critical to photosynthetic light-harvesting and carboxylation pathways (Salisbury and Ross 1992, Kozlowski et al. 1991), and carbon losses to maintenance respiration are directly related to temperature. Additionally, temperature is a critical variable in determining relative activity of ribulose bisphosphate carboxylase-oxygenase (rubisco) in carbon fixation (photosynthetic pathway) as opposed to oxygen fixation (photorespiratory pathway). In addition, T_{leaf} determines the saturation vapor pressure in the boundary layers of air at foliar surfaces, and thus leaf-to-air vapor pressure deficit (water vapor pressure of air at saturation minus actual vapor pressure) (Buck 198 1).

At higher temperatures (generally > 40 “C) enzymes denature, usually resulting from deterioration of secondary molecular structure (Salisbury and Ross 1992). This may inhibit the electron transport systems of the photosynthetic light reaction, enzymes

involved in carboxylation reactions, or pathways for enzyme repair and replacement, and these effects may be temporary or permanent (Levitt 1980). Vann et al. (1994) reported that red spruce showed signs of thermal inhibition, which they attributed to disruption of enzymatic or membrane systems, beginning at temperatures between 35 and 40 °C.

Foliar temperature can have substantial influence on carbon gain by increasing losses to maintenance respiration. Maintenance respiration is the carbon cost of routine "basal" metabolic activity, i.e. the carbon used to maintain established tissue primarily by replacing structural components and enzymes, and is a relatively complex function of temperature and other allogenic influences (Larcher 1983, Amthor 1984, Fitter and Hay 1987). As maintenance respiration rates are the integrated result of all physiological activity, they generally conform to the Q^{10} function that describes the relationship between temperature and rates of chemical (enzymatic) reactions (Amthor 1984). The Q^{10} function provides for an exponential increase in rate with temperature that is defined by its exponent (Q^{10}-value) (Salisbury and Ross 1992). For example a Q^{10}-value of 2 defines a function at which rates double for each 10 °C increase in temperature. Temperate conifers generally have Q^{10}-values of between 1.8 and 2.4 (Ryan et al 1996, Gower and Landsburg 1997). No Q^{10}-values specific to red spruce have been published.

Maintenance respiration rates are generally 0.5-l. 5 % of gross photosynthetic rates (Ryan et al. 1997, Sprugel 1995). However, fohar losses to maintenance respiration continue when light-levels are not sufficient for photosynthesis and are a significant carbon sink in tree species. From a whole-tree perspective (photosynthetic and nonphotosynthetic organs), temperate species may allocate 25-50% of the carbon fixed in photosynthesis to

maintenance respiration (Landsberg and Gower 1997, Ryan et al. 1997, Ryan et al. 1994, Edwards et al. 1980). In red spruce, shade-adapted individuals, although they exhibit lower absolute rates, may allocate a greater proportion of photosynthetically fixed carbon to maintenance respiration due to lower maximum photosynthetic rates (Day 2000, Alexander et al. 1995).

Temperature may also affect photosynthetic rates through its influence on the relative activities of photosynthesis and photorespiration (Monson et al. 1982, Ku and Edwards 1977a, Jolliffe and Tregunna 1968). In addition to its role as a catalyst in the carboxylation of ribulose-1,5-bisphosphate in the C-3 carboxylation cycle, the enzyme ribulose-bisphosphate carboxylase/oxygenase (rubisco) also acts as a catalyst for oxygenation in the C-2 or photorespiratory cycle. Temperature can influence the differential activity of rubisco as carboxylase or oxygenase through two pathways. The solubility ratio of 0, to CO, in the mesophyll symplast increases exponentially with temperature (Ku and Edwards 1977b), increasing 0, substrate concentration and enhancing oxygenase activity. Additionally, Ogren (1984) has proposed that temperature and specificity of rubisco for 0, are directly related. These consideration led Tolbert (1994) to estimate a 20 °C optimum for C3 species at current atmospheric concentrations of 21 % 0, and 300-350 μl CO, l^{-1} air. Because of the exponential nature of the 0, to CO, solubility ratio, Tolbert (1994) also suggested 40 to 65 μmol mol^{-1} atmospheric CO, concentration as an effective compensation point (zero net photosynthesis) for C3 plants at 20 “C, 110 μmol mol^{-1} at 30 “C, and 300 μmol mol^{-1} at 37 “C.

The effects of stand structure on microclimate

Stand structure exerts significant control over microclimatic variables such as light, temperature, and leaf-to-air vapor pressure deficit, which, in turn, exercise control over photosynthetic carbon gain. However, few studies have documented the relationship between canopy structure and multiple environmental variables.

Most published studies have focused on the environments created by treefall gaps, and most were carried out in tropical forests. Examples are Brandani et al. (1987), Fetcher et al. (1985), and Chazdon and Fetcher (1984) for Costa Rican rainforests, and Ashton (1992) for Sri Lankan rainforest. Due to great differences in insolation attributes and conditions in the bulk atmosphere, such studies reveal little about conditions in structurally similar forests at higher latitudes.

The most complete picture of micrometeorological conditions in temperate forest gaps comes from the research at the Harvard Forest by F.A. Bazzaz and his associates (summarized in Bazzaz and Wayne 1994). This study focused on patterns of environmental heterogeniety within gaps and between gaps and the surrounding intact forest and is unique in encompassing multiple environmental factors. Other research on gaps in temperate North American forests have addressed the influence of light regimes (e.g., Phillips and Shure 1990, Paulson and Platt 1989, Canham 1988b), or light and belowground resources (e.g., Finzi and Canham 2000, Walters and Reich 1997, Sipe and Bazzaz 1995) and their effect on regeneration or interspecific competition. However, none of these studies comprehensively addressed micrometeorological regimes.

For canopy gaps (which are analogous to those created by multiple-tree selection

harvests), direct beam (full strength) sunlight falls over the northern one-third to one-half of the gap area for some portion of the day. However, the duration of direct beam radiation is strongly dependent on gap size, gap shape, orientation of major axis (considering a roughly oval-shaped gap), height of surrounding canopy, and seasonal track of the sun (Bazzaz and Wayne 1994, Canham 1988b). On clear days air temperature in large (300 m^2) gaps in the Harvard Forest showed a direct, linear relationship to light intensity, and midday maxima in the northern aspect of the gaps were 4-5 °C higher than the surrounding intact forest (Bazzaz and Wayne 1994). Variability in air temperature across gaps was significant, with southern aspects showing midday highs close to those of intact forest. Rates of air movement are also an important factor in determining the similarity of air temperature in gaps to that of bulk air above the surrounding forest canopy and their within-gap heterogeneity, with high wind speeds resulting in more uniform temperatures both between gap air and bulk air and within gaps (Miller et al. 1991). Higher wind speeds are generally associated with larger gaps and lower and less uniform canopies in the surrounding forest.

The light and temperature environments created by shelterwoods are generally characterized as more moderate than clearcuts and less spatially variable than gaps (Oliver and Larson 1990). For example, Childs and Flint (1987) monitored air and soil temperatures and solar radiation over a growing season in shelter-wood (24 $m^2\ ha^{-1}$ overwood basal area) and clearcut stands in the Cascade Mountains of Oregon. Daily average solar radiation was 30-40% lower in the shelterwood stands; however, air temperatures were similar between the two stand-types with usually < 1 °C difference.

Surface soil temperatures, reflecting differences in radiation input, were 4-6 °C, higher in the clearcut during summer months. Survival of planted Douglas-fir seedlings over two growing seasons were significantly greater in the shelterwood, which the authors attributed to a more moderate temperature regime. Studies comparing environments in clearcuts with intact (closed canopy) forests have demonstrated that clear-cuts have greater input of solar radiation, higher daytime temperatures for both air and soil, and higher evaporative demand (greater atmospheric vapor pressure deficits) at seedling and/or sapling strata than intact canopies (Landsburg and Gower 1997). Nighttime temperatures are lower in clearcuts due to enhanced radiational cooling. These differences are consistent with predictions from stand-level heat budgets by the Pennman-Monteith relationship (McCaughey 1987).

Silvicultural systems, by controlling microenvironments in seedling and sapling strata, may be able to shift competitive balances between target species and potential competitors (Messier et al. 1999; Hannah 1991, 1988; Marquis 1979). While this is a basic tenet of selection and shelter-wood silviculture (Nyland 1996, Seymour and Hunter 199 1, Smith 1986), Messier et al. (1999) made a case that the principle may also apply among species with closely related silvical attributes. Numerous studies have investigated the relationship between microclimate and optimal conditions for growth. The least ambiguous results have generally come from studies that compare species pairs or groups of species with different degrees of shade-tolerance between varying environments (e.g., Finzi and Canham 2000, Wayne and Bazzaz 1993, Phillips and Shure 1990, Canham 1988a). Most of these have used light regime as an independent variable and have focused

on the heterogeneity of light environments present in gaps.

Studies that attempt to define optima for single species by using transects extending from high light to low light or multiple plots in different stands to provide a light-environment continuum have often produced more ambiguous results with respect to those predicted by observations of silvical properties. This uncertainty may be related to complexity introduced by variation in other environmental variables such as soil moisture or nutrient availability, or variables that are highly correlated with light environment such as transpirational demand (e.g., Holgrén and Hånell 2000, McConville 1998, Klinka et al. 1992). The clearest relationships between light and growth are reported for species with low shade-tolerances, where growth is strongly inhibited at low light levels and increases until full sunlight levels (e.g., mountain beech (Dignan et al. 1998), longleaf pine (Palik et al. 1997) and white pine (Stiell and Berry 1985)). With a few exceptions (e.g., Man and Lieffers 1997) these studies have not been explicitly linked to physiological mechanisms that are promoted or inhibited by explicit environmental variables.

Light is the principle factor causing variability in productivity or growth across stand-types with different canopy characteristics (Coates 2000, Finzi and Canham 2000, Bergqvist 1999, Dignan et al. 1998, Mailly and Kimmins 1997, Walters and Reich 1997, Sipe and Bazzaz 1995, Comeau et al. 1993). However, water availability may be a second-order limiting factor if it varies among microsites (Holgren and Hånell 2000, Walters and Reich 1997). If sites differ in edaphic attributes, nutrient availability (generally nitrogen) may influence differential growth rates (Sipe and Bazzaz 1995, Fahey et al. 1998, Reich et al. 1997). However, Finzi and Canham (2000) found that intersite nitrogen availability

explained only 7% of sapling growth in a New England hardwood forest, compared with 21-79% accounted for by light regime.

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Chapter 2: Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age

Abstract

The contribution of maturation-related changes in meristem behavior to age-related decline in forest productivity is poorly understood. While changes in morphological and physiological attributes associated with transition from juvenile to reproductively-mature phases have been described for many woody species, few studies have examined maturational changes that occur after the onset of reproductive development. We studied age-related needle morphology and gas exchange in a population of red spruce growing in a multicohort stand where tree ages ranged from first-year germinants to over 150 y, as well as grafted scions from these trees. Age-related trends in foliar morphology were evaluated, and differences in gas exchange characteristics were compared between 60- and 120-y age-classes in a field investigation. This was followed by a common-rootstock study, where scions from trees representing 20-, 60-, and 120-y cohorts were grafted onto juvenile rootstock and maintained for three growing seasons, after which morphological and physiological foliar attributes were evaluated.

The field study demonstrated significant age-related trends in foliar morphology, including decreasing SLA and increasing needle width, projected needle area, and needle width-to-length ratio. Similar trends were apparent in foliage from the grafted scions. Both ***in situ*** foliage and shoots resulting from grafted scions from the oldest cohort showed significantly lower photosynthetic rates than their counterparts from younger

trees; however, differences in stomatal conductance and internal CO, concentrations were nonsignificant. These results demonstrate that: (1) Foliage of red spruce shows significant age-related trends in both morphology and physiology. (2) Lower rates of photosynthesis contribute to age-related decline in the productivity of older red spruce. (3) These declines in photosynthetic rates result from nonstomatal limitations. (4) Age-related changes in morphology and physiology are inherent in meristems and persist for at least 3 y in scions grafted to juvenile rootstock.

Introduction

The production of biomass by both individual trees and forest stands decreases substantially with age, commencing well before trees reach the midpoint of their average lifespan (Assmann 1970). Age-related reduction in biomass accumulation is an important consideration in mechanistic models that predict forest growth and determines the capacity of forests to act as carbon sinks. With the current impetus towards silvicultural approaches that employ uneven-aged systems and extended rotations, understanding the physiological basis for age-related decline in productivity of dominant species has become increasingly important. Understanding this component of productivity is crucial to quantifying and manipulating carbon fluxes in forest ecosystems and their influence on global CO, cycles.

Although both stand-level and tree-level factors may contribute to age-related decline in productivity, those operating at the scale of individual trees are likely to play a major, if not principal, role (Ryan et al. 1997). Several contrasting hypotheses have been advanced to establish a physiological basis for age-related declines in individual trees.

Until the past decade, the textbook explanation has centered on a declining ratio of photosynthesis to respiration (e.g. Waring and Schleisinger 1984). This hypothesis was questioned by Ryan and Waring (1992) and subsequent studies (e.g. Murty et al. 1996) that indicated that differences in carbon allocation to maintenance respiration between mid-aged and old trees were insufficient to account for observed age-related declines in growth. However, Hunt et al. (1999) provided evidence that respiration plays a significant role in age-related decline in balsam fir forests of eastern Canada. Other mechanisms based on carbon allocation (i.e., increased carbon allocation fine roots, defensive compounds, and sexual reproduction) have been proposed, but little quantitative evidence has been advanced to support them (reviewed by Ryan et al. 1997).

An accumulating body of circumstantial evidence supports a model predicated on lower photosynthetic rates (or integrated photosynthesis) in older trees (Richardson et al. 2000, Hubbard et al. 1999, Yoder et al. 1994, Kull and Koppel 1987). Yoder et al. (1994) proposed that lower photosynthetic rates in older trees are caused by reduced stomatal conductance, which, in turn, results from lower hydraulic conductivity in their longer (or more complex) hydraulic pathways. Becker et al. (2000) has questioned the validity of this model based on observations that trees have an excess capacity in conductance and larger trees are able to compensate for limitations in conductivity by altering their hydraulic architecture. While circumstantial evidence in support of the hydraulic limitation model has been advanced (Hubbard et al. 1999, Kostner et al. 1996), attempts to manipulate photosynthetic rates in younger trees by decreasing hydraulic conductivity or increase rates in older trees by reducing transpirational demand have been largely unsuccessful

(Brooks et al. 2000, Hubbard et al. 1999).

Another explanation for age-related declines in productivity may lie in genetically based maturational changes in tree meristems with age. Dramatic changes in morphological and physiological attributes of foliage, including photosynthetic capacity, have been described for numerous species during their early development and have been attributed to different challenges to growth and survival at various life-stages (Greenwood and Hutchison 1993, Rebeck et al. 1992, Hackett 1985, Greenwood 1984). Emebiri et al. (1998) and Hutchison et al. (1990) have implicated a genetic basis for ontogenetic changes by identifying differential patterns of gene expression related to life-stages. Although little is known about age-related trends in foliar attributes beyond reproductive maturity or mid-age, there is some evidence that supports a concept of continuing change. Richardson et al. (2000) reported that changes in foliar morphology and gas exchange attributes continue past mid-age in hybrid Englemann x white x Sitka spruce (*P. emgelmanni x glauca x sitchensis).* Similar trends in foliar attributes have been described for Norway spruce, *P. abiea* (L.) Karst, (Kull and Koppel 1987), and in needle morphology of Sitka spruce, *P. sitchensis* (Bong.) Carr, (Steele et al. 1989). However, none of these studies have directly implicated ontogenetic changes in meristematic tissue as a contributing mechanism.

Herein we have evaluated trends in foliar morphology and physiology that continue beyond mid-age in red spruce (*Picea rubens* Sarg.) and have provided evidence that those trends are related to ontogenetic changes in meristems. Red spruce is a major component of several cover-types in the forests of northeastern North America, and its long lifespan (> 200 y) and propensity to occur naturally in multicohort stands make it ideally suited as

a model species for investigations of long-term maturational change. A study where scions from juvenile (2 y) and mature (~ 70 y) red spruce were grafted onto common rootstock (Rebbeck et al. 1992) clearly showed that maturation-related changes in meristems of red spruce persist for at least 2 y after grafting. In their results scions from mature (28 y) trees exhibited lower specific leaf area (SLA), stomatal conductance (G_s) and maximum photosynthetic rates (A_{max}) than those from juvenile donors.

We conducted an investigation to evaluate a possible ontogenetic basis for age-related decline in productivity of red spruce by addressing four questions: (1) Is there evidence that productivity in red spruce growing in multicohort stands declines with age of trees? (2) Is reduction in photosynthetic capacity associated with this decline? (3) Do trends of change in foliar morphological attributes continue beyond reproductive maturity or mid-age? and (4) Are maturation-related changes in meristem behavior (indicating differential gene expression) associated with age-related changes in foliar attributes?

Methods

Study site and population

This study focused on a population of red spruce growing in a multicohort stand of approximately 10 ha (Compartment C 16) at the Penobscot Experimental Forest (PEF), Penobscot County, Maine. Use of a multicohort population minimized site effects, particularly nutrient limitations. Stand-level differences in nutrient availability have been advanced as a potential explanation for age-related decline in productivity, either through direct influence on photosynthetic capacity or indirectly by stimulating greater allocation

of resources to roots (Crier et al. 198 1). The USDA Forest Service has managed C 16 under a selection system with a five-year cutting cycle since the early 1950s. Seymour and Kenefic (1998) have summarized the management history, edaphic conditions, and dynamics of this stand. Although the age structure is unbalanced, cohorts ranging in age from new germinants to approximately 150 years are present.

The upper canopy of Cl6 is dominated by two mature cohorts (Table 2.1A). The oldest originated following significant disturbance (perhaps harvesting) in the middle of the nineteenth century and shows a mean age at breast height (1.3m) of 117 years (nominal 120 y age-class). The younger cohort, with a mean age of 54 years at breast height (nominal 60 y class), was likely released by early Forest Service entries. Harvesting systems common during the time period in which the oldest cohort was released were diameter-limit cuts which selectively removed the largest individuals (Seymour 1992), resulting in disturbance patterns that would closely resemble those of the single-tree to small group selection system that released younger cohorts. Thus, it is doubtful that the earlier harvest favored regeneration of trees with different growth characteristics or foliar attributes than more recently released cohorts.

Growth efficiency

Growth efficiency was evaluated using a random sample (n = 58) of upper canopy individuals (defined as those trees with > 60% of south-facing crown exposed to direct sunlight for at least 6 hours per day during summer). DBH, height, and crown length measurements were made on sample trees in the summer of 1995. Two opposing increment cores (N and S aspects) were taken at breast height and the extent of sapwood

Table 2.1. Characteristics of the red spruce population used in this study. A. Mean attributes (n = 58) for the two upper canopy cohorts from Penobscot Experimental Forest selection stand C-16 used for field photosynthesis measurements, foliar morphometry, and as scion donors. B. Means (n = 32) for members of the two upper canopy cohorts selected for field gas exchange measurements. '±' = one standard deviation.

Age at 1.3 m	DBH (cm)	Height (m)	Live crown ratio
A. Field population			
53.8 ± 26.4	15.4 ± 4.6	10.6 ± 3.2	0.56 ± 0.15
117.1 ± 13.2	39.7 ± 2.6	20.3 ± 2.8	0.55 ± 0.15
B. Gas exchange sampling population			
57.7 ±21.3	16.5 ±3.0	11.5 ± 2.3	0.57 ● 0.14
116.5 ± 14.7	37.5 ± 2.7	20.7 ±1.2	0.53 ± 0.13

marked on the fresh cores by observing change in transparency. Ages, radial growth increments, and sapwood radii were determined with an optical core reading system (Measuchron, Bangor, Maine, USA) coupled to a computer using the PJKv5DOS software (P.J. Krusic, Lamont-Doherty Geological Observatory, Palisades, NY, USA). Active sapwood and total cross-sectional areas were calculated as concentric circles using averaged radii. Total leaf mass was calculated using regression equations of leaf mass on sapwood area at breast-height developed by Maguire et al. (1998) for red spruce growing in the PEF. For individual trees, total aboveground biomass for 1994 and 1989 was calculated from locally developed equations of biomass on diameter given in Young et al. (1980). Aboveground annual net production (ANP) was determined as the average annual change in aboveground biomass for the five-year period 1989-1994. Foliar efficiency (Waring 1983) was estimated as mean annual aboveground biomass production per unit

foliar mass over the same 5-year interval. This model incorporated the assumption that leaf mass remained essentially the same over that period. This assumption is supported by the relatively consistent longevity of red spruce foliage (Blum 1992) and the lack of any reports of defoliating disturbances during that period in the PEF (USDA Forest Service records). Correlations between productivity and age were assessed using Pearson r-values (SAS v. 6.1; SAS Institute, Cary, NC, USA).

Field gas exchange and water potential

In the summer of 1995, 16 trees from each of the two dominant canopy cohorts were randomly selected for gas exchange measurements (Table 2.1 b). From this set, 2 trees from each cohort were randomly assigned without replacement to each of 8 sampling dates (Julian dates 172, 173, 201, 206, 208, 233, 235, 237). On each sampling date, order of sampling (by cohort) was random, and the sampling sequence repeated twice between 1000 and 1200 hours EST, providing 2 subsamples from each tree. Foliage samples consisted of a terminal branch shoot from the southern aspect of the upper one-third of the crown. Samples were harvested using a shotgun and rushed to a portable field lab within 1 minute of sampling. A section of shoot with last season's foliage was excised for gas exchange measurements, and the balance of the sample placed on ice in a small insulated box for water potential measurements.

Gas exchange measurements were made with a Li-Cor 6200 closed-type photosynthesis system using a cuvette with 0.25 1 volume. Calibrations for flow meter, IRGA zero points, and CO, span values were made just prior to each measurement series. Light was provided by a halogen lamp and filtered through a water bath to minimize long-

wave infrared input, while maintaining saturating irradiance (1000-1200 $\mu mol\ m^{-2}\ s^{-1}$, Day 2000). Additional cooling was provided by external electric fans. This system allowed needle temperatures in the cuvette (measured with a fine-wire thermocouple) to be maintained near 25 "C, within the opimum range reported for sun-adapted foliage of this species (Day 2000). Three sequential measurements were made within 1 - 2 minutes, and average values used for analysis. Thus, all gas exchange measurements were completed within 3-4 minutes of sample harvest. Our preliminary measurements indicated that excision of branches has no deleterious effects on photosynthetic rates for at least 6- 10 minutes in spruce. All gas exchange samples were returned to the lab, dried at 65 °C for at least 72 hours and weighed on an analytical balance (test accuracy ± 0.001 g).

Xylem water potential was measured within 10 minutes of harvest using the pressure bomb technique (Koide et al. 1989) with 100% N_2. Pressurization endpoints were observed using a 10-45x zoom stereoscope. For each sample, 3 trials were made and the mean value reported for analysis. Material was maintained in the cooler until measured. In addition, dawn water potential measurements were made on all trees, except on day 233, as early as light conditions permitted sampling.

Gas exchange parameters were evaluated with analysis of variance (GLM procedure, SAS v.6.1) using a randomized block design with date as the blocking factor to account for variance due to phenological and meteorological factors. Concordance of analyses with the assumptions of ANOVA was evaluated with the Durban-Watson statistic for normality and Levene's test for heteroscedacity (Snedecor and Corcoran 1989). As a result, log-transformed data were used for the ANOVA of G_s.

Foliar morphometry

To minimize confounding effects of foliar adaptation to light environment, separate analyses were carried out on shade- and sun-adapted foliage. Shade foliage was collected from 15 randomly selected individuals in each of 6 nominal age-classes (2, 5, 10, 20, 60, and 120 years). Ages of the first 4 classes were determined by counting whorls. Ages of the older classes were determined by cores taken at 1.3 m; therefore, their class designations reflect age at breast height. The two oldest classes are the equivalent of the mature cohorts used for field gas exchange measurements. As light adaptation is a fluence response (Chabot et al. 1979), sun-adapted foliage was collected from only the three oldest classes. Trees in the younger classes were growing in canopy gaps and received substantially less integrated light flux than upper canopy trees. Sun-foliage was collected from the crown positions described for field gas exchange sampling. Shade-foliage was collected from the nor-them aspect of the lower one-third of crowns which were not likely to receive substantial input of direct sunlight.

Collections were made during the autumn, when current-year foliage was fully formed. For each individual, 3 subsarnples of approximately 3 cm twig length from the current foliar cohort were analyzed. Needles were stripped from twigs, scanned on a high-resolution flatbed scanner, and analyzed with WinSeedle (v.4.3, Regent Instruments, Quebec, PQ, Can.). Dry masses were determined as previously described. All analyses were ANOVAs for simple random design (GLM procedure; SAS v.6.1). The assumptions of ANOVA were tested as previously described and log-transformed data used when necessary.

Grafting study

Eighteen trees from each of the three oldest age-classes sampled for analysis of foliar morphology (mean ages of 2 1, 54, and 117 y), were randomly selected as scion donors. Scions for the grafting experiment originated as terminal branch shoots from canopy positions with sun-adapted foliage (as previously defined). Scions were collected during the last two weeks of February, 1997, with a hand pruner, pole pruner, or shotgun, depending on tree height. After collection, scions were placed in a cooler with ice and held dormant until grafting.

Three-year-old potted rootstocks that had satisfied their cold-requirement were brought into a heated greenhouse in mid February, and grafts were made shortly after rootstocks became physiologically active. This approach resulted in dormant scions being grafted onto non-dormant rootstock to enhance the establishment of vascular connections before scion budbreak. Scions, consisting of a terminal bud and approximately 4 cm of subtending stem with any associated lateral buds, were cleft-grafted onto leader stems of similar caliper. Trees were maintained in the greenhouse until danger of frost was past (15 May), then relocated to a nearby shade house (35% interception shadecloth) for the remainder of the growing season.

Of the initial 18 scions from each age-class, 8, 12, and 7 grafts from the 20, 60, and 120 nominal age-classes, respectively, were successful. Grafted trees were maintained in the shadehouse for three growing seasons, resulting in 4 foliar flushes. (Trees flushed twice in 1996 due to the extended growing season initiated in the greenhouse.) The shadehouse frame was covered with plastic sheeting during the winter months and

shadecloth during the growing season. Trees were transferred to 25 1 pots at the beginning of the second post-grafting growing season (1998), potted with peat, vermiculite, and sand mixed 2: 1: 1, and supplied with time-release fertilizer (Osmocote 18-6- 12 (NPK); Sierra Chemical Co., Milpitas, CA) at a rate of 0.124 kg m^{-2}. Potentially competing leaders from rootstocks were pruned following budbreak. Survival to the third growing season was 6, 8, and 4 trees from the 20-, 60-, and 120-y scion classes, respectively. Most losses were from whole-tree mortality, which may have been caused by freezing damage to roots.

Foliar attributes of scions

In the summer of 1999 (3^{rd} post-grafting growing season), 4 trees from each age class were selected for sampling. This included all 4 surviving trees with 120 year-old scions and individuals randomly selected from the other two classes. Gas exchange measurements were made on three shoot tips from the uppermost whorl of each selected scion. Control measurements were also made on 3 upper crown shoot tips from each of four randomly selected rootstocks. Measurements were taken on current-year foliage during the first two weeks of August. Shoot elongation and needle growth had ceased approximately one month before measurements. The standard 2 x 3 cm cuvette from a LI6400 (Li-Cor, Inc., Lincoln, NE) open-type photosynthesis system was clamped on the center portion of sample shoots and foliage acclimated for 30 minutes to a light intensity of 2000 $\mu mol\ m^{-2}\ s^{-1}$ PPFD using a LI6400-02B light source. Gas exchange measurements were subsequently made at 14 light intensities (2000, 1500, 1000, 750, 500, 350,200, 120, 90, 60, 40, 25, 10, and 0 $\mu mol\ m^{-2}\ s^{-1}$) in declining order. With each change in light

intensity a 3 minute adjustment period was provided, followed by a test for stability (< 0.5% maximum CV for ACO,), and the adjustment period repeated if necessary. The system's infrared gas analyzers were matched before each measurement, zero values were calibrated daily, and span values were checked weekly using a standard gas for CO, and a LI610 (Li-Cor, Inc.) dew point generator with pressure compensation correction for H_2O. Measurements were made on one tree per day with tree sampling order assigned randomly. On each day sampling began at 0800 EST and was completed in approximately 3 hours. After sampling, the shoot sections contained in the cuvette were severed, their needles detached, and morphology measured as described for the field samples. Gas exchange measurements were calculated on the basis of actual leaf mass (A_{net}) or area (G_s) using the algorithms in Licor, Inc. (1999). Apparent quantum efficiencies were calculated as the slope of the linear portion of the photosynthetic light-response curve using rates at PPFD levels $\leq 60\ \mu mol\ m^{-2}\ s^{-1}$ (Leverenz 1988).

Data analysis, using the means of the 3 subsamples in a simple random sample design, followed the procedures described for the field data. To meet the assumptions of ANOVA, analyses of photosynthesis and stomatal conductance were both performed on log-transformed data.

Results

Foliar efficiency index (Fig. 2.1) was inversely related to tree age. This demonstrated that either older individuals are producing less photosynthate per unit of foliar mass or a smaller proportion of production is allocated to accretion of aboveground biomass.

Red spruce exhibited age-related trends in several aspects of foliar morphology. Specific leaf area (SLA; cm^2 projected leaf area per g dry mass) declined with age in both sun- and shade-adapted foliage (Fig. 2.2a) The most pronounced decreases were across age classes < 40 y, with the rate of change lessening across the mature cohorts. Needle width (Fig. 2.2b), needle area (Fig. 2.2c), and, particularly, the ratio of needle width-to-length (Fig. 2.2d) showed a positive relationship to tree age that was consistent across foliar types (sun- or shade-adapted). The increasingly steep slope of the needle width-to-length (W:L) trend between the 60- and 120-y classes compared to the 20- and 60-y cohorts made this attribute particularly noteworthy.

Table 2.2 compares field gas exchange attributes between the upper canopy age-classes. ANOVA showed late-morning photosynyhetic rates in the 120-y upper-canopy cohort to be significantly lower than the 60-y cohort when calculated on a leaf-mass basis. Stomatal conductance (G_s) was not significantly different between the age classes, and internal CO, concentration (C_i) was slightly nonsignificant ($P = 0.06$) with the younger cohort showing the lower levels. Dawn xylem water potentials were about -0.4 Mpa, dropping to about -1.4 MPa during the midday. For both sampling series, differences between the cohorts were very close to those predicted by their differences in mean tree height (Table 2.1 b) and gravitational potential (approximately 0.01 $MPa\ m^{-1}$; Salisbury and Ross 1992).

For the grafted scions, ANOVA of foliar morphological attributes showed similar age-related trends to the field population in mean needle width (Fig. 2.3a), width-to-length

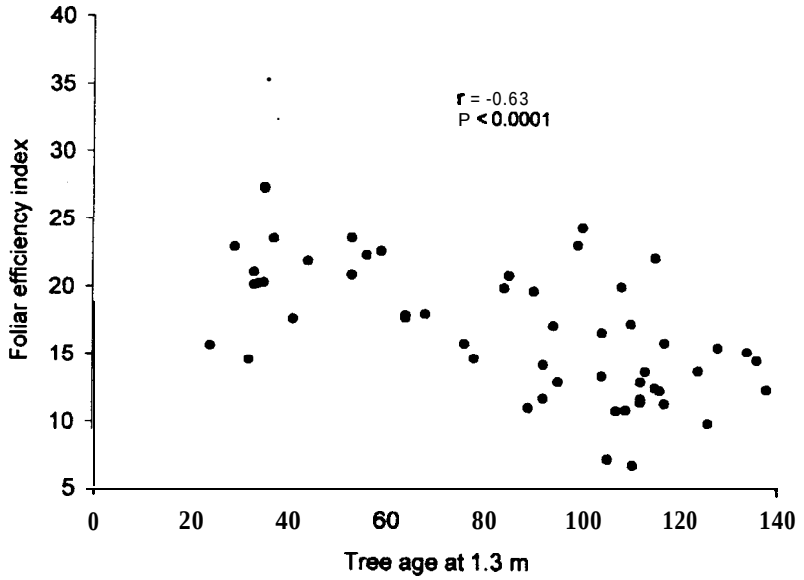

Figure 2.1. Relationship between tree age and foliar efficiency for upper canopy red spruce in C-16 (n = 58). Foliar efficiency index values represent g aboveground ANP per 100 g foliar biomass.

Table 2.2. Results of gas exchange and water potential measurements on the two upper canopy cohorts of red spruce in PEF Compartment 16. All entries are mean ± standard error. Abbreviations and symbols are defined in the text, and mensurational data for the two cohorts are summarized in Table 1A.

Cohort	60 y	120y	P > F
A_{max} (μmol g^{-1} s^{-2})	14.4 ± 0.86	11.7 ± 0.84	< 0.01
G_s (mmol m^{-2} s^{-1})	87.5 ± 6.58	92.1 ± 6.63	0.28
C_i (μl l^{-1})	261 ± 5.01	276 ± 5.08	0.06
Ψ_{midday} (MPa)	- 1.42 ± 0.046	- 1.52 ± 0.043	0.12
Ψ_{dawn} (MPa)	- 0.41 ± 0.053	- 0.45 ± 0.053	0.24

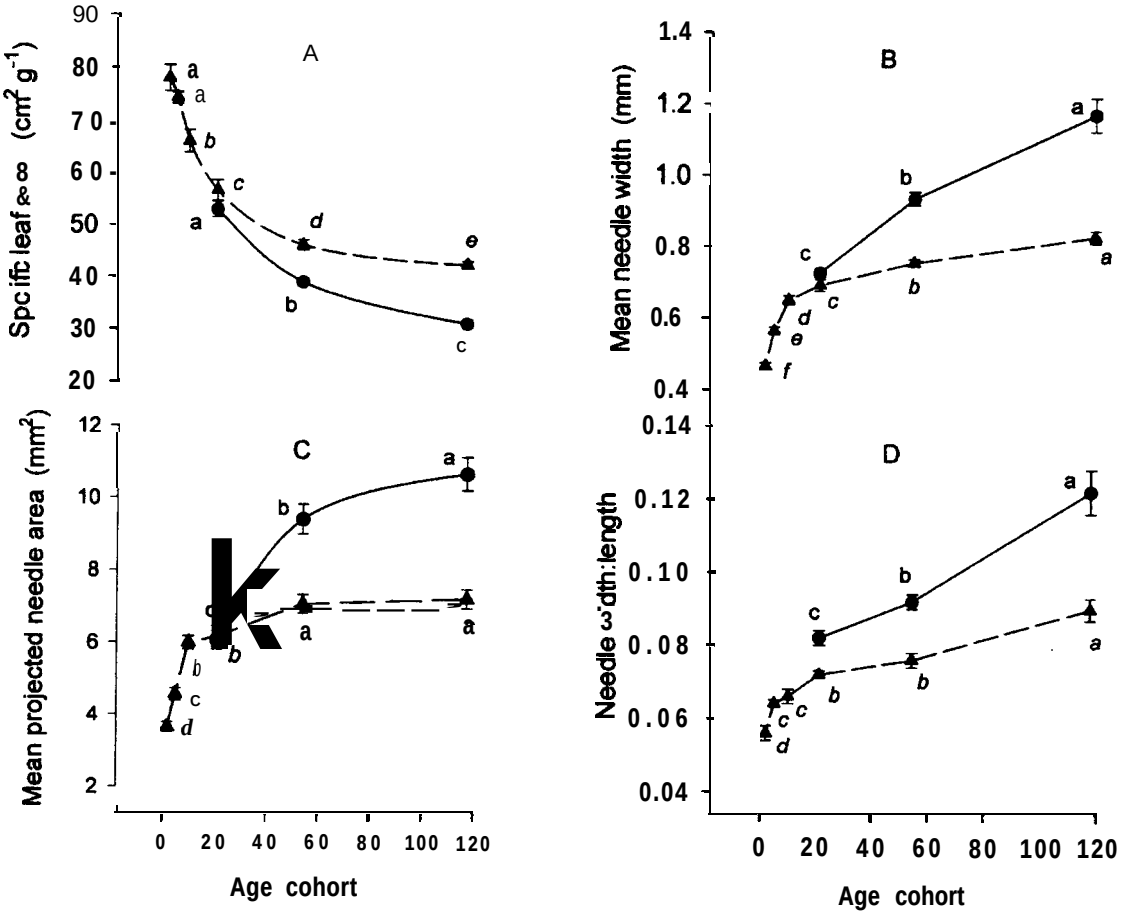

Figure 2.2. Trends in foliar morphological attributes with tree age in the multicohort red spruce field population: (A) specific leaf area, (B) mean needle width, (C) mean projected needle area, and (D) needle width-to-length ratio. Means were calculated from 15 trees of each age class, with 3 subsamples per tree. Bars represent one standard error. Letters represent significant differences between tree age-classes within foliage-types (sun- or shade-adapted) determined with Duncan's New Multiple Range Test at $\alpha = 0.05$. Sun-foliage trends are shown with solid lines and normal font, and shade-foliage with dashed lines and italics.

ratio (Fig. 2.3b), and needle area (Fig. 2.3c). Projected needle area was significantly different due to trends in needle width and length, while differences in SLA showed a declining trend with scion-donor age but were nonsignificant across age-classes (Fig. 2.3d).

A_{max} exhibited a decreasing trend across age classes, but only differences between 120 y scions and those of younger donors were significant (Fig. 2.4a). Stomatal conductance (Fig. 2.4b) showed a strong declining trend with scion age-class. Internal CO_2 concentration also decreased with scion age-class (Fig. 2.4c). However, the mean for the 120 y age-class was only 6% lower than that for the 60 y scions, and differences between these groups were nonsignificant. Apparent quantum efficiency (AQE) exhibited a decreasing trend with scion age-class, with AQE of 120 y scions only about 60% as efficient as those from 20 y donors (Fig. 2.4d).

Discussion

In the upper canopy cohorts, foliar efficiency (biomass production per unit foliar mass) declined with tree age (Fig. 2.1). Further, the trend in Figure 2.2 indicates that the decline in foliar efficiency with age appears to begin very soon after reproductive maturity. Similar patterns have been reported for other species (reviewed in Ryan et. al. 1997). Thus either (1) productivity per unit leaf mass is substantially lower in the older individuals, or (2) a greater proportion of primary production is being allocated to sinks other than accretion of aboveground biomass. For example, Crier et al. (1981) speculated that increasing nutrient-limitations in older stands could result in greater proportional

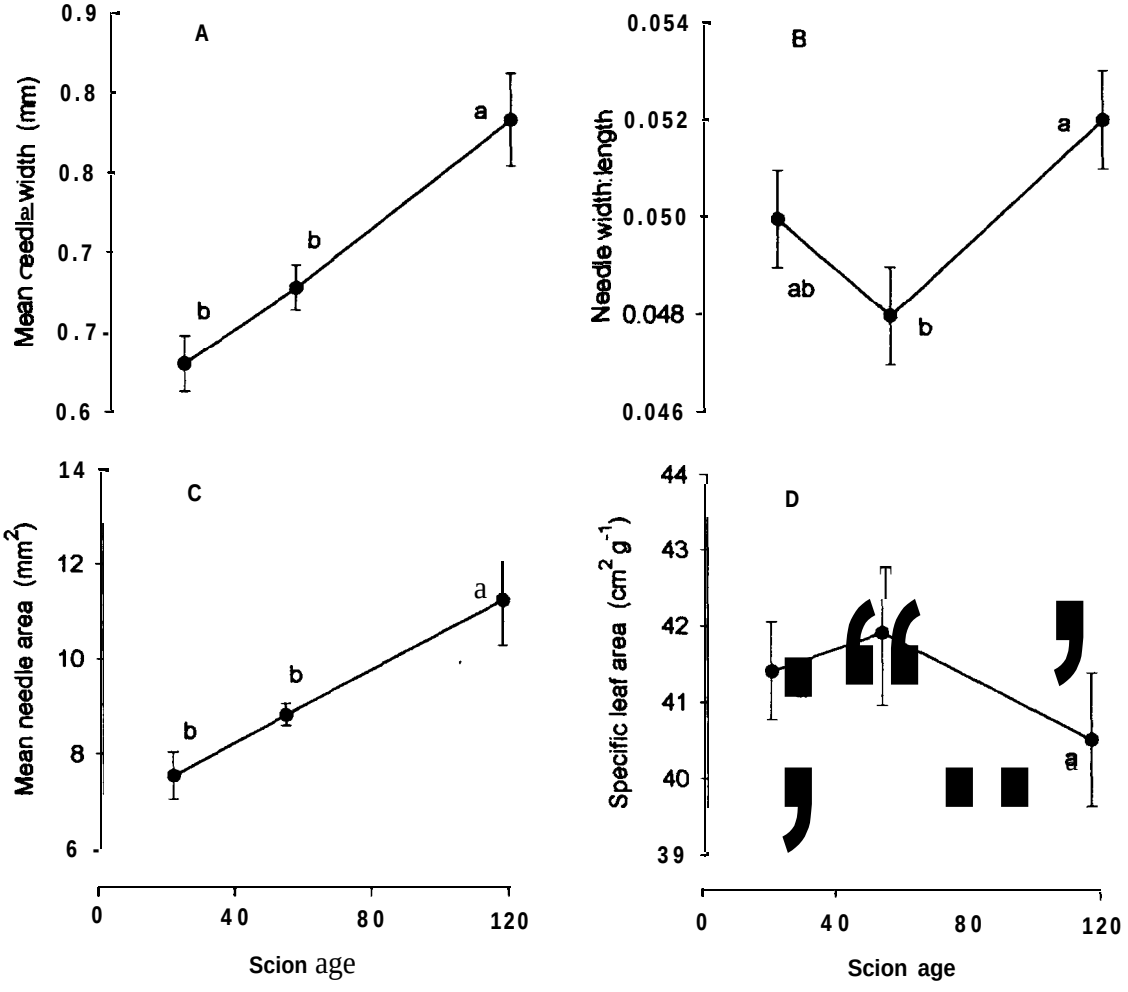

Figure 2.3. Trends in foliar morphological attributes of scions with age of donor in grafted scions after 3 growing seasons on rootstock of common age (n = 12): (A) mean needle width, (B) needle width-to-length ratio, (C) mean needle area, and (D) specific leaf area. Bars represent standard errors, and letters describe significantly different groupings of means separated by Duncan's New Multiple Range Test at $\alpha = 0.05$.

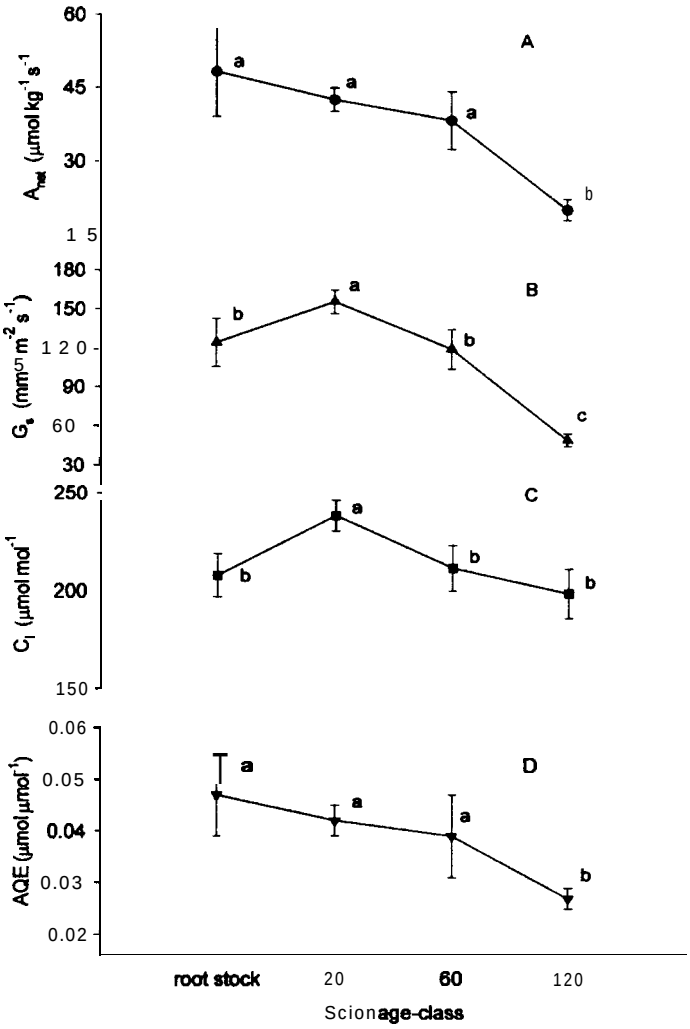

Figure 2.4. Gas exchange results from the grafted scion study during the third post-grafting growing season, with measurements from rootstock provided for comparison: (A) maximum rate of net photosynthesis, (B) maximum rates of stomata1 conductance to H_2O, (C) internal CO, concentration, and (D) apparent quantum efficiency (initial linear slope of photosynthetic light response curve). Bars represent standard errors, and letters describe significantly different groupings of means separated by Duncan's New Multiple Range Test at $\alpha = 0.05$.

allocation to root systems. However, in this multicohort stand, where individuals with contrasting foliar efficiencies were growing adjacent to one another, differential nutrient availability would be an unlikely cause of differing foliar efficiencies.

Morphological changes between juvenile and mature foliage (Fig. 2.2) correspond with those reported for red spruce by Rebbeck et al. (1994) and Sitka spruce by Steele et al. (1989). In red spruce growing in non-suppressed canopy positions, reproductive maturity usually occurs at about 25 years (Blum 1990). Thus, this study shows that age-related trends in foliar morphology continue well beyond reproductive maturity in both ***in situ*** shade- and sun-adapted foliage (Fig. 2.2), and in foliage of grafted scions growing on rootstock of common age (Fig. 2.3). Richardson et al. (2000) reported similar trends for hybrid Englemann x white x Sitka spruce, although they found that age-related morphological trends are complicated by canopy position (shade-sun adaptation). Richardson et al. (2000) also reported that foliar plasticity (defined as the relative difference between sun- and shade-adapted foliage) decreased with tree age. This is in contrast to the morphological differences found in this study where older age-classes showed greater morphological variation between sun- and shade-adapted foliage in all attributes tested (Fig. 2.2). This incongruity may represent true interspecific differences or be related to the greater PAR fluence intercepted by taller age-classes in multicohort stands. The lack of consistency in SLA trends between ***in situ*** foliage and that of the grafting experiment may be due to this, or, alternatively, may be an artifact of comparisons using one-year-old foliage in the field study and first year needles in the grafting experiment. Changes in SLA with needle age have been described in several conifers

(Gilmore et al. 1995, Hatcher 1990). In addition, physiological attributes such as A_{max} and G_s are significantly lower in one-year-old compared with current year foliage in red spruce (Day 2000).

The lower A_{max} of the 120 y cohort from both the field data and grafted scions supports the hypothesis that photosynthetic production decreases with tree age (Yoder et al. 1994, Ryan and Waring 1992). However, the lack of significant differences in G_s and C_i in the field study and the small differences in C_i between 60 y and 120 y scions in the grafting experiment do not support the hypothesis that lower maximum photosynthetic rates are due primarily to stomatal limitations to gas exchange (Yoder et al. 1994).

Alternatively, these results could be interpreted in a feedback model where stomatal conductance is in balance with lower inherent photosynthetic rates (Sharkey 1985). In turn, lower photosynthetic rates may be related to larger scale (branch-level or whole tree) carbon balance. In this model, investment in foliar photosynthetic capacity would be determined by demand for photosynthate or sink strength (Farrar 1992). Age- or size-related changes in meristematic activity would result in decreased sink strength in shoots of older trees (or grafts made with them), ultimately reflected in changes to foliar gas exchange attributes. Inverse relationships between inherent growth potential of scions and donor age have been reported for loblolly pine (*Pinus taeda* L.) by Greenwood (1984) and for eastern larch (*Larix Zaricina* (Du Roi) K. Koch) by Greenwood et al. (1989). In eastern larch, growth potential of grafted scions declines with donor age despite higher photosynthetic rates and chlorophyll content in their foliage (Hutchison et al 1990). After observing that meristems of larch scions from older donors produce cells of smaller

diameter than those of their younger counterparts when grafted on common rootstock, Takemoto and Greenwood (1993) proposed that resource acquisition of older scions may be limited by competitively weaker sink strengths.

In red spruce, a maturation-based sink-strength hypothesis is supported by the equivalent C_i levels between mid-aged trees with high A_{max} and G_s and old trees with lower rates for both processes. This relationship was consistent for both field (Table 2.2) and grafted scion (Fig, 2.4) studies. Further evidence of decreasing investment in photosynthetic capacity with tree age comes from the lower AQE of the older scion classes (Fig. 2.4d). The high-to-low light intensity protocol used for development of light-response curves in this experiment did not provide sufficient response times for G_s to equlibriate with photosynthesis at lowered light levels (20-30 minutes: M. Day, unpublished data). Thus, except at saturating irradiances, G_s was at a greater level than would normally occur for prevailing PPFD, and C_i would presumably not be limiting over the range of light intensities (10 - 60 $\mu mol\ m^{-2}\ s^{-1}$) used to determine AQE.

After three growing seasons, grafted scions exhibited age-related trends in foliar morphology and physiology corresponding to those found in the field population, indicating that age-related characteristics are retained for at least several growing seasons by scions grafted to juvenile rootstocks. Thus, red spruce meristems from older trees appear to retain a ‘memory’ with respect to the attributes of foliage they produce. Such a scenario may explain the lack of foliar response to experiments designed to alter stomata1 conductance or photosynthesis by manipulating leaf-specific conductivity of branches (Brooks et al. 2000, Hubbard et al. 1999).

It is unclear whether this meristematic memory is age-related in the strict sense (related to an internal timing mechanism) or is induced by signals related to tree size that cause changes in metistematic gene expression. In the latter model, attributes would ultimately be determined by such intrinsic factors as whole-tree conductivity or carbon sink strength. Foliage produced by the meristems would have characteristics that are adaptively superior for the changing challenges to survival faced by trees as they grow larger. Considering the ability of red spruce to persist for decades as suppressed individuals in forest understories then grow to upper canopy status following release (Davis 1991, Blum 1990), the internal clock model seems unlikely, and a model that incorporates induction by intrinsic or extrinsic factors would appear to offer the most promising explanation.

In either case, these results imply that the expression of genes in meristems is altered as trees grow older or larger beyond reproductive maturity or mid-age. Differences in genetic expression have been demonstrated during early growth (Emebiri et al. 1998) and linked to phase changes between juvenile and reproductively mature individuals for several species (Hutchison et al. 1990). New techniques that can simultaneously evaluate the activity of thousands of genes provide much promise for evaluating changes in genetic expression with respect to later life-stages.

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Chapter 3: Influence of temperature and leaf-to-air vapor pressure deficit on net photosynthesis and stomatal conductance in red spruce*

Abstract

A field study and controlled environment experiment were used to investigate the roles that temperature (T) and leaf-to-air vapor pressure deficit (VPD) play in regulating net photosynthesis (A_{net}) and stomatal conductance (G_s) of red spruce (*Picea rubens* Sarg.). The species exhibited a relatively flat response between 16 - 32 °C for both A_{net} and G_s. Apparent threshold effects markedly decreased both A_{net} and G_s between 32 and 36 "C. Vapor pressure deficit had significant effects on both A_{net} and G_s at values > 2 kPa. The influence of VPD fit a linear response model and did not interact significantly with T effects.

Introduction

In northeastern North ***America,*** red spruce ***(Picea rubens Sarg.)*** has historically been a major component of conifer and mixed hardwood-softwood associations and one of the most economically desirable species for lumber and fiber (Seymour 1995). However, recent evaluations of stand conditions in the northeastern forest have given rise to concerns about the continued abundance of red spruce in low-elevation forests. Recent USDA Forest Service inventory data (Griffith and Alerich 1996) indicate that red spruce has exhibited a dramatic decline and is being replaced by balsam fir ***(Abies balsamea Mill.)***

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and several hardwood species (Seymour 1985, Livingston 1998). Harvesting practices and/or climatic changes that decrease the presence of microenvironments favorable for regeneration and early growth of the species may be contributing to this decline.

Several lines of evidence suggest that this species is sensitive to high air temperatures and low atmospheric humidity. Optimum conditions for regeneration of *P. rubens* have been associated with partially closed canopies (Davis 1991, Seymour 1992), indicating that environmental conditions under more open or absent overstory canopies may inhibit early growth. Recent palynological evidence suggests that, during warmer and drier periods of the Holocene, spruce may have been restricted to refugia within the coastal 'fog belt' that subtends the Bay of Fundy (Schauffler 1998). Intolerance of high temperatures and a requirement for high atmospheric humidity have been cited as common attributes of tree species currently restricted to coastal ranges (Laderman 1998).

Alexander et al. (1995) reported a temperature optimum for net photosynthesis of about 20 °C for understory *P. rubens* saplings. Vann et al. (1994) found significant inhibition of photosynthesis at higher air temperatures (> 25°C) and related the response to current range limits and changes that might be associated with a warming climate. A 20 °C optimum is consistent with predictions for C3 species at current atmospheric concentrations of 21 % 0, and 300-350 µmol CO, mol^{-1} air, based on differential selectivity of ribulose-bisphosphate carboxylase/oxygenase (Rubisco) for CO, and 0, and effects of temperature on the water solubility of the two gasses (Ku and Edwards 1977a, Tolbert 1994).

Although no studies have been published on the effects of atmospheric humidity on carbon gain by *P. rubens*, work on related species suggests a possible influence. In Sitka spruce (*P. sitchensis* (Bong.) Carr.), a species of the moist maritime forests of western North America, increasing leaf to air vapor pressure deficits (WD) result in significant inhibitory effects on stomatal conductance (Ludlow and Jarvis 197 1, Running 1976, Sanford and Jarvis 1986). Kaufmann (1976) reported a similar response for the subalpine Engelmann spruce (*P. engelmannii* Engelm.). Research by Marsden et al. (1996) suggests that high WD may inhibit early growth of outplanted white spruce (*P. glauca* (Moench) Voss) seedlings.

In this study, I tested the hypothesis that increasing WD and T, acting singly or interactively, would reduce photosynthetic carbon gain in sapling *P. rubens*, and evaluated the potential for these factors to limit carbon gain in natural populations. A preliminary investigation determined responses under field conditions. This was followed by an experiment in a controlled environment to separate influences of WD and temperature, which were highly correlated in the field study, and to examine the possibility of interactive effects between those variables.

Methods

For the controlled environment experiment, nine individuals were randomly selected from a population of 4-year-old, 0.5-m high, potted red spruce. The trees were placed in a greenhouse in mid-January after cold requirements had been met, repotted in 25-L pots containing a mixture of 50% peat, 25% sand, and 25% vermiculite, and fertilized with 18-6-12 Osmocote (Sierra Chemicals) time-release fertilizer at a rate of

0.124 kg m^{-3}. While in the greenhouse, soil was watered to field capacity every 3 days. New foliage had flushed by early February and was fully expanded with bark of twigs appearing lignified by the time of the experiment (May 1 through June 7, 1998). Because of imperfect environmental controls in the greenhouse, trees were subjected to a highly variable environment with daytime temperatures of 15 to 38 °C and vapor pressure deficits (VPD) ranging from near zero to over 3.5 kPa. Midday n-radiances were typically 1200 to 1500 $\mu mol\ m^{-2}\ s^{-1}$ PPFD during clear weather.

The controlled experiment was carried out in an environmental chamber (I-37 Series, Percival Manufacturing Company, Boone, IA) where all components could be maintained at the test temperature (T,). This prevented condensation within cuvette and control systems at high T and low VPD. The chamber allowed three individuals to be treated per day. Temperatures were randomly assigned to each of 18 days, with each T_e occurring in each of three replicates. Three trees were assigned to each T_e without replacement; thus, each individual was tested at each T_e only once. Trees were placed in the chamber the day before measurement and held at a photoperiod of 16 h day (at T,) and 8 h night (at T_e less 7 “C). Four fluorescent lights provided about 250-300 $\mu mol\ m^{-2}\ s^{-1}$ PPFD within the chamber. Soil water was maintained near field capacity during the experiment. Twig samples removed following gas exchange measurements had a mean xylem pressure potential (ψ_{xylem}) of -0.3 MPa (pressure chamber method, Koide et al. 1989) and no correlation between T_e and ψ_{xylem}. Sampling order of trees within chamber runs was random.

A LI-6400 photosynthesis system equipped with a standard 2 x 3 cm leaf cuvette

and a model 6400-02B light source (Li-Cor, Inc., Lincoln, NE, U.S.A.) was used for gas exchange measurements. This system permitted accurate control of cuvette temperature and h-radiance. Constant VPD within the leaf chamber was maintained with a LI-610 dew-point generator (Li-Cor, Inc.) and a column of calcium sulfate desiccant in the input air stream. To compensate for changes in T,, the IRGAs were zero-calibrated on a daily basis. CO, and H_2O span values were calibrated weekly. Temperature control and VPD calculations were based on leaf temperature, measured by a fine wire thermocouple. h-radiance within the cuvette was maintained at 1400 $\mu mol\ m^{-2}\ s^{-1}$ (photosynthetically active radiation, 400 - 700 nm) based on preliminary determinations of saturating light intensity at the shoot-level.

Gas exchange was measured on attached terminal shoots of lateral branches from the upper one-third of the crown. Each measurement series began at 0900 and was finished by 1430. The cuvette was applied at the center of current-year growth. Gas exchange was permitted to stabilize for approximately 40 minutes before measurements were made. A preliminary study of response times to increases in VPD, using the same population, indicated that stability of stomatal conductance occurs within 20 to 30 minutes, and response to new light regimes stabilizes after less than 5 minutes. Before every measurement, stability of net photosynthesis and stomatal conductance were also verified using real time strip chart output. In all cases, VPD was manipulated from low to higher values. Previous work indicated that stable response of gas exchange to increasing humidity regimes can require several hours, which would preclude completing a series of measurements in a single day.

Measurements were made at six temperatures (16, 20, 24, 28, 32, and 36 “C) and three VPDs (2.0, 2.75, and 3.5 kPa). All VPDs were tested for runs where $T_e \geq 28$ “C. Because maximum VPD is constrained by temperature-related saturation vapor pressures, only a VPD of 2 kPa was tested at 20 and 16 “C, and 24 °C received VPD treatments of 2 and 2.75 kPa. Temperatures were maintained ± 0.2 °C and VPD ± 0.1 kPa during measurements.

After gas exchange measurements were completed, leaf areas were determined by stripping all needles from the section that was enclosed in the cuvette, scanning at high resolution, and analyzing the image with the computer program Needle 4.3b (Reagent Instruments, Quebec). Projected needle areas were converted to half-total areas using a ratio of width to perimeter (1.45) previously developed from analysis of 100 needle cross sections. Considering the quadrate cross-sectional shape of red spruce needles, even distribution of stomates on ab- and adaxil surfaces, and directional nature of the light source, a half-total area basis provides a good description of the active photosynthetic surface in this experiment. These needle areas were used to calculate net photosynthesis and stomatal conductance using the standard algorithms of Li-Cor’s Open 3.2 operating system (Li-Cor 1998) with broad band correction for water vapor.

Field measurements were made in July 1996, on one-year-old, randomly selected upper crown, terminal shoots from saplings (0.5 to 2 m high) growing in the Penobscot Experimental Forest, Bradley and Eddington, Maine. These trees were growing in the open after release by a shelterwood overstory removal cut two years before measurement. The same instrumentation (except the light source was a Licor 6400-02), calibration

procedures, and methods for determining needle area as described for the chamber experiments were used to collect field data and calculate gas exchange rates. In this case, temperature was maintained at ambient and VDP was measured at randomly selected levels of ambient, 75% ambient, or 50% ambient (if saturation vapor pressure permitted). Single measurements were made on individual trees.

Correlations were examined with Pearson's product-moment correlation coefficients, and probabilities for r = 0 tested by Bonferroni adjustment (Snedecor and Cochran 1989). Data from the controlled environment experiment were divided into subsets to test specific hypotheses by analysis of variance (ANOVA). In all analyses, each of the trees in a chamber run were considered subsarnples and effects tested with the replicate by effect variable error term. Specific temperature effects over the range of 16 to 36 °C were analyzed by holding VPD constant at 2 kPa, a typical midday value for forest canopies in this region (unpublished data, Forest Ecosystem Research Program, University of Maine). To minimize threshold effects that occur between 32 and 36 "C, influences of VPD were evaluated based on the data for $T_e < 36$ °C. Interactive effects were assessed with a balanced 3 x 3 factorial design over the temperature range of 28, 32 and 36 °C and VPD 2, 2.75, and 3.5 kPa. The SAS statistical package (Release 6.12, SAS Institute, Cary, NC, U.S.A.) was used for all analyses. To meet the assumptions of ANOVA, analysis of A_{net} and G_s responses were performed on log-transformed data. The SAS GLM procedure was used for ANOVA to compensate for the unbalanced design of the VPD response analysis. For T effects at VPD = 2, means were separated by Tukey's HSD test to control experiment-wise error rate with a large number of factor levels. Because of the

smaller range of factor levels in the other analyses, the more sensitive Duncan's multiple range test was selected to separate means. Polynomial contrasts (Snedecor and Cochran 1989) were used to analyze the forms of response that A_{net} and G_s exhibited to increasing WD.

Results

The field data (Fig. 3.1) indicated that both net photosynthesis (A_{net}) and stomatal conductance (G_s) were significantly correlated with leaf-to-air vapor pressure deficit (WD): Pearson's r of -0.80 and -0.78, respectively; both $P < 0.0001$. However, WD was also highly correlated with ambient temperature ($r = 0.76$, $P < 0.0001$) which varied from 16 to 29 "C. A strong correlation between A_{net} and G_s ($r = 0.91$, $P < 0.0001$) indicated that stomatal resistance provides significant control over gas exchange.

The scatter of the field data suggested that the influence of WD on G_s was much weaker at lower VPDs. Points representing WD < 2 kPa and included measurements from that range made during the growth chamber study (Fig. 3.2). At WD < 2 kPa, neither data set showed a significant correlation between WD and G_s ($r = -0.07$, $P = 0.75$ for field data and $r = -0.26$, $P = 0.27$ for growth chamber measurements). In Fig. 3.2 the cloud of data points for environmental chamber trees lies generally above that representing the field population. This is probably because of the difference in foliage cohort measured in the two studies: current-year needles for the chamber experiment and one-year-old foliage for the field survey. In mature (upper canopy) *P. rubens*, mean differences in G_s of 46% between the two cohorts have been observed (M. Day, unpublished data), presumably related to buildup of waxes in epistomatal cavities.

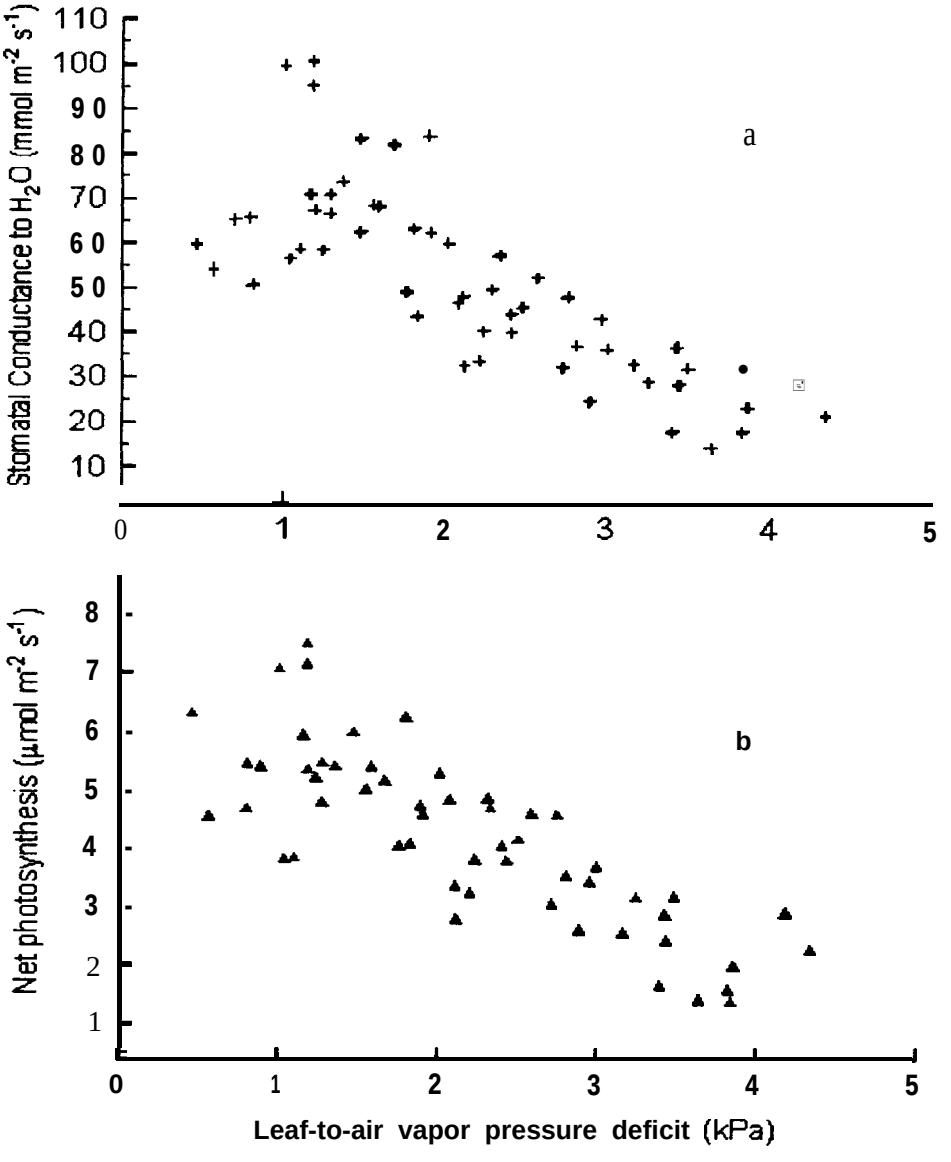

Figure 3.1. Field data showing the relationship between leaf-to-air vapor pressure deficit and (a) stomata1 conductance and (b) net photosynthesis for red spruce. Measurements are for l-year-old upper crown foliage on trees 0.5-2 m tall, growing in full sunlight (n=54). Pearson's r for stomata1 conductance = -0.80 ($P < O.OOOl$), and for net photosynthesis r = -0.78 ($P < 0.0001$).

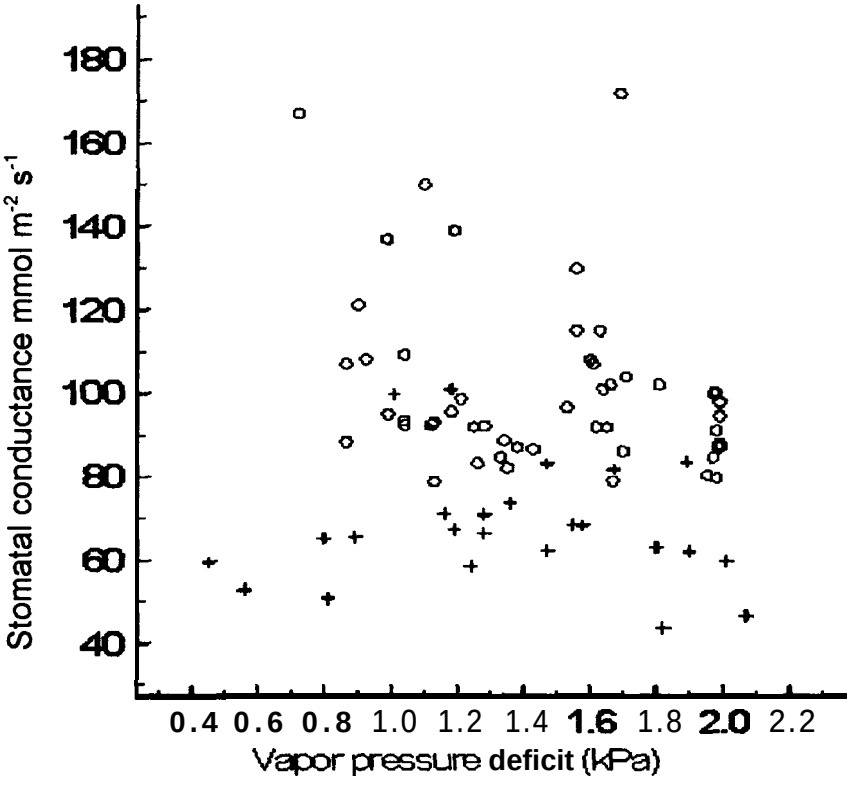

Figure 3.2. Response of stomatal conductance in red spruce to leaf-to-air vapor pressure deficits in the range of 0.4 to 2 kPa. '+' indicates data from l-year-old foliage in the field population and 'o' current year needles on potted trees in an environmental chamber. Ambient air temperatures varied between 16 and 24 °C for both data sets. Pearson's r for field data = -0.07 (P = 0.75). For environmental chamber data r = -0.26 (P = 0.27). The generally higher conductance values of the environmental chamber foliage are largely attributable to effects of needle age on stomatal resistance.

Results of the controlled environment experiment with VPD held constant at 2 kPa showed a broad temperature optimum (16 - 32 "C) for photosynthetic response to temperature (Fig. 3.3). A peak in A_{net} (statistically nonsignificant) occurred at 20 °C, and a conspicuous decline developed between 32 and 36 °C. Although G_s appeared to decrease monotonically with increasing temperature (Fig. 3.4), only the value at 36 °C is significantly below the rates at lower temperatures, suggesting a response threshold at 32 °C or slightly above.

Figure 3.4 also indicates that the relationship between internal CO, concentration (C_i) and G_s is inconsistent. This suggests that stomates are not responding in a predictable

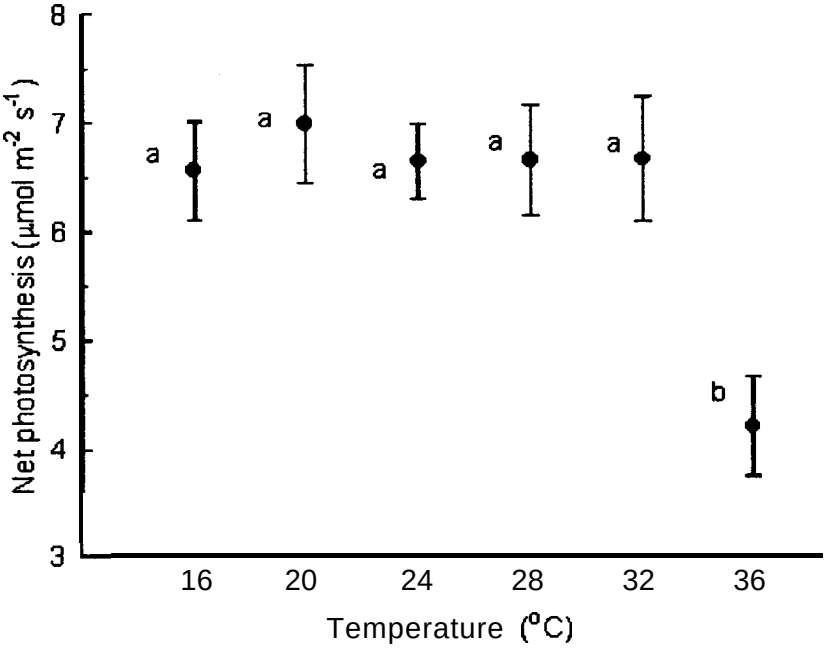

Figure 3.3. Response of net photosynthesis in red spruce to temperature at a constant leaf-to-air vapor pressure deficit of 2 kPa. Letters indicate Tukey's HSD groupings at $\alpha = 0.05$. Bars show 1 standard error.

fashion to C_i during the experiment. The C_i increased at higher temperatures, implying that the rapid decrease in A_{net} above 32 °C was not caused by stomatal limitation of gas exchange.

In contrast, responses of both A_{net} and G_s to increasing VPD showed appreciable decreases (Fig. 3.5). However, standardized rates of reduction were not proportional between G_s and A_{net}. Mean rates of G_s dropped 43.6% between 2 and 3.5 kPa, whereas A_{net} declined by 26.3% over the same range. Thus A_{net} appears to respond to VPD at about 60% of the standardized rate for G_s. This relationship between the two response

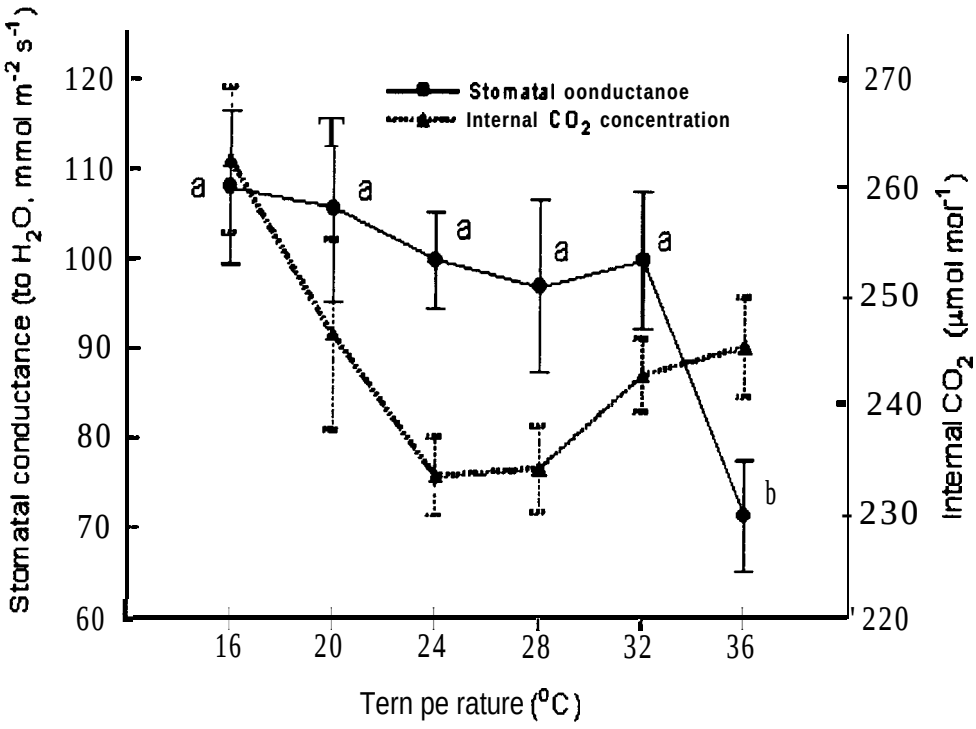

Figure 3.4. Responses of stomatal conductance (●) and internal CO_2 concentration (A) to temperature at constant vapor pressure deficit (2 kPa). Letters indicate Tukey's HSD groupings at α = 0.05. Bars show 1 standard error.

variables is similar to that found in the data of Sanford and Jarvis (1986) for Sitka spruce. For that species, A_{net} decreased less than 30% between 0.5 and 2.0 kPa, whereas G_s dropped by approximately 60%. Compared to *P. rubens*, the rate of decrease reported for *P. sitchensis* was much steeper on both unit and standardized bases. Polynomial contrasts indicated that the responses of A_{net} and G_s to increasing VPD were best described as linear. Higher order models tested as insignificant.

Factorial analysis of T and VPD responses at 28, 32, and 36 °C provided nonsignificant interaction terms for both A_{net} and G_s (Table 3.1).

Discussion

Response to temperature

In this C3 species adapted to cool temperate climates, the observed broad plateau for temperature response (Fig. 3.3) is somewhat surprising and qualitatively different from that described by Alexander et al. (1995). Those authors reported an unequivocal peak at 20 °C followed by a decline to 47% of maximum at 30 °C. Whereas, in this study there was a relatively flat response to temperatures ≤ 32 °C.

Alexander et al. (1995) attributed the decline in net photosynthesis (A_{net}) with increasing temperatures (> 20 °C) to a greater proportion of photosynthate allocated to maintenance respiration (R_{dark}). Their data suggest that at 20 °C shade-adapted saplings allocate approximately 18% of gross photosynthesis ($A_{gross} = A_{net} + R_{dark}$) to R_{dark}. This

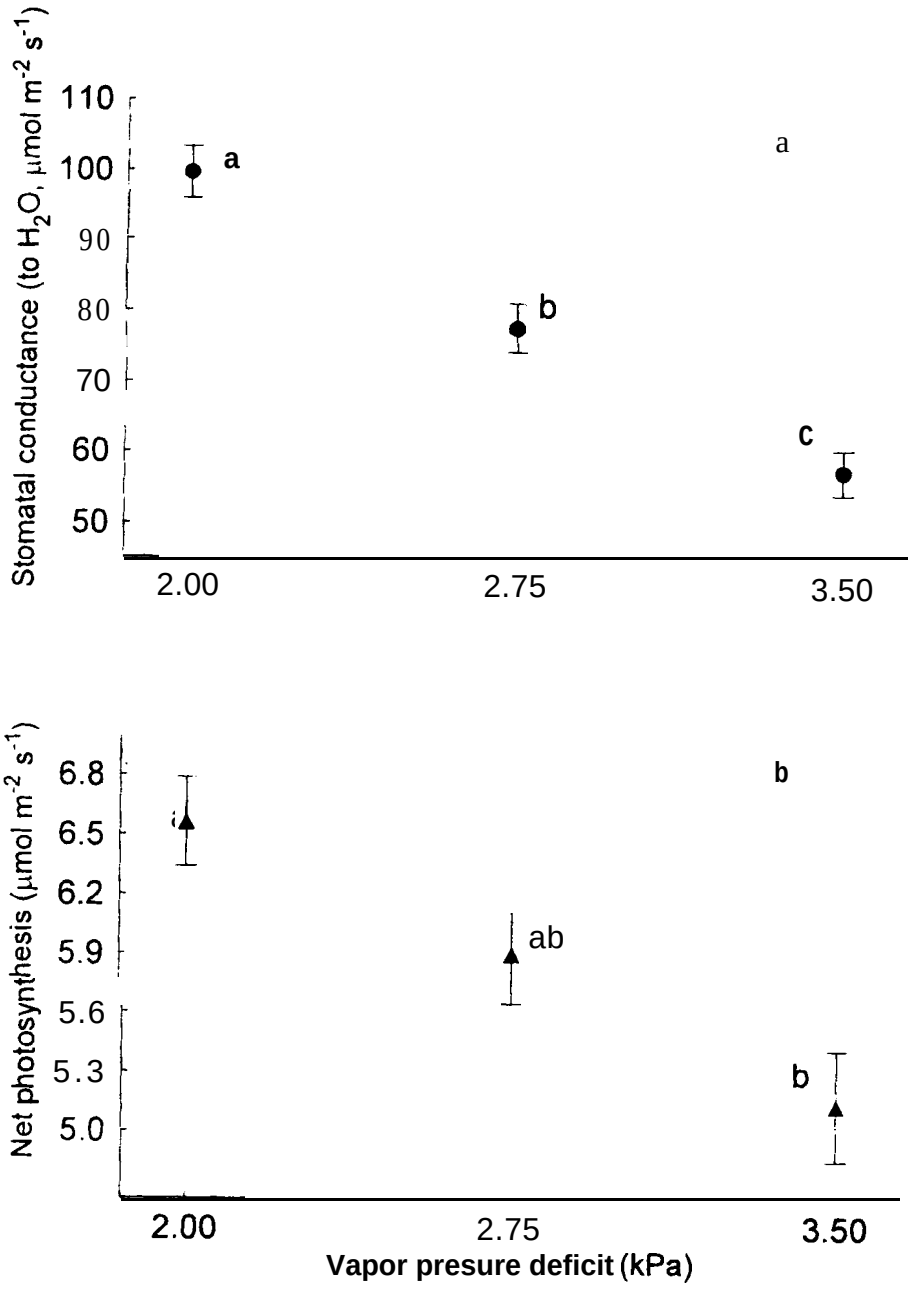

Figure 3.5. Rates of (a) stomatal conductance and (b) net photosynthesis at three levels of leaf-to-air vapor pressure deficit for the environmental chamber experiment. Bars give one standard error, and letters indicate Duncan's multiple range test groupings at $\alpha = 0.05$.

Response variable	Source	df	Type III MS	F value	P > F
Log, net photosynthesis:					
	Temperature	2	1.0735	26.79	0.0048
	VPD	2	0.3876	119.71	0.0003
	TxVPD	4	0.000945	0.16	0.9551
Log,, stomatal conductance:					
	Temperature	2	0.8399	8.36	0.0372
	VPD	2	1.6605	129.85	0.0002
	TxVPD	4	0.00924	0.93	0.4925

Response variable	T °C	Mean µmol m^{-2} s^{-1}	Duncan Grouping	VPD kPa	Mean µmol m^{-2} s^{-1}	Duncan Grouping
Net photosynthesis:						
	28	5.91	a	2.0	5.58	a
	32	5.75	a	2.75	5.11	b
	36	3.70	b	3.5	4.40	c
Stomatal conductance:						
	2%	74.96	a	2.0	86.05	a
	32	76.10	a	2.75	70.25	b
	36	55.66	b	3.5	52.55	c

Table 3.1. Response of net photosynthesis and stomata1 conductance to temperature and leaf-to-air vapor pressure deficit. Results of ANOVA for 3 x 3 factorial with temperature levels of 28, 32, and 36 °C and leaf-to-air vapor pressure deficit levels of 2, 2.75, and 3.5 kPa. Duncan's multiple range test groupings show significant differences between means at a = 0.05.

ratio increased to 28% at 25 °C and 52% at 30 °C. Over this range, A_{gross} exhibited a slight decrease from 2.7 $\mu mol\ m^{-2}\ s^{-1}$ at 20 "C, to 2.2 at 30 "C. Their A_{net} rates are consistent with *in situ* rates (2.5 $\mu mol\ m^{-2}\ s^{-1}$ at 20 °C) the author has measured for shade-adapted *P. rubens* of comparable size (0.5-l. 5 m height), although their ratio of R_{dark} to A_{gross} is higher (18% versus 12.8%). In contrast, sun-adapted foliage measured on open grown saplings showed a ratio of R_{dark} to A_{gross} of 6.6% (M. Day unpublished data). This comparison suggests temperature-related increases in R_{dark} have a much smaller effect on A_{net} in sun-adapted foliage.

Whole tree respiratory demand, which would be expected to increase proportionally with temperature, may also contribute to explaining the broad temperature plateau by another pathway. Weak carbohydrate sink strength or reduced phloem loading can have a negative feedback effect on photosynthetic rates (e.g., Leverenz 1981, Stitt 1991). In the environmental chambers, only the shoot section used for gas exchange measurements received saturating irradiance. The balance of foliage was exposed to the lower light levels provided by growth chamber lamps and would be a relatively poorer source for export of photosynthate.

Variation in temperature response among genetic lines or provenances and effects associated with plastic preconditioning may complicate comparisons across studies. Neilson et al. (1972) found that temperature optima varied among five provenances of Sitka spruce with one showing little change in A_{net} between 15 to 28 °C. This one was from stock with long term exposure to higher temperatures. Those authors also reported a correlation between time of year and T,, providing evidence of preconditioning effects.

Trees used by Alexander et al. (1995) were collected from forest understories in Vermont, U.S.A., at elevations of 380 and 945m, where temperature regimes would be expected to be moderately cool. In contrast, greenhouse-maintained stock used in this experiment had experienced temperatures greater than 30 °C on 10% of the days between initial budburst and sampling.

Measuring air temperature as opposed to leaf temperature may bias the resulting response curve. In both natural environments and gas exchange cuvettes conifer leaf temperature may diverge substantially from ambient air temperature under high n-radiance. For instance, Vowinckel et al. (1975) reported open air needles under mid day irradiance of *Picea mariana* exceeded air temperature by over 7 °C and in cuvettes by 5 °C. In a previous study with detached shoots of red spruce (M. Day, unpublished data), differentials of >5 °C were observed under both natural and artificial illumination in 0.25 to 1 .O 1 cuvettes that were equipped with circulating fans. It appears that neither Alexander et al. (1995) nor Vann et al. (1994) directly measured needle temperature. If needle temperature was higher than ambient, their reported photosynthetic optimums would show bias towards lower temperatures. Additionally, if needle temperatures exceed air temperature, VPD at leaf surface might be higher than that calculated on an air temperature basis, providing the potential of VPD-induced limitations to G_s.

The threshold response to temperature that occurs above 32 °C may indicate disruption of one or more components of the photosynthetic carboxylation pathway. However, this temperatures is lower than those generally associated with disruption of enzymatic and membrane systems (Salisbury and Ross 1992, Kozlowski et al. 1991).

Alternatively, the temperature-dependent influence of photorespiration on A_{net} (Jolliffe and Tregunna 1968, Ku and Edwards 1977b, Monson et al. 1982) may provide an explanation. The solubility ratio of 0, to CO, in the mesophyll symplast increases exponentially with temperature (Ku and Edwards 1977a), and Ogren (1984) has proposed that temperature and specificity of rubisco for 0, are directly related. Tolbert (1994) suggested 40 to 65 $\mu mol\ mol^{-1}$ atmospheric CO, concentration as an effective compensation point (zero A_{net}) for C3 plants at 20 °C, 110 $\mu mol\ mol^{-1}$ at 30 "C, and 300 $\mu mol\ mol^{-1}$ at 37 °C. Thus, at the highest temperature (36 "C) and 350-380 $\mu mol\ mol^{-1}$ CO, the trees in this experiment were close to their predicted CO, compensation points. In this conceptual model, the abrupt drop in A_{net} between 32 and 36 °C reflects a rapidly increasing 0, to CO, solubility ratio and perhaps shifts in the substrate afiinity of rubisco. This interpretation is consistent with the observed increase in C_i while G_s is decreasing at higher temperatures (Fig. 3.4) and the positive relationship between temperature and mesophyll resistance to CO, reported by Neilson et *al.* (1972) for *P. sitchensis.*

Increasing temperature also appeared to have an influence on G_s, independent of its effects on photosynthesis (Table 3.1). While decreases in A_{net} are known to be reflected by G_s and mediated by increased C_i (Mansfield 1985), the inconsistent relationship between G_s and C_i shown in Fig. 3.4 argues against this effect occurring here. A possible explanation may involve a stress-induced increase in active abscisic acid (Weiler et al. 1982) which could be mediated by changes in apoplastic pH (Wilkinson and Davies 1997) at the leaf level.

Effects of vapor pressure deficit

A negative response of G_s and A_{net} to increasing VPD has been described for several other members of the genus ***Picea*** and is confirmed here for ***P. rubens*** (Table 3.1, Figs. 3.1 and 3.5). In general, red spruce appears to be less sensitive to VPD at the lower end of the scale (Fig. 3.2) than its congeners from western North America. Ludlow and Jarvis (1971), Running (1976), Sanford and Jarvis (1986), and Warkentin et al. (1991) all describe response ***curves*** for ***P. sitchensis*** that drop precipitously as VPD becomes greater than 0.5 kPa. Kaufmann's (1976) curve for ***P. engelmannii*** showed a similar response. Interestingly, Darlington et al. (1997) found that ***P. mariana,*** which is closely related to and can hybridize with ***P. rubens*** in the sympatric portions of their ranges (Gordon 1976), showed no significant difference in biomass accumulation between seedlings grown in 0.3-0.8 kPa and 2.0-2.5 kPa VPD regimes. Although gas exchange rates were not measured in that experiment, their results are indicative of a relatively high threshold for VPD response and/or a response curve with low slope.

The pattern of response to VPD found in red spruce may relate to comparatively low maximum rates of G_s in this species (Figs. 3.la and 3.5a, Eamus and Fowler 1990). In contrast, Sanford and Jarvis (1986) report rates of G_s in ***P. sitchensis*** as approaching 300 mmol m^{-2} s^{-1}. When compared to its co-occurring conifer species and other members of the genus ***Picea,*** red spruce is relatively slow growing; thus, its low rates of G_s may reflect an adaptation to permit adequate gas exchange while minimizing water loss. This might help to explain its success on potentially water-deficient sites with shallow, primarily organic soils overlying bedrock or hardpan.

As with temperature, preconditioning or interactions with other environmental factors may alter response to VPD (Wiebel et al. 1993). The shade-adapted trees used by Alexander et al. (1995) may have had a lower threshold for VPD effects than the sun-adapted experimental stock used here. Additionally, interactions between soil moisture and VPD effects have been described for other species (e.g. Grieu et al. 1988). When Alexander et al. (1995) collected their sample trees they included a 20 cm diameter by 15 cm deep soil plug. As any roots extending outside of this zone were severed, it is likely that their trees (20-50 cm in height) would be experiencing water stress during laboratory treatments, even if soil was kept well-watered. These conditions may have lowered natural VPD thresholds and/or increased the steepness of that response.

Response differences between spruces may result from adaptation to regional humidity regimes and/or other factors in their overall (air + soil) moisture environments. Decreased sensitivity to VPD at higher humidity levels may represent an adaptation to the regional climate of northeastern North America, where VPD levels ≥ 2 kPa are common during the growing season. Data collected at a spruce plantation in the Penobscot Experimental Forest indicate that levels of greater than 2 kPa, based on leaf temperature, occurred on 91% of days during July and August, 1998, and on 83% under a partial canopy in a selection stand (unpublished data, Forest Ecosystem Research Program, University of Maine). This can be contrasted with the range of Sitka spruce in the Pacific Northwest where atmospheric VPD levels ≥ 1 kPa are uncommon (Warkentin et al. 1992).

Implications for population dynamics and management

It has been proposed that mean annual temperature decreases of approximately 1 °C allowed red spruce to expand its range across northeastern North America during the past 1 ka (Schauffler 1998), and that future success of the species may be inhibited by increases in temperature predicted for the next century (Vann et al. 1994). The relatively robust response of A_{net} and G_s to temperature reported here suggests that modest increases in daytime temperatures during the growing season are unlikely to significantly hinder gas exchange in *P. rubens*. However, daytime maxima that result in needle temperatures in excess of 32 °C could have a dramatic effect on carbon gain. Increases in overnight temperatures may elevate losses to dark respiration, which would be expected to have a greater negative effects on shade-adapted individuals. Also, small changes in carbon balance stress may have long term consequences for population dynamics by limiting reproductive output (Harper and White 1974) or increasing susceptibility to pests or pathogens (Warkentin et al. 1992).

The influence exerted by VPD could be a factor in presettlement range movements and may be related to restriction of the species to coastal refugia during periods of warmer (and potentially drier) climate prior to 1 ka and in the future. However, a complete characterization of environmental controls on population dynamics in red spruce will also require an understanding of the role of other factors (such as soil temperature and moisture, disturbance regimes, and seedbed availability) that influence establishment and early growth.

While red spruce commonly regenerates under partially closed canopies, it also

appears to be capable of tolerating, in terms of gas exchange responses, the temperature and VPD environments found in large canopy openings. In those environments, higher light intensities could maximize growth, while lower night time temperatures (Childs and Flint 1987, McCaughey 1989) would reduce losses to R_{dark}. Supporting this suggestion, Hughes and Bechtel(1997) found, along transects running from intact forests into clear-cuts, that *P. rubens* saplings farther from overstory shade exhibited greater stem diameters.

This study supports the hypothesis that current decreases in the abundance of *P. rubens* in low-elevation forests has been more a consequence of harvesting practices and interspecific competition than environmental variables. Seymour (1992) has proposed its abundance in presettlement forests was favored by a combination of shade-tolerance and longevity. These results suggest that the cool temperatures and decreased VPD associated with understory environments are not intrinsic requirements for regeneration under the current climatic regime, thus its shade-tolerance can be viewed as an adaptation to surviving competition from faster growing associates. Nevertheless, differences in physiology of sun- and shade-adapted foliage and preconditioning appear to be important determinants of this species' ability to take advantage of environments with higher h-radiance.

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Chapter 4: Microclimates created by silvicultural systems and their influence on photosynthetic carbon gain in red spruce

Abstract

Micrometeorological conditions were monitored over a growing season at sites in stands (two replicates each) managed under three diverse silvicultural systems: selection, shelterwood, and clearcut-plantation. The resulting data were input into a carbon gain model, based on physiological response functions of red spruce to light, temperature, and leaf-to-air vapor pressure deficit. Summaries of micrometeorological data and output from the model were used to (1) assess microclimatic differences among stand-types and variation within stand-types, (2) evaluate the relative influence of environmental factors on photosynthetic carbon gain in sapling red spruce, (3) determine how microclimatic differences translate into differences in net carbon gain among and within stand-types, and (4) estimate how these differences would affect net photosynthetic carbon gain under scenarios of cooling or warming climates.

The silvicultural regimes evaluated (selection, shelterwood, and clearcut systems) resulted in substantially different microclimates. However, the magnitude of differences may not be apparent if bulk air properties alone are monitored. Dissimilarities become clearer when physiologically relevant attributes, such as foliar temperature, are considered.

While gross photosynthesis, thus potential photosynthetic carbon gain, is highly correlated with incident light flux density, the interaction of this variable with photosynthetic light-response curves is of significant importance in integrated carbon gain.

Attributes of these response curves not only vary between species, but are also due to differences in light-adaptation status within species.

Modeling the integrated influence of microclimate on photosynthetic carbon gain variables indicated that the indirect effects of temperature (vapor pressure deficit and maintenance respiration) are more significant than direct inhibition of photosynthesis by temperature. Vapor pressure deficit was found to be the factor having the greatest inhibitory effects on photosynthetic carbon gain in red spruce. Among silvicultural systems, photosynthetic carbon gain is most strongly limited by light in selection stands and by temperature related factors (inhibition by temperature and vapor pressure deficit) in shelterwood and clearcut systems.

The effects of competition on availability of belowground water resources influences transpirational flux and loss of foliar heat through latent energy transfer. This aspect is especially important in controlling temperature-related inhibitions to carbon gain in the high-energy environments of clearcuts.

With respect to net photosynthetic carbon gain of upper-crown foliage in red spruce saplings, stand-types were ordered selection < clearcut ≈ shelterwood under current-climate temperature regimes. In cooler-climate scenarios this relative order was maintained, but, in absolute terms, the superiority of clearcut and shelterwood over selection systems increased. Under warmer-climate scenarios the order was selection ≈ clearcut < shelterwood , with the latter showing clear superiority over the other stand-types. This may provide a partial explanation for reported changes in distribution of red spruce in the

Acadian region during the Holocene, and has implications for future distribution and management under predicted climate change scenarios.

Introduction

Numerous factors in the external environment can influence photosynthetic carbon gain (reviewed by Teskey et al. 1995). These may act either directly on photosynthetic rates (e.g., light intensity) or indirectly by regulating supply of reaction substrates (e.g., stomatal effects on CO, uptake). Additionally, external factors may influence carbon gain through complex internal pathways, such as low soil water potential causing production of abscissic acid in roots which, when transported to leaves, induces stomatal closure (Zhang and Davis 1990).

Leaf temperature (T_{leaf}) has direct effects on photosynthetic carbon gain through high temperature inhibition. At moderately high temperatures (30-40 °C in red spruce) inhibition can result from changes in the relative efficiency of ribulose-bisphosphate carboxylase-oxygenase (rubisco) to fix CO, as opposed to 0, (Day 2000, Ogren 1984). At higher temperatures disruption of electron transport and enzymatic systems can occur (Vann et al. 1996, Leavitt 1980). In addition T_{leaf} can have indirect effects through at least two pathways. Rates of maintenance respiration (R_m) increase exponentially with temperature. As temperate tree species have Q^{10} values (Eq. 4.2) of approximately 2 (Amthor 1994, Ryan et al. 1994), R_m rates can be expected to double with each 10 °C increase in T_{leaf}. In addition, T_{leaf} determines the saturation vapor pressure in the boundary

layers of air at foliar surfaces, therefore leaf-to-air vapor pressure deficit ($VPD_{,,}$ = water vapor pressure of air at saturation - actual vapor pressure at leaf surface).

VPD_{leaf} is the driving force for transpiration, therefore, movement of water through the soil-plant-air continuum. As water flux is limited by a series of resistances between soil and leaf (Pallardy et al. 1995), high rates of transpiration can result in internal plant water stress. Plants minimize harmful effects of water stress, such as xylem embolism, by controlling transpiration rate through stomata1 closure (Mansfield 1985). Partially closing stomata not only decreases transpiration, but results in increased resistance to CO_2 uptake, lowering CO_2 concentration in internal air spaces of the leaf Therefore, potential photosynthesis, the possible rate under prevailing irradiance, may become substrate-limited.

Plants appear to have developed several pathways by which stomata1 aperture is regulated to prevent internal water stress. Decreasing water potential in roots can induce production of abssicic acid (ABA), which is transported through the xylem to leaves where it causes stomata1 closure by altering ion transport across the membranes of guard cells (Zhang and Davies 1990). Alternatively, transpiration rate appears to be an initiating factor for inducing stomatal closure, even in the absence of significant plant water stress (Grantz 1990). Although the physiological details of this cause-and-effect pathway have not been fully described, Wilkinson and Davies (1996) provided evidence that this process may be mediated by changes in apoplastic pH in the leaf mesophyll, which induces conversion of ABA from an inactive form bound to cell walls to a free, active form. The latter pathway is consistent with rapid responses of stomata to increasing VPD_{leaf} in tree foliage, which have been described for numerous tree species (e.g., Day 2000, Weibel et al. 1993, Warkentin et

al. 1992, Sanford and Jarvis 1986, Kaufmann 1976). Day (2000) has proposed that interspecific differences in stomatal sensitivity to leaf-to-air vapor pressure deficit may be the result of adaptation to the microclimates of different regions or stand-types of varying structural characteristics.

Red spruce (*Picea rubens* Sarg.) is a common to dominant species in coniferous and coniferous-deciduous forests of northeastern North America, where the species is valuable as a sawlog and pulpwood resource. Historically, red spruce was substantially more abundant than on the present landscape (Seymour 1992), and recent forest inventory data indicate that its decline in abundance is accelerating (Griffith and Alerich 1996). Seymour (1992) has suggested that this phenomenon is linked to changes in forest management, as harvesting practices have moved from diameter-limit removals of large trees (a defacto selection approach) to more complete harvests under even-aged systems. Across the landscape this has resulted in red spruce being replaced by species better adapted to grow under this harvest-imposed disturbance regime, such as balsam fir (*Abies balsamea* Mill.) and early- to mid-successional hardwoods.

Red spruce is a long-lived, shade-tolerant species that primarily regenerates from established advance regeneration (Davis 1991). Thus, it is commonly assumed that the existence of a partial overstory canopy provides an ideal microclimate for growth in young red spruce saplings. McConville (1998) suggested that height growth in red spruce saplings may be optimum under partial shade; however, the relationship was not strong. In contrast, Hughes and Bechtel(1997) presented evidence indicating that growth in red spruce saplings is positively correlated with distance from the canopy edge in clearcuts. The

palynological record from the late Holocene also suggests that abundance of red spruce is correlated positively with episodes of climatic cooling (Schauffler 1999). Although the record remains sketchy at present, red spruce distribution in the Acadian region appears to have expanded and contracted with changes in mean temperatures of a few degrees. This suggests that the species may have a relatively narrow realized niche with respect to its competitors, and its competitive abilities may be strongly influenced by climatic variables, principally temperature.

Several studies on the photosynthetic physiology of red spruce suggest that stresses associated with the microclimates resulting from substantial canopy removals may reduce growth by inhibiting photosynthetic carbon gain. Alexander et al. (1995) provided evidence that high-temperature microclimates substantially inhibit photosynthetic carbon gain in red spruce growing in understories and proposed a temperature optimum of about 20 °C for photosynthesis. Likewise a study by Vann et al. (1996) found substantial declines in photosynthesis in red spruce at temperatures above 24 “C. Day (2000) has shown that photosynthesis in this species is not only directly inhibited by high temperatures, but is sensitive to increasing leaf-to-air vapor pressure deficit, which is highly correlated with foliar temperature. The relative importance of these potential environmental stresses and their influence on ***in situ*** photosynthesis is poorly understood.

In even-aged stands, red spruce shows slow height growth rates relative to co-occurring tree species in its early sapling stages, making it a weak competitor that is easily overtopped by balsam fir and other species until it reaches a height of 3-4 m (Meng and

Seymour 1992). Therefore, factors inhibiting carbon gain during that life-stage may be particularly important to its population dynamics.

Studies on the microclimatic conditions created by various silvicultural systems generally show that more open canopies provide higher daytime temperature and lower humidity (Reynolds et al. 1997, McCaughey 1989, Childs and Flint 1987) at levels near the ground. However, the light available for photosynthesis in sapling strata is also directly related to canopy openness. Thus, saplings growing at more open sites have greater light resources, but may face substantially greater microclimatic stresses.

This study is an attempt to answer several questions posed above. (1) What is the importance of inhibition of net carbon gain by temperature (direct effects and indirectly through R_m) and VPD relative to gross photosynthesis, and which factors provide the most substantial limitations to photosynthesis? (2) How do the microclimates produced by various silvicultural systems differ or not differ, and what factors are responsible for these differences? (3) Do these differences in microclimate translate into dissimilarities in photosynthetic carbon gain among and within the stand-types created by these silvicultural systems? (4) How would past or future climatic changes affect photosynthetic carbon gain by red spruce saplings growing in these stand-types. Answers to these questions were addressed using cumulative carbon gain functions, based on physiological response curves to the environmental factors of interest, and hourly time-step micrometeorological data collected over an entire growing season at replicated stations in clearcut, shelterwood, and selection stands.

Methods

Study site

Research was carried out in the Penobscot Experimental Forest (PEF), Penobscot County, Maine (44°50'N, 68°35'W). Briggs and Lemin (1992) place the PEF on the border of Maine's central and southern climatic zones. Forest soils are variable but principally Aquic or Typic Haplorthods or Podzols in the Thorndike, Buxton, Dixmont, and Monarda-Burnham series (USDA Forest Service 1959). Slope phase is generally less than 8%.

The PEF lies in the Acadian region of northeastern North America. This region is defined by moderate precipitation (100-l 30 cm) that is evenly distributed throughout the year (Seymour 1995, 1992), and contains numerous softwood, hardwood, and mixed-wood forest types with distributions primarily controlled by soil drainage patterns (Westveld 1953). Except on excessively drained sandy soils, moisture is generally not limiting to forest productivity, but may exert significant influence on regeneration and interspecific competition (Seymour 1995, Meng and Seymour 1992). Small scale disturbance patterns likely dominated the presettlement Acadian forest. Large scale fires and windthrow events are believed to have been relatively rare (Lorimer 1977). Fires are limited by the precipitation regime, and windthrow events by the region's geographic position with respect to tropical storm tracks and relatively low frequency of strong convective storms.

The PEF is dominated by conifer-deciduous forest-types. This forest is jointly managed by the University of Maine and the Northeast Forest Experiment Station of the U.S.D.A. Forest Service and contains stands maintained under a number of traditional and nontraditional silvicultural systems. Prior to Forest Service management, which began in

195 1, this area had a complex harvest history. Early harvests apparently focused on saw timber (pine and spruce) with some hardwood cutting for firewood and removals of hemlock to extract tannic acid from bark. Because of this history, the PEF has changed in both composition and structure from what is believed to be that of the region's presettlement forests. However, the area is typical of 'second-growth' forests in the southern part of the Acadian region (Seymour and Kenefic 1998). The diversity of stand-types in the PEF and their occurrence in at least two replicates within l-2 km of each other presented ideal conditions for this study.

Response curves

Photosynthetic light-response curves were developed for 2 sets of 12 red spruce saplings (l-2 m height), one growing in full sunlight, and the other in multi-treefall gaps of 200 to 500 m^2. The latter group would be exposed to direct beam sunlight for several hours (perhaps not contiguous) on clear days but would receive substantially lower fluence of photosynthetically active radiation (PAR; 400-700 nm) than those growing in full sunlight (Bazzaz and Wayne 1994). This approach was designed to develop response curves specific to individuals adapted to partially shaded (gap-adapted) or full sun (sun-adapted) conditions. As light-adaptation is a fluence response (Chabot et al. 1979), differences in the form of response curves would be expected between individuals adapted to habitats with large differences in integrated PAR flux.

Photosynthesis measurements were made between 0800 and 1100 hours EST, in mid-July through mid-August 1996. All trees were exposed to full sunlight at time of sampling, therefore capable of photosynthesis at maximum rates. For each tree, a sample

branch was randomly selected by whorl and quadrant from the upper one-third of the crown, and measurements were taken on current-year foliage. Shoot elongation and needle growth had ceased at least two weeks before measurements. The standard 2 x 3 cm cuvette from a LI6400 (Li-Cor, Inc., Lincoln, NE) open-type photosynthesis system with LI6400-02 light source was clamped on the center portion of sample shoots and foliage acclimated for 30 minutes to a light intensity of 2000 $\mu mol\ m^{-2}\ s^{-1}$ PPFD. Gas exchange measurements were subsequently made at 14 light intensities (2000, 1500, 1000, 750, 500, 350,200, 120, 90, 60, 40, 25, 10, and 0) in declining order. With each change in light intensity a 3 minute adjustment period was provided, followed by a test for stability (< 0.5% maximum CV for ΔCO_2 + ΔH_2O), and the adjustment period repeated if necessary. The system's infrared gas analyzers were matched before each measurement, zero values were calibrated daily, and span values were checked weekly using a standard gas for CO, and a LI6 10 (Li-Cor, Inc.) dew point generator with pressure compensation for H_2O. All measurements were made at a standard temperature of 23 ± 1 °C and VPD of < 1.5 kPa.

Response curves were developed based on the non-rectangular hyperbola model (Prieul and Car-tier 1976)

$$A = \frac{q \cdot PPFD + a - \sqrt{(q \cdot PPFD + a)' - 4 \cdot q \cdot PPFD \cdot k \cdot a}}{2k} \qquad \text{Eq. 4.1}$$

where A is apparent photosynthesis, q is apparent quantum efficiency (μmol A . μmol $PPFD^{-1}$), $PPFD$ is incident photosynthetic photon flux density, a is maximum net photosynthetic rate, and k is a bending factor that described the flex of the curve above the

initial linear portion. Maximum photosynthetic rates were determined from mean rates at 2000 $\mu mol\ m^{-2}\ s^{-1}$ PPFD. To control the tendency of this model to become unstable in the initial linear portion of the response curve (Leverenz 1988), a least-squares linear regression was performed on subsets of data defined by PPFD $\leq$ 60 $\mu mol\ m^{-2}\ s^{-1}$, and the resulting slope input as the q parameter. Subsequently, estimates of k-parameters were determined with the Gausss-Newton algorithm of Systat (v. 8.0, SPSS, Inc., Evanston, IL, USA), and derived using data for PPFD > 60 $\mu mol\ m^{-2}\ s^{-1}$. Table 4.1 gives parameter and error estimates for linear (4.la) and nonrectangular hyperbola functions (4.lb), and Fig. 4.1 shows the resulting photosynthetic light-response curves for gap- and sun-adapted foliage.

Photosynthetic response curves for leaf temperature (T_{leaf}) and vapor pressure deficit (VPD_{leaf}) were generated by fitting least-squares linear regression models to the data given in a previous study of the influence of those factors on photosynthesis in red spruce (Day 2000). As the preceding analyses indicated, the response of photosynthesis to both factors was nonsignificant below threshold levels (2.0 kPa for VPD and 32 °C for T). Above the VPD threshold red spruce has been shown to respond in a linear fashion to increasing VPD until at least 4 kPa (Day 2000). Table 4.la gives parameter and error estimates for the regression of photosynthetic rates on VPD. As data were only available for one T_L level (36 “C) beyond 32 “C, the response was assumed to be linear and was defined by the slope of the line connecting those Cartesian coordinates. This assumption is substantiated by the concurrence of the high temperature compensation point (x-intercept) of the model (43 “C) with the high temperature photosynthetic compensation point for red spruce reported by Vann et al. (1994).

Table 4.1. Parameter statistics for linear (A) and nonlinear (B) functions used in the photosynthetic carbon gain model. SE = standard errors for parameter estimates.

(A) Linear functions ($y = a + bx$). The function for response to vapor pressure deficit (VPD) was a slope-only equation ($y = bx$), thus given intercepts relate only to the dataset used for parameter estimation. PLR = Initial linear slope of photosynthetic light-response curve (see text for methods of estimation).

Function name	Parameter	Parameter estimate	SE of estimate	R^2 of model
VPD response				*0.66*
	a	*5.79*	*0.240*	
	b	-1.01	0.101	
PLR: sun foliage				*0.94*
	a	*-0.49*	*0.073*	
	b	*0.032*	*0.003*	
PLR: gap foliage				*0.88*
	a	*-0.30*	*0.057*	
	b	*0.028*	*0.002*	

(B) Non-rectangular hyperbola (NRH; Eq. 4.1). Parameter q of the NRH (apparent quantum efficiency) is the initial slope of the light-response curve and is equivalent to parameter a in the PLR models of Table 4.1A. Parameter q was fixed in the estimations of the other NRL parameters. R^2 values reflect mean corrected estimates (1 -residual ss / corrected ss).

Foliar type	Parameter	Parameter estimate	SE of estimate	R^2 of model
Sun foliage				*0.98*
	a	11.89	*0.370*	
	k	0.81	*0.009*	
Gap foliage				*0.83*
	a	8.81	*1.482*	
	k	0.91	0.188	

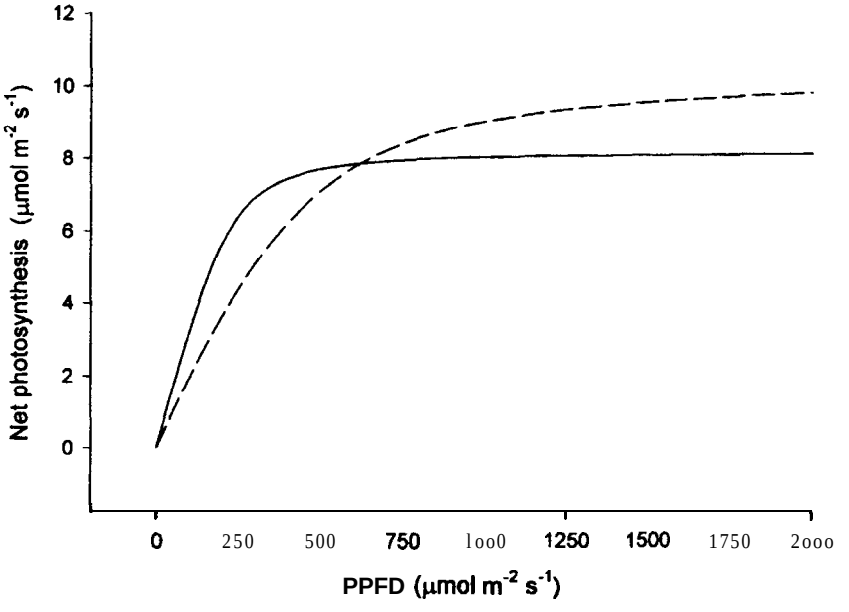

Figure 4.1. Photosynthetic light-response curves for red spruce. Curves were predicted by the non-rectangular hyperbola model (Eq.4.1) with the fixed parameters given in Table 4.1. The curve of sun-adapted foliage is shown with a solid line and that of gap-adapted foliage with a dashed line.

Rates of daytime foliar maintenance respiration (R_m) were calculated from the linear regressions (y-intercept values) of photosynthesis on PPFD ≤ 60 µmol m^{-2} s^{-1} described above. Separate values were derived for gap-adapted and sun-adapted foliage at the standard measurement T_{leaf} of 23°C. To predict R_m at higher and lower T_{leaf}, Response models were developed based on the Q^{10} function (Salisbury and Ross 1992)

$$R_i = R_0^{Q\left(\frac{T_i - T_0}{10}\right)} \qquad \text{Eq. 4.2}$$

where R_i is the rate at temperature i, R_0 is the rate at temperature o, $T_i - T_0$ is the difference in temperature, and Q is the change in rate for each 10 °C change in temperature. A Q^{10}-

value of 2.0 was selected based on reported values for related species and conifers in general (Ryan et al. 1994, Amthor 1984). The influence of R_m and direct temperature limitations to photosynthesis were partitioned by subtracting estimated R_m from total temperature inhibition (TFAC) when foliar temperatures exceeded the 32°C threshold.

Micrometeorological stations

Micrometeorological stations were established in the summer of 1998 in a silvicultural clearcut, a selection stand, and an expanding gap shelter-wood stand in the Penobscot Experimental Forest (PEF). Three additional stations were installed in a set of replicate stands in the spring of 1999. At each station site in selection and shelterwood stands basal area and canopy gap fraction were determined along a north-south transect that passed through the stations. At three points (south edge of gap, gap center, and station location in the northern sector) basal area was measured with a variable-radius prism plot, and gap-fraction with a LI2000 canopy analyzer (Li-Cor, Inc., Lincoln, NE, USA). The means of these values for each site are given in Table 4.2.

The USDA Forest Service has managed the selection stands under a 5-y cutting cycle since the 1950s. Harvesting has varied from individual tree to small group selection harvests, resulting in various sizes of harvest gaps in diverse stages of regeneration. Seymour and Kenefic (1998) have described their management and structure in detail. In the selection stands, stations were installed adjacent to red spruce saplings of 0.5-l .O m height situated to the north of gap center in gaps of approximately 250 m^2 area . The selected positions received direct sunlight for at least a portion of the day.

The shelterwood stands were established in 1996 and 1997 as part of the University of Maine's Forest Ecosystem Research Program (FERP). Silvicultural treatment of these stands was designed to provide an operable output of timber, to simulate the

Table 4.2. Site characteristics for locations of micrometeorological stations in the Penobscot Experimental Forest, Penobscot County, Maine.

Stand-type	Station	Basal area (m^2 ha-')	Fraction of canopy in gaps
Selection	SL-1	26	0.172
	SL-2	24	0.158
Shelterwood	SW-1	16	0.346
	SW-2	12	0.328
Clearcut	cc-1	0	0.100
	cc-2	0	0.100

natural disturbance regimes of mixed-wood forests in the Acadian region, and to provide regeneration niches for diverse overstory species (Seymour and Day, unpublished manuscript). The initial harvests were broadly oval-shaped gaps of approximately 0.2 ha, usually centered on preexisting multiple tree-fall gaps. Within the harvest gaps, shelterwood regeneration cuts removed approximately two-thirds of the preharvest canopy. In many cases, these entries released substantial accumulations of conifer advance regeneration, primarily balsam fir (*Abies balsamea* Mill.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and red spruce. Gaps selected for stations had advance regeneration of red spruce (0.5-l .O m height) located just north of the harvest area center, making station sites similarly situated to those in the selection stands.

To monitor micrometeorological conditions in clearcut areas, stations were located in two spruce plantations that had been established by FERP in 1995 and 1997. The older plantation (about 3 ha) had an ample sapling (>0.5m ht) population around the monitoring site. However, as the existing trees in the newer plantation were <0.2m tall, two larger (0.5-0.7m) individuals were planted near the plantation center for monitoring of leaf temperatures. Both plantation sites were on former hardwood (birch-maple-poplar) stands and produced large numbers of competing hardwood stump and root sprouts after planting. To control competing sprouts, the smaller (older) plantation (CC-l) had been treated with a ground application of herbicide in 1997 and all hardwood sprouts were removed with motor-manual (brushsaw) release in May, 1999, immediately before collection of microclimate data was initiated. The larger (newer) plantation (CC-2) had not received any post-planting treatments and had numerous hardwood sprouts of l-3 m height, as well as herbaceous and graminoid competitors.

Collection of micrometeorological data

Each micrometeorological station consisted of a 2m high tripod and mast mounted on 1.5 cm diameter metal rods driven approximately 0.75m into the ground. Tripods were always set to the north of sample trees to minimize shading. PPFD was measured with LI-160 quantum sensors (Li-Cor, Inc., Lincoln, NE, USA) suspended immediately above the crowns of sample trees on a 0.5m arm. Air temperature and vapor pressure were monitored with Vaisala 50Y thermistor-humiters (Vaisala, Inc., Boston, MA, USA) in radiation shields attached to the mast below the quantum sensor arm. Foliar temperature was sensed by two fine-wire (38 ga), type-T thermocouples (Omega, Inc., Stamford, CT, USA)

located on current-year foliage of upper crown branches. Thermocouple junctions were rested on top of foliage, the two wires extended down opposite sides of the shoot, and the shielded wire secured to branches with very fine stainless steel strands. Wires passed through a small clear plastic ring on the underside of the shoot, which provided a tension-weight to keep the thermocouple junctions in contact with foliage. Sensors were calibrated against laboratory standards (thermistor-humiters and thermocouples) or by the manufacturer (quantum sensors) before deployment. Sensors were scanned at 60 s intervals and hourly mean maximum, and minimum values recorded with dataloggers (4 Campbell model 10X, and 2 model 21X; Campbell Scientific, Inc., Ogden, UT, USA).

Modeling integrated photosynthetic attributes

A deterministic photosynthetic carbon gain (PCG) model that input the hourly time-step micrometeorological data was developed using the SAS language (SAS Institute 1998). Figure 4.2 provides a flow diagram illustrating the relationships between model components and pathways, and the complete model code is given in Appendix A. The model calculated apparent net photosynthesis (APS) based on the nonrectangular hyperbola function. APS was combined with maintenance respiration (R_m), which was calculated from baseline rates at 23 °C using a Q^{10} of 2.0 (see previous discussion), to estimate potential photosynthetic carbon gain (PPCG). Factors were then developed to reduce PPCG by the actions of leaf temperature (T_{leaf}) and leaf-to-air vapor pressure deficit (VPD_{leaf}). As the original response functions for these constituents were determined from measurements of A_{net}, that model variable was used for calculating reduction factors. The influences of T_{leaf} and VPD_{leaf} have been shown to act independently in red spruce (Day 2000), allowing them

to be treated additively. For each hourly timestep, net photosynthetic carbon gain (NPCG) was then calculated as:

$$NPCG = PPCG - TFAC - VFAC \quad \text{Eq. 4. 3}$$

where TFAC and VFAC are the reduction factors for the functions of APS on T_{leaf} and VPD, respectively. TFAC included both direct temperature inhibition (T_d) and losses to R_m. T_d was subsequently determined by subtracting R_m from TFAC. The model output values of NPCG and its constituents for the growing season by summing hourly values for the 126-day interval, 1 June - 30 Sept, 1999. To provide insight into within harvest-type variability, output was generated independently for each replicate (2 per harvest-type).

To evaluate the influence of climatic changes on NPCG, the model was run under cooling (mean T_{air} of -2.5 and -5 °C from current-climate data) and warming (mean T_{air} of +2.5 and +5 °C from current-climate data) scenarios. The former represents a range of values that have been proposed to reflect temperature conditions during Holocene cooling periods (Gajewski 1988, 1987), while the latter are based on estimates of temperature increases due to global warming (Mitchell et al. 1992). For these scenarios, runs were made that modeled changes in T_{leaf} as both additive and proportional functions of T_{air}. As an additive function

$$T_{leaf}' = T_{air}' + (T_{leaf}^{\circ} - T,") \quad \text{Eq. 4.4}$$

and, as a proportional function

$$T_{leaf}' = T_{air}' \cdot (T_{leaf}^{\circ} / T,") \quad \text{Eq. 4.5}$$

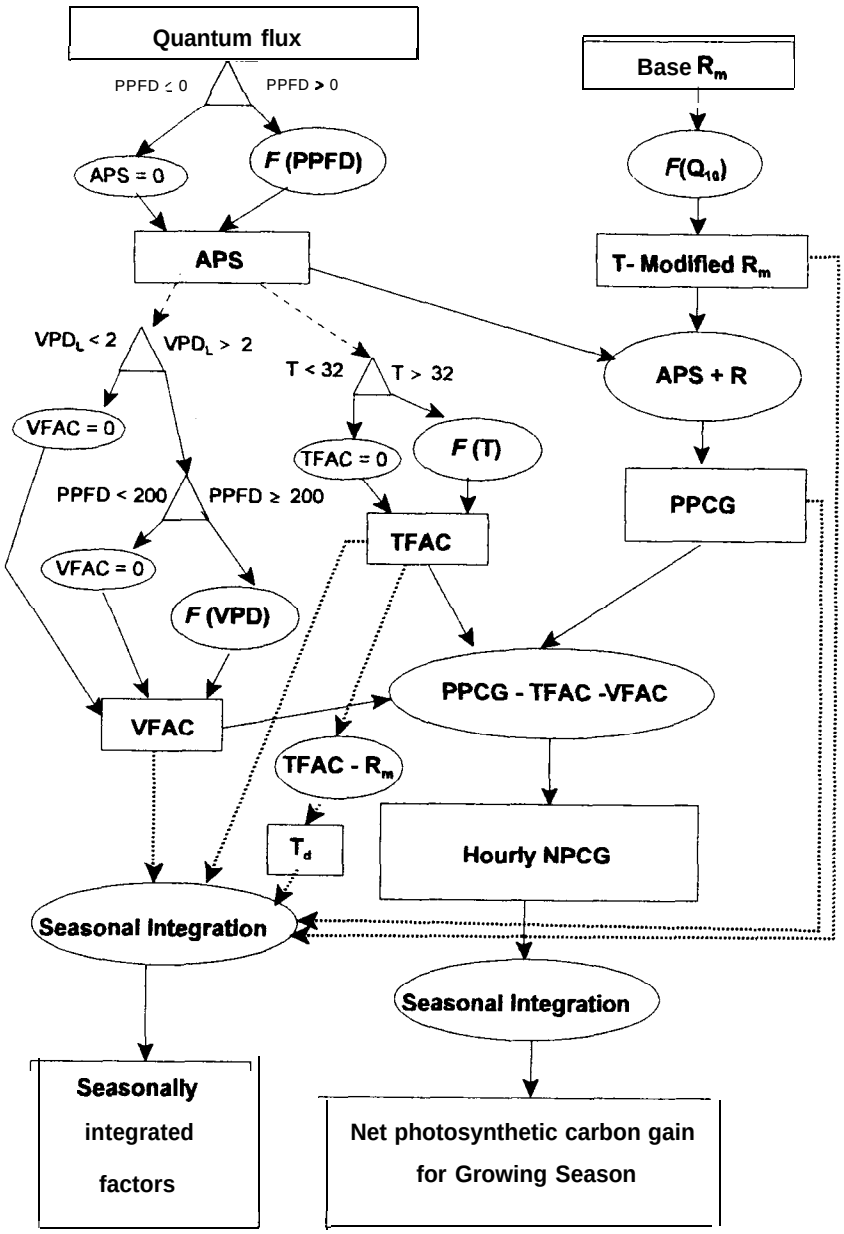

Figure 4.2. Flow diagram for the carbon gain model. Rectangles indicate factor states, triangles show switches, and ovals contain functions. Direct input pathways for calculating net photosynthetic carbon gain are given as solid lines, and use of outputs from factor states in other functions is indicated with dotted lines. TFAC is inhibition due to temperature, VFAC is inhibition due to vapor pressure deficit, R_m is maintenance respiration, APS is apparent (net) photosynthesis, PPCG is potential photosynthetic carbon gain, NPCG is net photosynthetic carbon gain, and T_d is direct temperature limitation.

where T_{leaf}' and T_{air}' represent values of those variables under the climate change scenarios, and T_{leaf}° and T_{air}° hourly mean values in the growing season 1999 dataset. Predictions of models incorporating either of these functions were nearly identical, and predictions from runs using the proportional function are reported here. Only temperature was varied in the climate change scenarios, and it was assumed that solar energy input, ambient vapor pressure, and photosynthetic response to light would remain constant.

Results

Microclimates created by silvicultural systems

Selection systems showed the lowest mean hourly photosynthetic photon flux densities (PPFD, Fig. 4.3a), and mean integrated hourly PAR (400-700 nm) fluence (Fig. 4.3b). Shelterwood sites were intermediate, but still substantially less than clearcuts in all PAR attributes. On a growing-season basis (1 June - 30 Sept.), total fluence reaching the sensors above the crowns of saplings was (mean of two stations): 73 1 moles m^{-2} at selection stand sites, 1477 moles m^{-2} at shelterwood sites, and 4459 moles m^{-2} in the clearcuts. These substantial differences in input of solar radiation were not directly reflected in differences in hourly mean (Fig. 4.4a) and maximum (Fig. 4.5a) air temperature (T_{air}).

The trend among stand-types in foliage temperatures (T_{leaf}) during daylight hours better followed the pattern expected from solar energy input, showing an average maximum T_{leaf} range of 5.0 °C across stand types in early afternoon (Fig. 4.4b). However, this relationship failed during midday when one of the selection sites (SL-1) and both

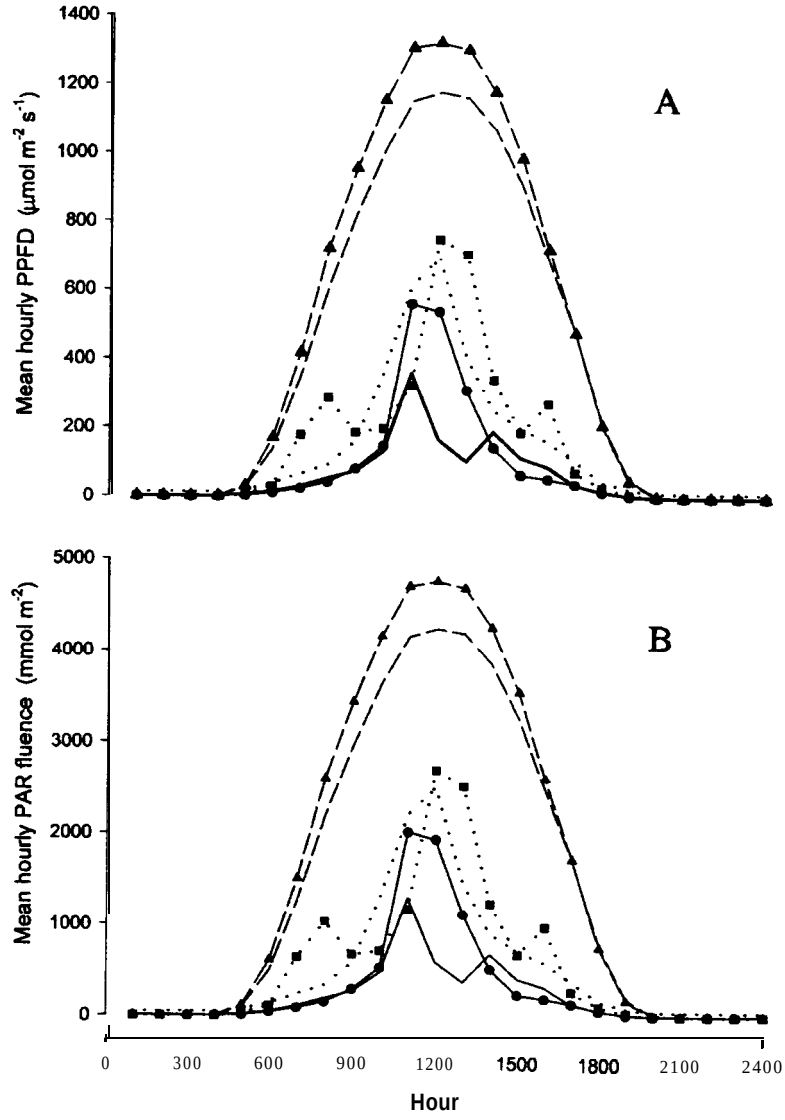

Figure 4.3. Light characteristics for the 1999 growing season at Penobscot Experimental Forest microclimate monitoring sites. Mean hourly photosynthetic photon flux density (PPFD) is shown in (A),and photosynthetically active radiation (PAR) quantum fluence in (B). Selection system sites have solid lines, shelterwood sites dotted lines, and clearcut sites, dashed lines. Symbols for individual stations are: SL-1 –●–, SL-2 —, SW-l ··■··, SW-2 •••, cc-1 -A-, cc-2 – – –.

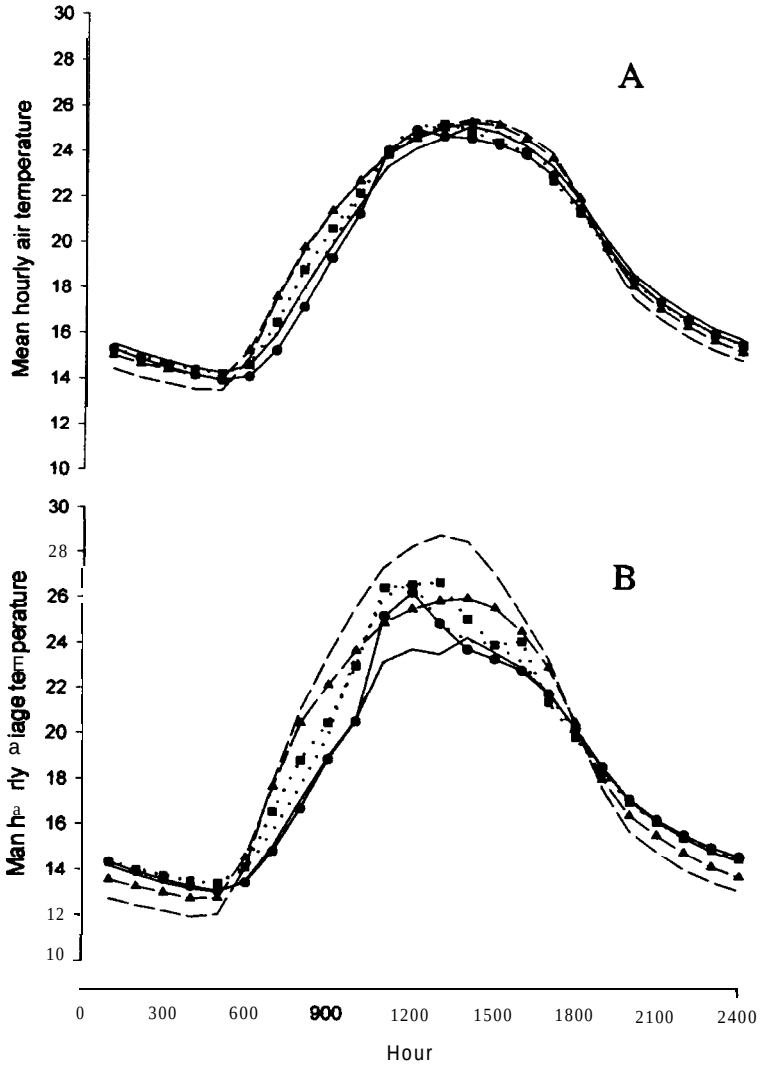

Figure 4.4. Mean hourly air (A) and foliage (B) temperatures for the 1999 growing season at Penobscot Experimental Forest microclimate monitoring sites. Selection system sites have solid lines, shelterwood sites dotted lines, and clearcut sites, dashed lines. Symbols for individual stations are: SL- 1 —●—, SL-2 ——, SW- 1 ● -m**, SW-2 . . •, CC- 1 -A-, CC-2 — — .

shelterwood sites showed higher mean leaftemperatures than one of the clearcuts (CC-2). An extensive correspondence with solar energy input was found with maximum daily T_{leaf} (Fig. 4.5b), but here a complex relationship was also evident. Maximum T_{leaf} were generally ordered clearcut > shelterwood > selection sites. However, the highest foliage temperatures were recorded in shelterwood stands on numerous days (Fig. 5b), and the above order was occasionally reversed. These days corresponded with the occasion of cool, damp air masses when thermal energy radiating from the ground and surrounding vegetation would be expected to maintain higher foliar temperatures at the selection sites. A similar scenario occurred at night when re-radiated thermal energy inputs were lowest, and losses to the sky greatest, for foliage in the clearcuts (Fig. 4.4b).

Differences within stand-types are also evident from the number of hours that T_{leaf} is above the physiological threshold (32 “C) for limitation of photosynthesis (Table 4.3a). This value ranges over an order of magnitude, from a low of 12 in SL-2 to 177 in CC-2. Based on mean values for stand-types, selection < shelter-wood < clearcut for both mean hourly temperatures and maximum hourly temperatures. Maximum hourly T_{leaf} implies that photosynthesis is temperature-limited for at least part of each hour. Considering that these values represent number of hours over the growing season, the ranges within selection and shelterwood stand-types would translate into only modest differences in temperature-inhibition. However, the range of values within clearcuts is substantial. CC-l had integrated hours (based on either mean or maximum T_{leaf}) of less than those for either shelter-wood site and close to the number for SL-1. In contrast CC-2 had over 2x the inhibition-hours of CC-l.

Trends in temperature differences between ambient air and foliage ($T_{leaf} - T_{air}$) mirrored the patterns found for mean hourly needle temperature (Fig. 4.6a) and maximum daily foliar temperature (Fig. 4.6b). At the selection site with the greatest intact canopy cover and smallest gap size (SL-2), mean hourly T_{leaf} remained negative (lower than T_{air}) throughout the diel cycle, while that at SL-1 was slightly (about 1 "C) positive at midday. In the shelterwood stands $T_{leaf} - T_{air}$ was positive for 4 to 6 midday hours, with a noon

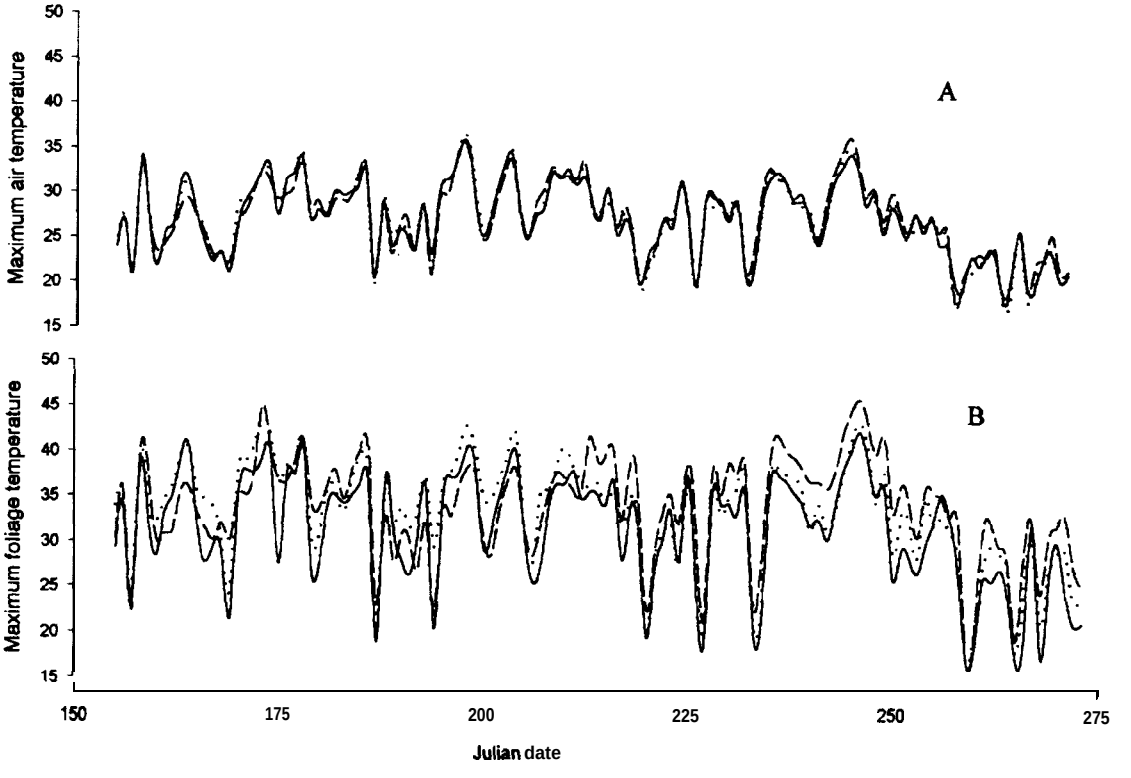

Figure 4.5. Daily maximum temperature tracks for the 1999 growing season at Penobscot Experimental Forest microclimate monitoring sites. Maximum air temperatures are shown in A, and maximum foliage temperatures in B. Each track is the mean of the two sites for each stand-type. Selection system sites have solid lines, shelterwood sites dotted lines, and clearcut sites, dashed lines.

Table 4.3. Number of hours above threshold levels for direct temperature inhibition of potential photosynthetic carbon gain based on (a) T_{leaf} and T_{air}, and for vapor pressure deficit inhibition (b) based on T_{leaf} and T,.

(a) Number of hours showing direct temperature inhibition based on T_{leaf} compared with T_{air} using mean and maximum hourly temperatures.

Stand -type	station	Mean leaf T	Mean air T	Maximum leaf T	Maximum air T
Selection	mean	34	18	122	37
	SL-1	55	21	151	43
	SL-2	12	16	93	31
Shelterwood	mean	70	29	231	56
	SW-1	85	26	270	44
	SW-2	54	32	192	57
Clearcut	mean	122	32	307	55
	cc-1	66	31	202	52
	cc-2	177	33	412	58

(b) Number of hours showing VPD inhibition by sites and basis (T_{leaf} compared with T_{air}). Some inhibition of photosynthesis is implied by VPD > 2 kPa, moderate inhibition by VPD > 3 kPa, and severe inhibition by VPD > 4 kPa.

Stand -type	station	VPD based on T_{leaf}			VPD based on T_{air}		
		> 2 kPa	> 3 kPa	> 4 kPa	> 2 kPa	> 3 kPa	> 4 kPa
Selection	mean	136	28	3	156	14	0
	SL-1	192	49	5	199	19	0
	SL-2	82	6	0	112	9	0
Shelterwood	mean	229	69	12	213	25	0
	SW-1	247	84	18	201	22	0
	SW-2	210	55	6	225	27	0
Clearcut	mean	381	119	30	247	35	4
	cc-1	306	51	9	235	33	2
	cc-2	486	186	51	259	37	5

difference of 2.5 “C. In contrast, mean hourly T_{leaf} - T_{air} at the clear-cut sites remained positive from shortly after sunrise until after sunset. However, in magnitude of response the two clear-cut curves varied greatly. The curve for CC-2 reached a mean difference of 3.7 °C, the greatest mean value of any site, while that for CC-l showed midday levels below the two shelter-wood sites and slightly less than the highest for selection site SL- 1. Nighttime differences in clearcuts were slightly greater (more negative) than those at sites with an overstory canopy, an effect of enhanced radiational cooling at sites without an overstory canopy (McCaughey 1989).

Table 4.3a uses the hours in which mean temperatures exceed the response threshold for inhibition of photosynthesis to illustrate differences between T_{leaf} and T_{air} on a physiological level. If based on T_{air}, the number of inhibition-hours were underestimated by approximately 50% at selection and shelter-wood sites, and by roughly 75% for clearcuts compared with estimations based on T_{leaf}. Underestimation based on maximum hourly temperatures was even greater. At selection and shelter-wood sites inhibition-hours as determined by maximum T_{leaf} and T_{air} differ by 3.5x and > 4x, respectively, while they varied by nearly 6x for clearcuts.

Trends in mean hourly atmospheric vapor pressure deficit (VPD_{air}) closely followed those of mean hourly T_{air} (compare Figs. 4.4a and 4.7a), although SL-2 exhibited midday means below any other site. Maximum levels occurred between 1300 and 1500 hours at all sites except SL-1, where the highest mean levels occurred before noon. This coincided with peak input of solar radiation at that site (Fig. 4.1).VPD in the boundary

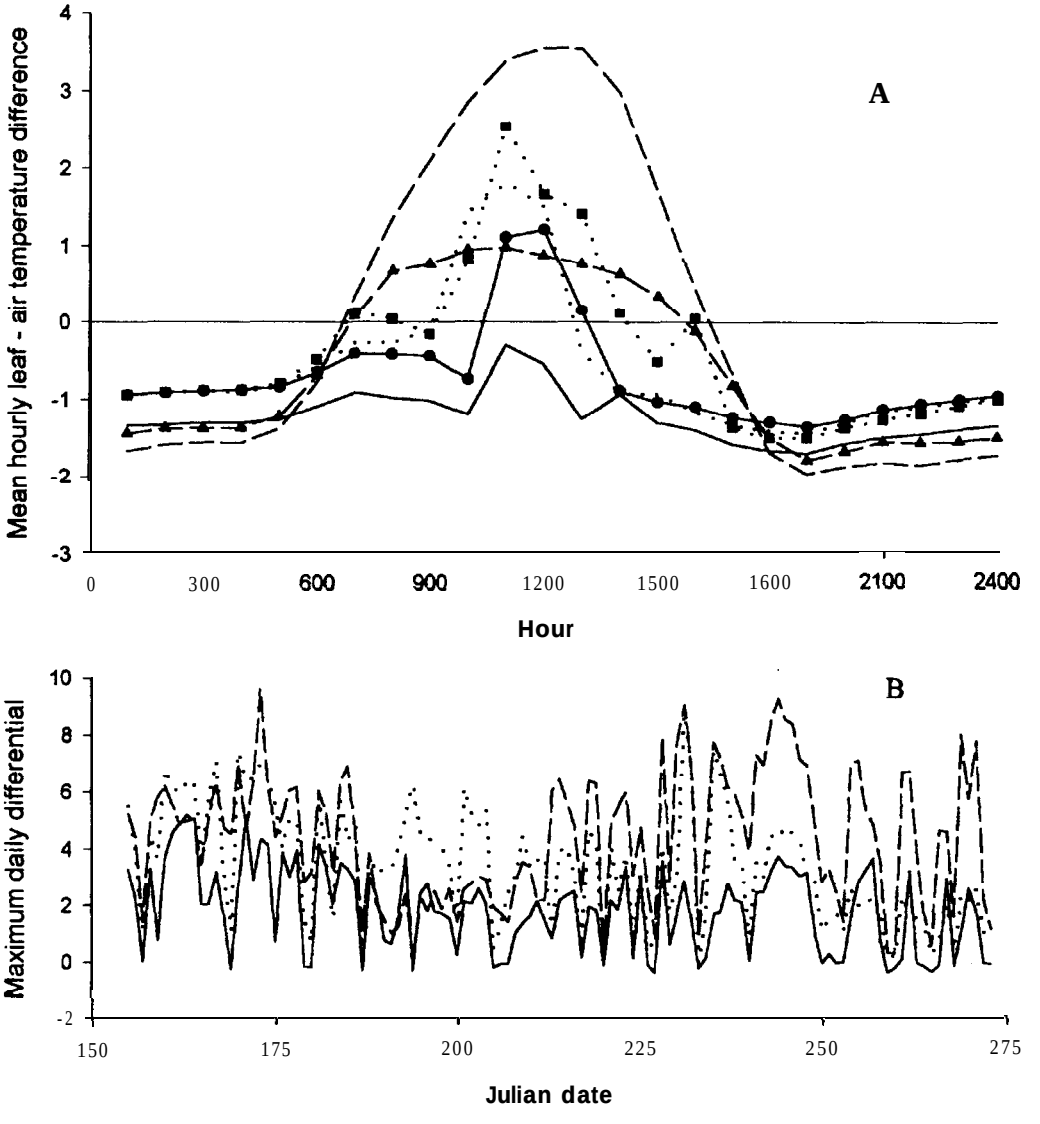

Figure 4.6. Differences between leaf and air temperatures for the 1999 growing season at Penobscot Experimental Forest microclimate monitoring sites. Mean hourly difference is shown in (A), and maximum daily differencefor stand-types in (B). Selection system sites have solid lines, shelter-wood sites dotted lines, and clearcut sites, dashed lines. Symbols for individual stations are: SL-1 —•—, SL-2 ——, SW-l ● *w**, SW-2 . . •, CC-l -A-, CC-2 — — .

layers at foliar surfaces (VPD_{leaf}) followed similar trends to that in the bulk air, however, absolute levels and differences between sites were greater (Fig. 4.7b). Shelterwood sites showed the greatest similarity in trends, while those of the other stand-types diverged for at least part of the day. For all stands except CC-2 mean hourly levels were below the 2 kPa threshold for stomatal response to VPD in red spruce reported by Day (2000).

However, using mean values of VPD may mask important influences of these environmental factors on foliar physiology. As Table 4.3b demonstrates, hours during which photosynthesis is down-regulated by VPD_{leaf} range from 82 at SL-2 to 486 at CC-2, and those exhibiting a moderate reduction due to VPD, are only 6 at SL-2, but 186 at the CC-2 site. Again, within stand-type ranges in VPD show the two shelterwood stands to be most similar. Between the clear-cut sites, differences are proportionally less than those for temperature inhibition (Table 4.3a) and the stand-types are most dissimilar when compared on the basis of moderate to severe (>3 kPa - >4 kPa) inhibition-hours.

Compared with VPD_{leaf}, VPD_{air} exhibited much smaller differences between and within stand-types (Table 4.3b). Using VPD_{air} to estimate inhibition-hours resulted in substantial underestimation of its influence on photosynthesis at the clearcut sites: 47% at CC-2 and 23% at CC-l. Shelterwoods exhibited nearly no difference between the approaches with a 16% underestimation at SW-l and a slight overestimation at SW-2. At both selection stands, using VPD_{air} as opposed to VPD_{leaf} resulted in small overestimations of inhibition-hours.

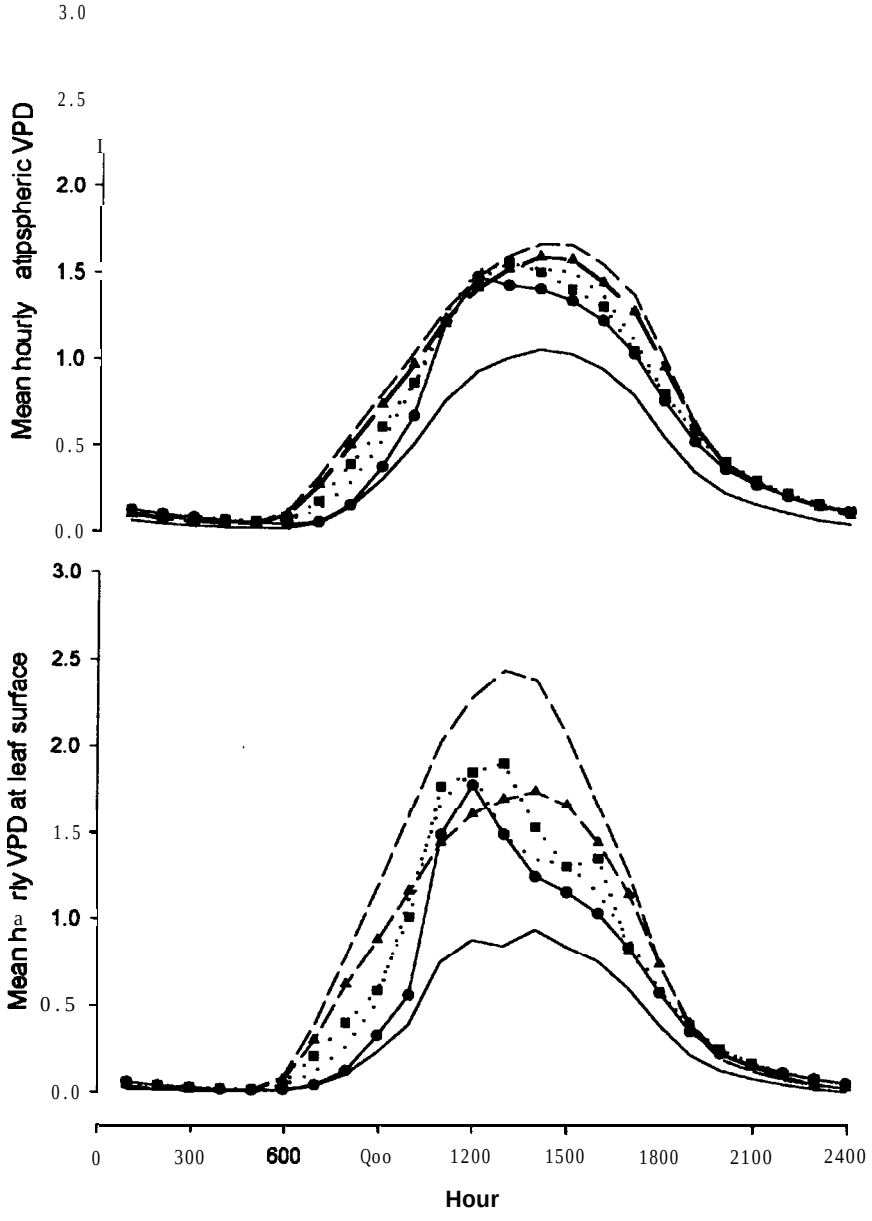

Figure 4.7. Differences in mean hourly vapor pressure deficit during the1999 growing season at Penobscot Experimental Forest microclimate monitoring sites. Mean hourly atmospheric VPD is shown in (A), and VPD based on leaf temperature (B). Selection system sites have solid lines, shelterwood sites dotted lines, and clearcut sites, dashed lines. Symbols for individual stations are: SL- 1 -•-, SL-2 —, SW- 1 ••■••, SW-2 . . •, CC- 1 -A-, cc-2 – –.

Influences of microclimate on photosynthetic carbon gain

Due to large differences in light availability, potential photosynthetic carbon gain (PPCG) was greatest at the clearcut sites and about 40% less at the selection stations (Fig.4.8, Table 4.4). However, estimates for the clearcuts and shelterwood sites were very close (about 6% lower in the shelter-woods). Ranges were small within all stand-types, which correspond to narrow ranges of light fluence within stand-types.

For all stand-types the major limiting factor for PGCG was inhibition from leaf-to-air vapor pressure deficit (VFAC) (Table 4.4), and its relative influence was of the order clearcut > shelterwood > selection (Fig.4.8). Diminution of VFAC was substantial along this continuum with the effect at shelter-wood sites 65% of that estimated for clearcuts, and at selection sites only 46% of the clearcut level (Table 4.4). The greatest range of VPD-inhibition within stand-types (2.6 mol y^{-1}) was found for the clearcut sites (Fig. 4.8). This compares with a much narrower range (0.1 mol y^{-1}) for the shelterwood sites, and an intermediate range for the selection sites (1.3 mol y^{-1}).

Relative to inhibition by VPD, temperature inhibition of PPCG (TFAC; a combination of direct effects and maintenance respiration) varied in importance among stand-types (Table 4.4). TFAC and VFAC were approximately equivalent at the selection sites, VFAC was about 1.5x the level of TFAC at the shelterwood sites, and VFAC was roughly 2x the level of TFAC for the clearcuts. Trends in ranges also mirrored those for VPD-inhibition (Fig. 4.8). Such parallel trends would be expected due to the use of T_{leaf} as a fixed variable in calculating both factors (see methods).

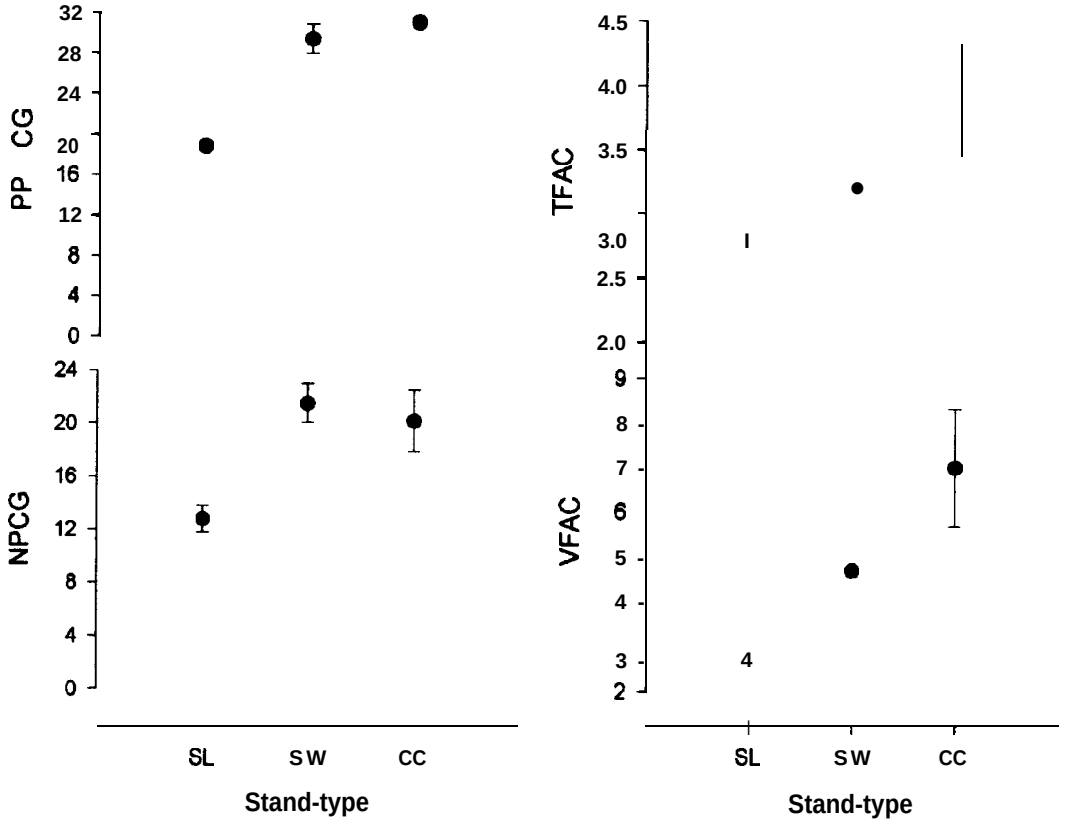

Figure 4.8. Differences among stand types in carbon gain and inhibitory factors. Units (y-axes) for all factors are moles m^{-2} for the growing season 1 June through 30 September, 1999. PPCG is potential photosynthetic carbon gain NPGC is net photosynthetic carbon gain, TFAC is temperature inhibition of PPCG, and VFAC is inhibition of PPCG due to vapor pressure deficit. SL designated selection sites, SW shelter-wood sites, and CC clearcut sites.Circles give mean values for sites and bars give ranges for the two replicate of each stand-type.

Table 4.4. Model estimates of NPCG and model factors for the 1999 growing season (1 June - 30 September). Estimates in moles m^{-2}. Sites 1 and 2 are the two stations in replicates of each stand-type, referred to in the text as SL-1, SL-2, SW-l, SW-2, CC-l, and CC-2.

Factor	Stand type	Mean	Site 1	Site 2
Potential carbon gain				
(PPCG)	selection	18.9	18.8	19.1
	shelterwood	29.4	27.0	30.9
	clearcut	31.2	31.4	30.9
Net carbon gain				
(NPCG)	selection	12.8	11.8	13.8
	shelterwood	21.5	20.0	23.1
	clearcut	20.2	22.2	18.2
Temperature-inhibition				
(TFAC)	selection	2.9	3.0	2.7
	shelterwood	3.2	3.3	3.2
	clearcut	3.9	3.5	4.4
Maintenance respiration				
(R_m)	selection	2.8	2.8	2.7
	shelterwood	3.0	3.0	3.0
	clearcut	3.4	3.3	3.6
Direct T-inhibition				
(T_d)	selection	0.1	0.2	<0.1
	shelterwood	0.3	0.3	0.2
	clearcut	0.5	0.2	0.8
VPD-inhibition				
(VFAC)	selection	3.2	3.9	2.6
	shelterwood	4.7	4.7	4.8
	clearcut	7.0	5.7	8.3

The breakdown of temperature-inhibition factors (Table 4.4) shows that losses to maintenance respiration (R_m) are an order of magnitude greater than inhibition due to direct temperature effects (T_d). Integrated direct temperature inhibition was < 1 mole m^{-2} for the growing season at all sites, ranging from <0. 1 mole m^{-2} at SL-2 to 0.8 mole m^{-2} at CC-2.

When the model was run with T_{air} substituted for T_{leaf} (Table 4.5, NPCG remained virtually the same for the selection sites (+0.8 %), increased slightly for the shelterwoods (3.3 %), and exhibited an 11.4 % increase for the clear-cuts. This was the result of the negative leaf-to-air temperature differentials at the selection sites and the more positive daytime differences at the shelterwood and clearcut stations (Fig. 4.6), and the effects of temperature basis on VFAC (Table 4.3b). Within the clearcuts, CC-l was more similar to the shelterwoods with a 4% increase in NPCG relative to the T_{leaf}-based run, while CC-2 showed a 28% increase. Again, this reflects the difference in $T_{leaf} - T_{air}$ between the two

Table 4.5. Percent under (-) or over (+) estimation in photosynthetic carbon gain factors and net carbon gain (NPCG), if estimated on the basis of air temperature as an alternative to foliage temperature. Values are means for two sites located in replicate stands of each type. TFAC = inhibition of potential photosynthetic carbon gain due to temperature (maintenance respiration + direct temperature inhibition), and VFAC = inhibition due to leaf-to-air vapor pressure deficit,

Stand type	TFAC	VFAC	NPCG
selection	+3.5	+3.1	+0.8
shelterwood	-3.1	-10.6	+3.3
clearcut	-12.8	-25.7	+11.4

sites (Fig. 4.6). The range of differences within the other two stand categories were < 1%. In the selection system using T_{air} overestimated TFAC and VFAC, while in the shelterwoods and clearcuts TFAC and VFAC were underestimated, most substantially at clear-cut sites (Table 4.5).

Runs of the model with shifts in mean hourly air temperatures (-5, -2.5, +2.5, and +5 °C from 1999 'current-climate' temperatures) gave estimates of changes in NPCG and its constituents under climate change scenarios (Table 4.6a). Under cooling scenarios NPCG is increased for all stand types relative to current-climate conditions, with the largest relative increases predicted for the clearcuts (Table 4.6b). Similarly the clearcuts suffered the greatest relative decreases in NPCG with rising temperatures, showing a maximum decline of 54% relative to current-climate in the +5 °C scenario. Under the cooling scenarios the stand-types retained their same relative order of NPCG rates (selection < shelterwood ≈ clearcut) as under current conditions (Fig.4.9). However, under the heating scenarios NPCG of clearcuts becomes substantially lower than that of shelterwoods at +2.5 °C and slightly less than that of the selection stands at +5 °C. At the highest temperature, NPCG of the shelterwoods is approximately double that of either of the other stand-types (Table 4.6a, Fig. 4.9).

Under the cooling scenarios TFAC decreases relatively more in the clearcuts than in the selection stands (Table 4.6b). This would be expected due to the cooler T_{leaf} values at the selection sites, and the relatively lower rates of absolute change in R_m at lower temperatures predicted by the Q^{10} function (Eq. 4.3). In the heating scenarios, relative increases in R_m, therefore TFAC, are similar across stand-types. Thus, carbon allocation to

Table 4.6. Factor values (a) and percent changes relative to current-climate (b) for net photosynthetic carbon gain, temperature- and VPD-induced inhibition, and maintenance respiration for changes in air temperature of -5 to +5 °C from temperatures recorded during the 1999 growing season as predicted by the PCG model. In (b), negative values indicate a reduction and positive values show an increase in factors.

(a) Predicted values of factors

Factor	Stand type	Hourly mean T_{air}: difference with 1999 values				
		-5	-2.5	0	2.5	5
Net carbon gain						
	selection	14.6	13.8	12.8	11.2	8.5
	shelterwood	24.5	23.3	21.5	18.8	15.2
	clearcut	25.2	23.4	20.2	15.8	9.2
Temperature-inhibition						
	selection	2.0	2.5	2.9	3.7'	4.6
	shelterwood	2.2	2.5	3.2	4.4	6.1
	clearcut	2.5	3.0	4.0	5.6	8.3
VPD-inhibition						
	selection	1.8	2.5	3.2	4.3	5.5
	shelterwood	2.2	3.2	4.7	6.5	8.8
	clearcut	2.8	4.5	7.0	10.0	13.7

(b) Percent increase (+) or decrease (-) in factors relative to current-climate conditions.

Factor	Stand type	Change in ambient air temperature			
		-2.5		2.5	
Net carbon gain					
	selection	+14.1	+7.8	-12.5	-33.3
	shelterwood	+14.0	+8.4	-12.6	-29.3
	clearcut	+24.8	+15.8	-21.8	-54.5
Temperature-inhibition					
	selection	-30.0	-13.8	+27.6	+58.6
	shelterwood	-31.3	-21.9	+37.5	+90.6
	clearcut	-37.5	-25.0	+40.0	+107.5
VPD-inhibition					
	selection	-43.8	-21.9	+34.4	+71.9
	shelterwood	-53.2	-31.9	+38.3	+87.2
	clearcut	40.0	-35.7	+42.9	+95.7

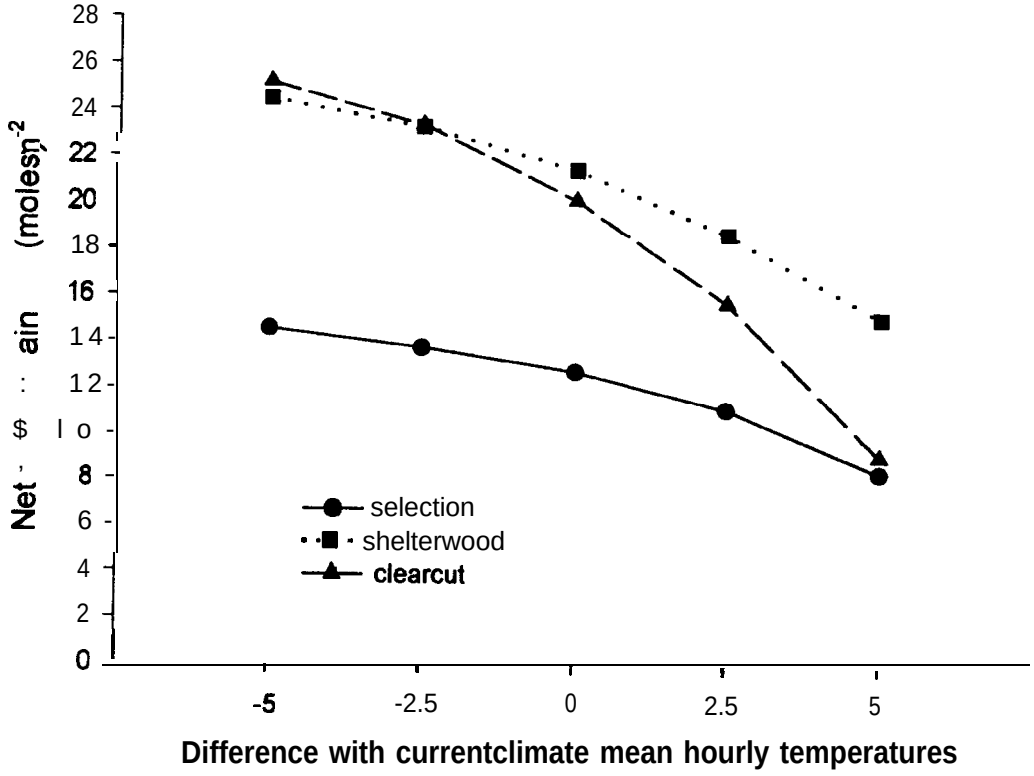

Figure 4.9. Changes in net photosynthetic carbon gain under cooler and warmer climate scenarios for selection, shelterwood, and clearcut silvicultural systems. Points represent means of two replicates for each stand-type.

R_m remained proportional to current-climate rates, and that factor had minimal influence on changes in the relative order among stand-types in NPCG (Fig. 4.9). Under cooler climate scenarios direct temperature inhibition became virtually nonexistent. With climatic warming, losses to direct temperature inhibition, which were very small compared to those due to R_m in output from the current-climate model run, became substantially more significant. Results from the +5 °C run, indicated that direct temperature inhibition would account for 41% of TFAC at the clearcut sites. Under those conditions, selection stands showed the lowest proportional losses to direct temperature limitations (22% of TFAC), and shelterwoods were intermediate (31% of TFAC).

VFAC decreased dramatically for all stand-types under cooling scenarios (Table 4.6a). Under the warming scenarios, proportional increases in VFAC were greatest in the clear-cuts, and the smallest proportional increases were at the selection sites. For all stand-types VFAC remained the principal limitation to NPCG under current-climate scenarios.

Discussion

The effects of silvicultural systems on microclimate

Differences in air temperature (T_{air}) and ambient vapor pressure deficit (VPD_{air}) on a mean-hourly scale were small across stand-types (Figs. 4.4a and 4.7a). On a daily scale (Fig. 4.4b) maximum temperatures on clear, calm days were commonly < 2 °C warmer in the clear-cuts than the selection stands. This shows that T_{air} and VPD_{air} in this forest are primarily a function of larger scale meteorological phenomena such as air-mass origin and interception of solar radiation by cloud cover. However, leaf-based microclimatic factors

varied substantially both between stand-types and within stand-types (Figs. 4.5 and 4.7b), and it is at this scale that temperature and vapor pressure deficit influence foliar physiological processes. Accordingly, type and scale of climatic information must be considered when evaluating the effects of microclimate on plant growth and other ecological attributes.

This study shows that two inherent characteristics of micrometeorological monitoring have implications for the development of comparisons between sites and for input into ecophysiological process models. First is the temperature basis. As Fig. 4.6 shows, differences between T_{leaf} and T_{air} can be substantial under certain conditions and may vary significantly not only among silvicultural treatments but also between individual stands or sites within a stand-type. Temperature basis is important not only for accurately determining the effects of temperature itself, but also for its influence on vapor pressure deficit and other parameters of physiological importance. At a coarse scale, the error introduced by basing estimates on T_{air} as a surrogate for T_{leaf} is directly proportional to input of solar radiation (compare Fig.4.3 and Table 4.5). However, the characteristics of individual stands may alter this relationship (discussed below). Second, in cases where the magnitude of physiological activities are determined by threshold functions, an important microclimatic parameter is the number of measurement intervals at which thresholds are exceeded. T and VPD effects on photosynthesis in red spruce are examples of such functions. Therefore, use of data based on bulk air measurements may tend to obscure physiological influences of microclimate, and the results of this study demonstrate that this effect is potentially stronger at sites with greater input of solar radiation.

Within stand-type differences in light, T_{leaf}, and VPD_{leaf} were relatively small between shelter-wood sites compared to the other stand-types (Figs. 4.5 and 4.7). This was likely due to the high-shade nature of light interception by the widely spaced upper canopy trees. This overstory type would tend to produce a more even pattern of moderately intense light (Oliver and Larson 1990) than the gaps surrounded by dense canopy that characterize selection stands. Differences in these attributes between the selection stands may be related to gap size (Bazzaz and Wayne 1994), which was slightly greater in SL- 1 than SL2.

Although both clearcut sites lacked an overstory canopy and showed very similar solar energy inputs, they exhibited the greatest variation within stand-types for T_{leaf} and VPD_{leaf}. CC-2 was over 3x the size of CC-l (3 ha and 10 ha, respectively). However, monitoring sites were centrally located in the openings and well away from shade cast by the surrounding intact forest, making it unlikely that size of opening resulted in microclimatic differences between the sites. As shown by their similarity in PAR fluence (Fig. 4.3), T_{air} (Fig. 4.4), and VPD, (Fig. 4.7), atmospheric meteorological conditions were substantially the same between these sites. Edaphic conditions (USDA Forest Service 1959) and preharvest stand composition (Forest Ecosystem Research Program, unpublished data) were also similar. The only apparent dissimilarity between the clearcut sites was in their post harvest treatment with respect to control of competing vegetation. CC-1 had received an application of herbicide 2 years before the measurement period and all surviving hardwood sprouts and competing shrubs were cut with brushsaws a few days before the 1999 micrometeorological monitoring began. As a result spruce saplings in CC-

1 had minimal competition, while those in CC-2 faced potential competition from *Populus* root sprouts and stump sprouts of *Betula* and *Acer*. Similarity in PAR fluence (Fig. 4.3) suggests that any competition was primarily for belowground resources.

Studies at the Fallingsnow Ecosystem Project in Ontario, Canada, indicated that control of competing vegetation for belowground resources was the predominant limitation to conifer growth (Reynolds et al. 1997). Their data showed that soil water availability was greater in plots with vegetation control as opposed to untreated plots through most of the growing season. Reynolds et al. (1997) attributed increased productivity in the treated plots to greater nitrogen mineralization from higher soil temperatures and enhanced mineral uptake in moister soils. Alternatively, vegetation control could enhance growth by increasing the water supply to transpiring foliage. This would increase heat loss to latent energy transfer and reduce leaftemperature, limiting the inhibitory effects of T and VPD on photosynthetic carbon gain. Such a competitive limitation to soil water availability would explain the divergence between $T_{leaf} - T_{air}$ curves for the two clearcut sites (Fig. 4.6). This effect may have been enhanced by monitoring transplanted saplings at the CC-2 site (see methods). Although the saplings had been transplanted over a year before measurements began, their root systems may not have been exploiting as great a volume of soil as those at the CC-l site which had been in place for 4 years. The high peaks for midday $T_{leaf} - T_{air}$ curves at the shelterwood sites (Fig. 4.6) may also be due to reduced latent heat removal, resulting from competition for soil moisture with remaining overstory trees and advance regeneration.

The influence of silvicultural systems on photosynthetic carbon gain

Potential photosynthetic carbon gain (PPCG) is clearly dominated by light availability (compare Figs. 4.3 and 4.8), although PPCG was not consistently proportional to fluence. Although fluence in the clearcuts was over 6x that at the selection sites and nearly 3x that of the shelter-wood sites, PPCG at the selection sites was 60% of that in the clearcuts, and that of the shelterwoods was only 6% less than the mean value for the clearcuts. This can be explained by the interaction of light intensity (photosynthetic photon flux density; PPFD) with the shape of photosynthetic light-response curves. A primary factor in this incongruity was the percentage of light fluence that was above the light-saturation point at the clearcut sites. As indicated by the photosynthetic light response functions (Fig. 4.2) rates representing 95% of maximum rates* in red spruce sun-foliage occur at a PPFD of approximately 1000 $\mu mol\ m^{-2}\ s^{-1}$. Therefore, much of the available h-radiance at the open sites is not photosynthetically utilized. However, this 'excess' PAR input may decrease the effects of mutual shading in lower parts of the crown (not examined in this study), which could enhance photosynthetic carbon gain at the tree level (Leverenz 1996).

A second factor contributing to the discrepancy between PAR fluence and PPCG may be the greater photosynthetic efficiency of gap-adapted red spruce foliage at intermediate light intensities. These light levels are associated with the strongly nonlinear

*As mathematical models of light response curves generally asymptotically approach maximum rates, Bazzaz and Carlson (1982) recommend that a value representing 95% of estimated maximum rates is of greater utility in comparisons of photosynthetic attributes than maximum rates.

portion of the photosynthetic light-response curve (Fig. 4.2), and Terashima and Hikosaka (1995) suggested that it is in this range of PPFD that photosynthetic systems may show the greatest divergence in their abilities to efficiently utilize incident PAR. Decreased efficiency at intermediate light intensities results from mutual shading that may occur at many levels: mutual shading by grana within chloroplasts, by chloroplasts within mesophyll calls, by mesophyll cells within needles, by foliar elements (needles), and by shoots or higher-level crown factors. The k-parameter (bending factor) of the nonrectangular hyperbola is a quantitative estimate of this phenomena at any scale at which photosynthetic light-response is considered (Evans et al. 1993, Leverenz 1988), and incorporates the effects of mutual shading at all lower levels. If no mutual shading occurred, then the resulting response curve would be of the Blackman-type, where the initial linear slope (defining apparent quantum efficiency) would continue until the light-saturation level of PPFD was reached. In this case the k-parameter would equal 1. Bending factors between 0 and 1 describe response curves that deviate from Blackman-types with lower values indicating increasingly shallower bends in their nonlinear portions. Physiologically, lower values of the k-parameter indicate decreasing efficiency of photosynthesis at PPFD levels between those associated with the initial linear response and saturating h-radiance (Terashima and Hikosaka 1995). In red spruce, the light response curve of sun-adapted foliage shows a higher maximum rate of photosynthesis than that of gap-adapted foliage (Fig.4.2). However, through a range of moderate light intensities the response curve of gap-foliage shows a higher photosynthetic rate than sun-foliage. This would be expected due to the thicker needles (lower specific leaf area) of red spruce sun-foliage compared to shade-adapted needles (Chapter l), which

implies enhanced mutual shading at cellular levels and below. Additionally, shoots of sun-adapted foliage in red spruce tend to exhibit greater needle packing (number per unit shoot length) and lower ratios of shoot silhouette-to-total-needle area compared to shade-foliage (M.E.Day, unpublished data). Both of these attributes would be expected to enhance mutual shading at the shoot-level. Although differences in photosynthetic rates at mid-levels of PPFD are small (Fig. 4.2), light intensities in this range are typical of incident levels in selection and shelter-wood stands, and represent mean levels during nearly one-half the daylight hours in the clearcuts (Fig. 4.3). Consequently, the accumulated influence of this factor may be significant in explaining the incongruity between PAR fluence and PPCG with respect to the clearcut and shelterwood sites.

Inhibition by vapor pressure deficit (VFAC) proved to be the greatest factor restricting PPCG and accounted for approximately 75% of the difference between PPCG and NPCG in all stand-types. Stomatal conductance in red spruce is far less sensitive to vapor pressure deficit than its western North American congeners *Picea sitchensis* (Bong.) Carr (Warkintin et ***al.*** 1992) and ***P. engehnanni*** Engelm. (Kaufmann 1976), for which rates decrease significantly above an ambient VPD of 0.5 kPa. However, this study demonstrates that under current climatic conditions VFAC exerts a substantial stress on gas exchange. That stress is increased under high irradiance conditions due to higher foliage temperatures and the temperature dependence of VPD (Buck 198 1). Alexander et al. (1994) and Vann et al. (1996) have proposed that current and future southern range limits of red spruce are controlled by temperature. The results of this study are consistent with their proposition in the broad sense. However, it appears that the major environmental stress on this species

will result more through the indirect influence of temperature on vapor pressure deficit than through direct pathways (Table 4.4).

Several studies have indicated that low soil water potentials enhance the response of stomata to VPD (Ellsworth 1999, Thomas and Eamus 1999, Nonami et al. 1990, Grieu et al. 1988). As the modeled assessments of inhibition of photosynthesis presented do not address this factor, they are likely underestimating actual rates of inhibition. This potential source of error would vary by site. If this underestimation is proportional to the degree of water stress, then rates of VFAC for sites with presumed high water stress (e.g. CC-2) would much greater than the model suggests, while those for the sites with low water stress (e.g. CC-l) would be closer to the predicted values.

In this study integrated carbon allocation to foliar R_m (Table 4.4) is approximately 10% of gross carbon gain in all stand-types. This is broadly consistent with estimates for other temperate conifers (Landsberg and Gower 1997, Ryan et al. 1997, Ryan et al. 1994, Edwards et al. 1980). Due to higher T_{leaf} and the temperature-dependence of R_m, allocation to foliar R_m is greater in the clearcuts. However, foliage in the clearcuts allocated proportionally less carbon to R_m, relative to PPCG, than that at the selection sites. Day (2000) has proposed that R_m may be a more significant carbon sink proportional to gross photosynthesis in shade-adapted red spruce foliage. In shade-foliage maximum photosynthetic rates are approximately one-fourth of those given in Table 4.2 for sun-foliage but respiration rates are 70-80% of sun-foliage rates (Alexander et al. 1994).

Compared to estimates for R_m, estimates of direct temperature limitation (T_d) under current climatic conditions were small in all stand-types (Table 4.4). This is a result of the

relatively few hours under which substantial effects from this factor occurred. Thus, temperature inhibition to NPCG is primarily a result of losses to R_m. However, inhibition of photosynthesis by T_d was significantly greater under warmer climate scenarios (Table 4.6). From these results, it appears that, under current-climate conditions, red spruce is growing near a turning point for this factor, and an increase of a few degrees in mean ambient temperature will result in large increases in T_d inhibition of photosynthesis.

These modeling results indicate that net photosynthetic carbon gain (NPCG) in upper canopy foliage of red spruce saplings was roughly equivalent at the shelterwood and clearcut sites (Fig. 4.4) under current-climate conditions, with ranges of estimates for the two stand-types showing significant overlap. When the shelterwood sites are compared with CC-Z, NPCG in the former is clearly superior, but this order is reversed when NPCG values of the selection sites are compared with those of CC- 1. This' comparison demonstrates the importance of the interaction of microclimate and competitive environment as determinants of carbon gain. Where competition for belowground water resources is strong (shelterwood and CC-Z sites; see discussion of microclimates), limitations to NPCG from temperature-related factors (TFAC and VFAC) increase. This is likely due to decreased transpiration rates resulting in lower dissipation of incident solar radiation energy by latent heat transfer. When belowground competition in clearcuts is low (CC-l), clearcuts and shelter-woods are roughly equivalent in NPCG. If belowground resources are not limiting, greater light availability in the absence of an overstory canopy may further enhance growth by providing higher PAR levels at lower crown levels in the canopies of regenerating saplings (Johnson et al. 1998, Lamhamedi et al. 1998, Palik et al.

1997, Klinka et al. 1992). The greater growth rates of red spruce saplings with distance from the edge of intact canopies reported by Huges and Bechtel (1997), may be due to this interaction of limiting (T-related and competition) and enhancing (PAR fluence) factors. This conceptual model may partially explain the inverse relationships between competition and growth of conifer seedlings in numerous studies (Walstad and Kuch 1987).

By extrapolation, growth efficiency of red spruce saplings should be equal in both shelterwood and clearcut silvicultural systems, but only if competing vegetation is controlled in the latter. However, achieving the almost complete control of competing vegetation at CC- 1 involves substantial costs (Nyland 1996), which are minimized under a shelterwood system (Seymour 1995). In addition, establishment of red spruce seedlings is enhanced by the partial shade of shelterwoods, which lowers temperatures and increases moisture availability in the uppermost soil strata (Hannah 1988). Growth of some species appears to be enhanced by early overwood removal in shelterwood systems (Bergqvist 1999, Dignan et al. 1998), but this has been shown to inhibit growth for others (Messier 1999, Dey and Parker 1997). For red spruce, these results argue for extended over-wood retention in shelterwood systems unless stand prescriptions call for a high level of vegetation control after removal.

In contrast to the shelter-wood and clearcut sites, the primary factor limiting NPCG at the selection sites was PAR fluence. While cooler leaf temperatures minimized inhibition of NPCG by VFAC and TFAC, mean estimated PPCG at the selection sites was roughly equal to levels of NPCG in the other two stand-types (Table 4.4). Thus, photosynthetic carbon gain of red spruce saplings is substantially lower under selection systems than

shelterwood or clearcut approaches. Selection systems may provide other advantages that are desirable from a tree growth perspective, however, such as limiting regeneration to shade-tolerant species, and from a forest ecosystem perspective by enhancing such aspects as structural diversity and consistency of soil microclimates over time (O'Hara 1998, Seymour 1995). While the focus of this study is on photosynthetic carbon gain by sapling-sized trees, there is evidence that selection systems may provide levels of productivity that rival even-aged systems at the stand level (O'Hara 1996). These results suggest that growth of sapling cohorts in uneven-aged red spruce stands, if desirable, can be substantially enhanced by silvicultural prescriptions that improve light fluence at the sapling strata (e.g., harvesting of larger groups and thinning of older cohorts).

Microclimatic conditions in stands with irregular overstory canopies are highly heterogeneous (Finzi and Canham 2000, Baldoccchi and Collineau 1994), and great variability is also typical within disturbance gaps (Bazzaz and Wayne 1994). Therefore, conditions encountered by saplings in selection stands will exhibit high levels of spatial and temporal variation, This is illustrated by the ranges of microclimatic and carbon gain factors for the two selection sites in this study, which are apparent notwithstanding the similarities in basal area and canopy gap-fraction between the sites (Table 4.1). Such variations have been shown to influence competitive differentiation between species regenerating in gaps (Finzi and Canham 2000, Wayne and Bazzaz 1993, Canham 1988). In contrast, the more consistent canopy structure in the shelterwoods appeared to minimize these variations and is more congruous with the close ranges of mensurational attributes of the shelterwood sites. This difference between stand-types supports the maxim that the high-shade of

shelterwoods provides relatively uniform conditions for regeneration (Oliver and Larson 1990, Hannah 1988). However, at the level of the individual sapling, competitors in overstory and understory strata have the potential to produce small-scale variation in resources that may effect the growth rates of individuals (McCaughey and Schmidt 1982).

Aboveground conditions would be expected to be relatively uniform in clearcuts, which is apparent in the ambient light and atmospheric climatic attributes. However, the competitive influence of surrounding vegetation on belowground resources that this study suggests and their effects on foliar physiology may also create variability in growing conditions at the scale of individual saplings. Microsite variability may also be introduced by the composition of competing vegetation. For example, Peltzer et al. (2000) reported that white spruce growth was lower in competition with aspen (*Populus*) as opposed to grass and forbs.

These sources of variability have implications for the results of this research. Because microclimatic monitoring was carried out at only single points in each stand, the results are not likely to adequately address inherent variation within stand-types. The conclusions drawn here should be entertained with respect to this caveat, and viewed as a tentative overview. A definitive understanding of how micoclimatic influences enhance or inhibit carbon gain in relation to stand structure will require finer-scale long-term monitoring of microclimates to evaluate both within-stand heterogeneity and the effects of interannual climatic variation.

Implications for the population dynamics of red spruce under changing climates

The base climate year (1999) was exceptionally warm in northeastern North America, with the mean annual temperature at the nearest long-term monitoring station (Caribou, Maine; lat. 46" 52', long. -68" 2') reported at 1.9 °C above the 30-year mean (NCDC 2000). During the microclimate monitoring period the mean departure from normal temperatures was slightly less (1.8 "C). However, this growing season difference was skewed by mean September temperatures of 4.4 °C above normal mean temperatures. June showed departure from normal of 1.9 °C, July 0.9 °C, and August 0.1 °C. Precipitation for 1999 was 5.3 cm above the 30-year mean. Again, this data was skewed by abnormally high levels during September (13.6 cm, about 20% of the mean annual total).

The difference between factors limiting NPCG in red spruce saplings between selection systems (light) and the other stand-types (T-related: TFAC and VFAC) are apparent in the cooler climate model runs (Fig. 4.9). Under cooling scenarios selection systems respond little in absolute NPCG (Table 4.6a.), albeit increases relative to current-climate conditions are proportionally similar between selection and shelterwood stand-types (Fig. 4.6b). The most dramatic shifts in NPCG were seen with the warmer climate scenarios. At +5 °C, NPCG in the clear-cuts was approximately equal to that of the selection stands (Fig. 4.9). The modeling results indicated that NPCG at the shelter-wood sites would be clearly greater than that of the other stand-types with a warming climate. In this scenario, the shelter-wood stand-type offers the combined advantages of greater quantum fluence than the selection sites and lower T_{leaf} (therefore, decreased inhibition by TFAC and VFAC) than the clearcuts. Thus, under predicted scenarios of climatic warming

(Mitchell et al. 1990), the advantages of shelterwood and selection systems for managing red spruce will increase relative to clearcut systems.

Schauffler (1998) has suggested that red spruce in the Acadian region was restricted to coastal refugia, and perhaps some favorable inland sites, during warmer periods of the Holocene. As the climate cooled, the species was able to spread across the landscape to become an important component of most Acadian forest-types. Schauffler's (1998) hypothesis is consistent with the climate-change modeling results from this study. During warmer periods, red spruce would have been a poor competitor in most plant communities due to temperature-related limitations to carbon gain. Coastal refugia may have offered slightly cooler, and perhaps moister, microclimates, which would minimize those limitations. Inland sites with a combination of overstory protection from solar radiation input and sufficient soil moisture to permit rapid transpiration and latent heat transfer may have also offered safe-sites for this species during climatic warming. Under climatic regimes that were somewhat cooler than the current-climate, as have been proposed for the centuries immediately proceeding European settlement (Gajewski 1988, 1987), the species would have been a strong competitor following disturbances at many scales. This may explain the apparently rapid spread of red spruce across the Acadian landscape between approximately 1 k BP and the time of European settlement that Schauffler's (1998) hypothesis implies.

These extrapolations of red spruce carbon gain under different climatic regimes assume that temperature is the dominant climatic variable. Thus, the estimates presented here ignore changes in bulk air vapor pressure, precipitation regime, solar radiation input,

and CO, concentration that may accompany changes in temperature regime. How these related factors might change climatic warming or cooling is highly uncertain (Mitchell et al. 1990), so their interactive effects, although potentially significant, are not addressed here.

Conclusions

The silvicultural regimes evaluated (selection, shelterwood, and clearcut systems) result in substantially different microclimates. However, microclimatic differences may not be apparent if bulk air properties alone are monitored. Dissimilarities become clearer when physiologically relevant attributes, such as leaf temperature and vapor pressure deficit in the boundary layers of air at foliar surfaces, are considered. If physiological responses to microclimatic variables are best described by threshold-type functions, the number of measurement periods during which thresholds are exceeded may be a useful metric for evaluating the relative influence of microclimates.

While gross photosynthesis, and, therefore, potential photosynthetic carbon gain, is highly correlated with incident light flux density, the interaction of this variable with photosynthetic light-response curves is of significant importance in integrated carbon gain. Attributes of these response curves not only vary between species, but within species, due to differences in light-adaptation status, and can explain the incongruities between light fluence and integrated carbon gain in shade-tolerant species such as red spruce.

Modeling the integrated influence of microclimatic on photosynthetic carbon gain variables indicates that the indirect effects of temperature (vapor pressure deficit and maintenance respiration) are more significant than direct inhibition of photosynthesis by

temperature. Vapor pressure deficit provides the greatest inhibition to photosynthetic carbon gain in red spruce, with its effect approximately equal to the combined influences of direct temperature inhibition and losses to maintenance respiration.

Among silvicultural systems, photosynthetic carbon gain is most strongly limited by light in selection stands and by temperature related factors (inhibition by temperature and vapor pressure deficit, and losses to maintenance respiration) in shelterwood and clearcut systems. Lower levels of microclimatic inhibition in the shelterwoods tended to equalize net carbon gain between shelterwoods and clearcuts.

Both among and within stand-types, the effects of competition on availability of belowground water resources influences transpirational flux and loss of foliar heat through latent energy transfer. This aspect is especially important to controlling temperature-related inhibitions to carbon gain in the high energy environments of clearcuts.

With respect to net photosynthetic carbon gain of upper-crown foliage in red spruce saplings, stand-types were ordered selection < clearcut ≈ shelter-wood under current-climate temperature regimes, In cooler-climate scenarios this relative order was maintained, but in absolute terms the superiority of clearcuts and shelterwoods over selection systems increased. Under warmer-climate scenarios the order was selection ≈ clearcut < shelterwood , with the latter showing clear superiority over the other stand-types. This may provide a partial explanation for reported changes in distribution of red spruce in the Acadian region during the Holocene, and has implications for future distribution and management under predicted climate change scenarios.

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Appendix: Code for the carbon gain model

Figure 4.1 presents model pathways and steps in a graphic form. Using hourly time-step data from micrometeorological stations, the model outputs potential photosynthetic carbon gain, net photosynthetic carbon gain, losses to maintenance respiration, and inhibition of potential photosynthesis by direct temperature effects, vapor pressure deficit, and total temperature effects (direct temperature effects + losses to maintenance respiration) on a growing season basis (depending on the range of dates in the dataset). Model code is in capital letters, and italicized print describes steps and provides comment.

Identifies input dataset and input variables

```
FILENAME JSDATA 'C:\MYFILES\MIKESTUF\PEFMET99\JS99.DAT';
DATA A; INFILE JSDATA;

INPUT STA DAY HR PPFD FLU AT ATMAX ATMIN VPD VPDMAX STAVG
STMAX STMIN AMLT LVD MaxLT LTAT;

DATA B; SET A;
```

Identifies stations by stand-type

```
IF (STA = 1) OR (STA = 5) THEN TYPE = 1;
IF (STA = 4) OR (STA = 6) THEN TYPE = 2;
IF (STA = 2) OR (STA = 3) THEN TYPE = 3;
```

Used to switch temperature basis

```
MLT = AMLT;
/*MLT = (AMLT/AT)*(AT + 2.5);*/
MLT = AT;
```

Calculates leaf-to-air vapor pressure deficit (VPDL)

```
AVPSAT = 0.61365*EXP((17.502*AT)/(240.97 + AT));
AVP = AVPSAT - VPD;
LVPSAT = 0.61365*EXP((17.502*MLT)/(240.97 + MLT));
VPDL = LVPSAT - AVP;
IF (VPDL < 0) THEN LTVPD = 0;
IF (VPDL = 0) OR (VPDL > 0) THEN LTVPD = VPDL;
```

Parametizes non-rectangular hyperbola function by foiliage light-adaptation type

```
IF (TYPE = 3) THEN A = 10;
IF (TYPE = 1) OR (TYPE = 2) THEN A = 9;
IF (TYPE = 3) THEN Q = 0.03;
IF (TYPE = 1) OR (TYPE = 2) THEN Q = 0.05;
IF (TYPE = 3) THEN K = 0.81;
IF (TYPE = 1) OR (TYPE = 2) THEN K = 0.91;
```

Calculates potential net photosynthesis (APS) using non-rectangular hyperbola function

```
IF (PPFD = 0) THEN APS = 0;
IF (PPFD > 0) THEN APS =
(Q*PPFD+A-SQRT((Q*PPFD+A)**2-4*K*Q*PPFD*A))/2*K;
```

Calculates maintenance respiration (RM) rates using Q_{10} function from a 23 °C base and Q_{10} of 2

```
RQ10 = 2;
IF (PPFD > 0) AND (TYPE = 3) THEN R = 0.47;
IF (PPFD = 0) AND (TYPE = 3) THEN R= 0.33;
IF (PPFD > 0) AND ((TYPE = 1) OR (TYPE = 2)) THEN R = 0.43;
IF (PPFD = 0) AND ((TYPE = 1) OR (TYPE = 2)) THEN R= 0.301;
IF (MLT < 23) THEN RM = EXP (LOG(R)-LOG(RQ10)*((23-MLT)/10));
IF (MLT = 23) OR (MLT > 23) THEN RM =
EXP(LOG(R)+LOG(RQ10)*((MLT-23)/10));
```

Calculates potential gross photosynthetic rates (GPS) from net photosynthetic rates + maintenance respiration rates

```
IF (PPFD = 0) THEN GPS = 0;
IF (PPFD > 0) AND (MLT < 23) THEN GPS = APS + RM;
IF (PPFD > 0) AND ((MLT > 23) OR (MLT = 23)) THEN GPS = APS + R;
```

Calculates direct temperature inhibition of photosynthesis (DTFAC) when foliar temperatures exceed the threshold of 32 °C

```
IF (APS = 0) THEN TPS = 0;
IF (APS NE 0) AND ((MLT = 32) OR (MLT < 32)) THEN TPS = APS;
IF (APS NE 0) AND (MLT > 32) THEN TPS = APS-(0.534*(MLT - 32));
IF (TPS < 0) OR (TPS = 0) THEN TCPS = 0;
IF (TPS > 0) THEN TCPS = TPS;
DTFAC = (APS - TCPS);
```

Calculates inhibition of net photosynthesis by vapor pressure deficit (VFAC) when threshold is exceeded and incident light flux is above the level for 50% ***of maximum photosynthetic rates (Assumes that stomata1 conductance is not limiting to photosynthesis at low light levels.)***

Sets thresholdfor inhibition of photosynthesis by vapor pressure deficit

```
VPT = 2.0;
IF (APS = 0) THEN VPS = 0;
IF (APS NE 0) AND ((ltvpd < VPT) OR (ltvpd = VPT)) THEN VPS = APS;
IF (APS NE 0) AND (ltvpd > VPT) THEN VPS = APS-( 1.009*ltvpd);
IF (VPS < 0) OR (VI'S = 0) THEN VCPS = 0;
```

Removes vapor pressure inhibition at PPFD levels < 200 $\mu mol\ m^{-2}\ s^{-1}$

```
IF (VPS > 0) AND (PPFD < 200) THEN VCPS = APS;
IF (VPS > 0) AND ((PPFD = 200) OR (PPFD > 200)) THEN VCPS = VPS;
VFAC = (GPS - VCPS);
```

Scales gas exchange and inhibitory factors from $\mu mol\ m^{-2}\ s^{-1}$ to moles $m^{-2}\ h^{-1}$:

Potential photosynthetic carbon gain (PPCG)

```
IGPS = GPS *(60**2)*(10**-6);
```

Maintenance respiration (R_m)

```
IRM = RM*(60**2)*(10**-6);
```

Direct temperature inhibition of photosynthesis (T_d)

```
DTFAC = DTFAC*(60**2)*(10**-6);
```

Inhibition of photosynthesis by vapor pressure deficit (VFAC)

```
IVFAC = VFAC*(60**2)*(10**-6);
```

Calculates total inhibition of PPCG due to temperature (TFAC)

```
ITFAC = IRM +IDTFAC;
```

Calculates net photosynthetic carbon gain (NPCG)

```
INCG = IGPS - IRM - ITFAC - IVFAC;
```

Sorts dataset for integration by stand-type

```
PROC SORT; BY TYPE ;
```

Integrates by stand-type

```
PROC MEANS MAXDEC=3 SUM;
VAR INCG IGPS IRM INRM ITFAC TTFAC IVFAC;
 BY TYPE ;
```

Sorts data for integration by site

```
PROC SORT; BY TYPE STA;
```

Integrates by site

```
PROC MEANS MAXDEC=3 SUM;
 VAR INCG IGPS IRM INRM ITFAC TTFAC IVFAC;
 BY TYPE STA;
```

Ends model run

```
QUIT;
```

Biography of the Author

Michael E. Day was born in Portland, Maine, on March 27, 195 1, and graduated from Portland High School in 1969. He studied biology at the University of Maine at Portland-Gorham from 1970 - 1975. Michael worked as a technician in marine ecological research, mariner, boatbuilder, and cabinetmaker before returning to The University of Maine in 1992, He graduated from the University of Maine in May, 1994, with a Bachelor of Science degree in Forestry. He is a member of Xi Sigma Pi forestry honor society and the Society of American Foresters.

Michael entered the graduate program in Forest Resources at The University of Maine in 1994, and served as a research assistant in the University's Forest Ecosystem Research Program from June, 1994, until December, 1996. He has been employed since December, 1996, by the University of Maine as an Assistant Scientist in Forest Ecosystem Science. Michael is a candidate for the Doctor of Philosophy degree in Forest Resources from The University of Maine in December, 2000.