I. Introduction

Forests cover approximately 33% of the land surface of the earth, yet they are responsible for 65% of the annual carbon (C) accumulated by all terrestrial biomes (Schlesinger, 1991). In general, total C content and net primary production rates are greater for forests than for other biomes, but C budgets differ greatly among forests. Despite several decades of research on forest C budgets, there is still an incomplete understanding of the factors controlling C allocation. Yet, if we are to understand how changing global events such as land use, climate change, atmospheric N deposition, ozone, and elevated atmospheric CO₂ affect the global C budget, a mechanistic understanding of C assimilation, partitioning, and allocation is necessary. Numerous abiotic and biotic factors influence C allocation patterns, which in turn affect the capacity of plants to obtain resources from the atmosphere and soil.

Although reviews on various components of conifer forest C budgets, such as photosynthesis (see Chapter 4, this volume) and detritus production (Vogt et al., 1986), are available, a synthesis of the influence of abiotic and biotic factors on leaf, canopy, and stand-level C budgets of conifer forests is lacking. The objective of this chapter is to review the major factors that influence C allocation and accumulation in conifer trees and forests. In keeping with the theme of this book, we will focus primarily on evergreen conifers. However, even among evergreen co-
nifers, leaf, canopy, and stand-level C and nutrient allocation patterns differ, often as a function of leaf development and longevity (Gower and Richards, 1990; Gower et al., 1993a; Reich et al., 1994).

The terminology related to C allocation literature is often inconsistent, confusing and inadequate for understanding and integrating past and current research. For example, terms often used synonymously to describe C flow or movement include translocation, transport, distribution, allocation, partitioning, apportionment, and biomass allocation. A common terminology is needed because different terms have different meanings to readers. In this paper we use C allocation, partitioning, and accumulation according to the definitions of Dickson and Isebrands (1993). Partitioning is the process of C flow into and among different chemical, storage, and transport pools. Allocation is the distribution of C to different plant parts within the plant (i.e., source to sink). Accumulation is the end product of the process of C allocation.

II. Distribution of Conifer Forests

Evergreen conifers occur from tropical to boreal forests and from temperate rainforests to dry woodlands (Walter, 1979; Kikuzawa, 1991). Conifers commonly dominate in temperate regions only after disturbance or where soil infertility is low. The dominance of evergreen conifers in the Pacific Northwest of the United States can be explained partly by the unique environmental conditions of dry, warm days and cool nights in the summer and mild, moist conditions in the winter (Waring and Franklin, 1979). Although conifers occur on many of the major soil orders, conifers, especially pines, are more abundant on nutrient-poor soils (Miller et al., 1979). Nitrogen availability commonly limits net primary production (NPP) in temperate and boreal conifer forests whereas phosphorus availability limits NPP in subtropical and tropical environments (Ballard, 1984). In summary, temperature, moisture, and nutrient conditions differ greatly among evergreen conifer forests.

To help understand assimilation and allocation patterns of conifer forests, we briefly contrast the major differences in C and nutrient cycles of evergreen conifer and deciduous forests. Perhaps the most striking difference between evergreen conifers and broadleaf deciduous species is leaf longevity, which is correlated to a number of leaf, canopy, and ecosystem structural and functional characteristics (Gower et al., 1993a; Reich et al., 1994). Even among conifer species leaf longevity ranges from less than a year for *Larix* spp. and *Taxodium* spp. to greater than 40 years for *Pinus longaeva*. Leaf litterfall nitrogen content is often less for evergreen conifers than for broadleaf deciduous forests (Vogt et al., 1986). The litter of evergreen conifers decomposes slower than that from deciduous trees due to its lower litter quality (i.e., higher lignin and lower nitrogen concentrations), resulting in greater forest floor mass beneath conifer forests compared to broadleaf deciduous forests. Soil nitrogen availability is commonly lower in evergreen conifer forests than in deciduous forests due to the positive feedback of leaf litterfall quality on soil nitrogen dynamics (Gower and Son, 1992). In addition, evergreen conifer forests have lower annual nitrogen uptake rates compared to deciduous forests (Gosz, 1981; Nadelhofer et al., 1984; Son and Gower, 1991).

III. Controls on Carbon Assimilation

Net primary production of a seedling, tree, or forest is the balance between total canopy photosynthesis (gross primary production; GPP) and the amount of C lost via respiration (autotrophic respiration). There are numerous direct and indirect feedbacks on C assimilation and allocation in forests (Fig. 1). For example, net canopy photosynthesis is the product of net photosynthetic rate and photosynthetic surface area integrated over selected daily and seasonal time periods, and net primary production is the difference between net canopy photosynthesis and autotrophic respiration of woody tissues. Clearly, net primary production cannot be estimated without a complete understanding of the influence of biophysical controls on physiological processes such as photosynthesis and respiration (Chapter 4) and on the allocation of C to components such as leaf area and live woody biomass.

Under optimal environmental conditions, NPP is linearly related to intercepted photosynthetically active radiation (IPAR) for crop plants and tree seedlings (Monteith, 1977) and forests (Linder, 1985; Landsberg, 1986). Factors that influence the relationship include (1) canopy reflectance, (2) canopy architecture and persistance of the canopy during the year, and (3) light use efficiency (Cannell, 1989). The first factor that affects the relationship between NPP and IPAR is canopy albedo, which averages 15-20% for deciduous forests versus 10-15% for conifer forests (Rosenberg et al., 1983). Canopy characteristics related to architecture include rate of leaf area development, maximum leaf area, and leaf area duration. The rate of leaf area development in the spring, although important for deciduous species, is gradually less important for evergreen conifers that retain their needles for a greater number of years because the new foliage comprises an increasingly smaller fraction of the total leaf area (Gower et al., 1993a). Leaf area duration positively influences annual IPAR. For example, Cannell et al. (1987) reported a
linear decrease in IPAR with later dates of canopy development for a Salsola kali stand. Another important factor influencing IPAR is the leaf area index (LAI) of the tree or forest. IPAR is curvilinearly related to LAI, with 95% of the incoming radiation being absorbed in a forest with a LAI of 6 (Fig. 2), assuming radiation attenuation approximates the Beer–Lambert Law. Major factors governing LAI include environmental constraints (see Section V.B) and biotic factors such as leaf longevity (Gower et al., 1995a; Reich et al., 1994).

Crown architecture also influences radiation attenuation, which affects IPAR. Light extinction coefficients (k) for conifers range from 0.4 to 0.6 (Jarvis and Levenzer, 1983) and for a constant LAI, IPAR generally increases with k, especially for forests with LAMs from 1 to 6 (Fig. 2). Factors that influence k include shoot angle, clumping of foliage on the shoot, and spectral reflectance. As conifer shoots are held more erect (i.e., perpendicular to the soil surface), k decreases (Jordan and Smith, 1993). Clumped foliage such as needles on conifer shoots allows more radiation to penetrate deeper in the canopy. In fact, Leverenz (1980) speculated that the shoot morphology of conifers maximizes radiation use efficiency within the canopy and later demonstrated that the ratio of shoot silhouette area to total projected needle area of shade shoots was positively correlated to aboveground net primary production (ANPP) of evergreen conifer forests (Leverenz and Hinckley, 1980; Leverenz, 1992).

The third major factor influencing the relationship between NPP and IPAR is light use efficiency, or e, defined as dry biomass accumulated per unit of intercepted radiation (Monteith, 1977). Values of e from field studies range from 0.5 to 1.4 (Cannell, 1989), falling well short of the theoretical maximum value of 6.0 calculated by Jarvis and Leverenz (1983). Most estimates of e do not include belowground NPP, but including belowground dry matter production would increase e by 20–50% for conifer forests (see Section V.C). Multiple constraints on photosyn-
thesis imposed by environmental stresses may in part explain the inefficient use of radiation (Teskey and Whitehead 1994). For example, Runyon et al. (1994) reported a strong positive linear relationship between ANPP and IPAR for seven conifer forests located along a large environmental gradient in western Oregon only if they excluded the proportion of IPAR that was not utilized because of environmental constraints on net canopy photosynthesis (Runyon et al., 1994) (Fig. 3). Efforts to model environmental constraints cannot simply use leaf responses because of differences in physical structure and nonlinear relationships between light and photosynthesis (Norman, 1998). For example, changes in photosynthetic photon flux density (PPFD) have similar effects on C assimilation of a canopy and of its constituent needles; however, the canopy is light saturated at a higher PPFD than are needles at the top of the canopy because C assimilation of needles lower in the canopy increases with PPFD (Chapter 4).

IV. Carbon Allocation Patterns in Conifers

Carbon allocation patterns within conifers are highly integrated and are determined at early stages of development. These patterns are regulated by complex interactions between competing sources and sinks within the plant (Dickson, 1989), where a source is a net exporter of photosynthetic and a sink is a net importer of photosynthate (Dickson, 1991). Moreover, an intimate interdependency between the shoot and root exists throughout the life of a plant (Kozlowski, 1971a,b). Carbon allocation patterns in all woody plants are closely related to the source–sink interactions determined by shoot growth (Fig. 4). Sink strength varies markedly by species, genotype (clone), shoot type, age of plant, location within the plant, season, and environmental conditions (Kozlowski, 1992).

A. Plant Genetic Factors

There are three basic phenological patterns of C allocation to shoots in woody plants (Dickson, 1991; Kozlowski, 1992). The first pattern is typical of many conifers and is associated with determinate (or fixed) shoot growth that is characterized by a single, short burst of shoot growth in the late spring and early summer followed by a long lag period of bud set. Distribution of assimilate is dependent on the flush cycle, with most of the assimilate (i.e., >50%) allocated to shoots during the flushing episode, but is largely directed (i.e., >95%) to the lower stem and roots during the lag stage (Fig. 4). Conifers with this pattern include many cold-tolerant and boreal genera (or species) such as Abies, Picea, Pseudotsuga, Tsuga, Pinus ponderosa, Pinus taeda, and Pinus strobus. The second pattern is associated with indeterminate (or free) shoot growth, characterized by continuous shoot growth over most of the growing season. Distribution of assimilate in these plants varies with the stage of leaf development. Developing needles are net importers of assimilate until they become fully expanded, at which time they export both acropetally to developing shoots and basipetally to the stem and roots. Mature leaves export assimilate almost exclusively to the lower stem and roots. Conifers exhibiting this pattern include Gymnos, Larix, and some tropical pines. The third pattern is associated with semideterminate (or recurrent flushing) shoot growth, characterized by periodic flushes of shoot growth with intermediate lag stages. Assimilates are transported to developing shoots during a flush and downward to the stem and roots during the lag stage; the cycle is repeated during each successive flushing episode. Conifer species within this pattern include warm-temperate pines such as Pinus echinata, Pinus elliottii, Pinus palustris, and Pinus taeda, and subtropical pines such as Pinus caribaea and Pinus radiata.

B. Mechanisms of Carbon Allocation

To understand fully C partitioning and allocation in conifers, it is important to understand their patterns and the underlying mechanisms, of which there have been numerous reviews of the mechanisms of C partitioning

Figure 3 Relationship between aboveground net primary production (NPP) and intercepted photosynthetic active radiation (IPAR) for seven conifer forests along a precipitation gradient in Oregon. Closed symbols are for total IPAR and open symbols are for utilized IPAR after subtracting the IPAR that was not utilized by the trees due to environmental constraints (cold temperature, vapor pressure deficits, and water stress) on photosynthesis. (Adapted from Runyon et al., 1994.)
and allocation in herbaceous plants (Gifford and Evans, 1981; Geiger, 1986; Wyse, 1986; Ho, 1988; Stitt and Quick, 1989) and entire books have been written on the subject (Gronnow et al., 1986). Less is known about woody plants, especially conifers, but there is little reason to believe that the controls for C allocation will differ between herbaceous or crop plants and woody plants if similar plant ontogenetic stages and temporal factors are considered (Dickson, 1991) (see Table I). Unfortunately, the controlling mechanisms of C allocation still remain largely unknown, although some of the genetic, biochemical, and physiological aspects of the regulation of transport from sources and sinks are becoming more clear (Gronnow et al., 1986; see also Chapter 6, this volume).

<table>
<thead>
<tr>
<th>Table I: List of Carbon Allocation and Partitioning Studies in Conifers</th>
</tr>
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<tbody>
<tr>
<td>Genus and species</td>
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</tr>
<tr>
<td>Abies balsamea</td>
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<td>Abies spp.</td>
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<tr>
<td>Picea glauca</td>
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<td>Larix spp.</td>
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<tr>
<td>Pinus radiata</td>
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<tr>
<td>Pinus banksiana</td>
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<tr>
<td>Pinus elliottii</td>
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<td>Pinus ponderosa</td>
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<td>Pinus resinosa</td>
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<td>Pinus resinosa</td>
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<td>Pinus taeda</td>
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<tr>
<td>Pinus taeda</td>
</tr>
<tr>
<td>Pseudotsuga menziesii</td>
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<tr>
<td>Pseudotsuga menziesii</td>
</tr>
<tr>
<td>Pseudotsuga menziesii</td>
</tr>
</tbody>
</table>

*List includes representative references in each genus, published in English only.
toning may not be universal and may be specific to species, genotypes, tissue type, or ontogenetic stage (Cronshaw et al., 1986). For example, there are differences in C partitioning and allocation patterns in seedlings and in trees, making extrapolation from seedlings to trees problematic (Cregg et al., 1989). Genetic control is more important in C assimilation and allocation processes than once thought (Huisseg et al., 1992; Gower et al., 1994). Also, the root and shoot interdependently produce the essential growth substances needed to maintain a functional balance in plants (Kozlowski, 1971a). The main control of C allocation between roots and shoots is related to sink activity, including sucrose synthesis (Stitt and Quick, 1988; Dickson, 1991), respiration (Gifford and Evans, 1984), phloem loading and unloading (Ho, 1988), hormone synthesis (Gifford and Evans, 1981), and cell turgor and genetic control (Wyse, 1986). Another important factor is the proximity of the source to the sink and their vascular connections (Gifford et al., 1984; Dickson, 1989). Thus, the key to understanding the mechanisms of C allocation in plants seems to be with the properties of sinks, including the initial establishment of the sink at an early developmental stage, duration of sink growth, as well as sink effects on photosynthesis (Gifford and Evans, 1981).

V. Controls on Carbon Allocation

Cost-benefit theory suggests that plants have evolved to maximize resource use efficiency (Bloom et al., 1985); therefore, C allocation patterns should theoretically vary depending on the availability of resources that vary at different temporal and spatial scales. With few exceptions, environmental conditions differ enough during the year that different resources control C assimilation and allocation during different times of the year. Furthermore, C assimilation and allocation patterns vary within and among conifers due to changes in the magnitude of resource limitations. Below, we briefly examine controls on C allocation.

A. Respiration

Autotrophic respiration is a poorly understood component of forest C budgets. Respiration is commonly separated into construction and maintenance components. For uptake respiration is also recognized (Anthon, 1986; Ryan, 1991), but so few estimates exist for plants that our focus is on the two former components. Together, construction and maintenance respiration are a significant C cost. For example, Ryan and Waring (1992) estimated that maintenance respiration comprised about 18% of GPP for a subalpine Pinus contorta forest; Linder and Axelson (1985) estimated that autotrophic respiration comprised 34% of annual photosynthesis for a P. sylvestris tree; Kinerson et al. (1977) estimated that autotrophic respiration comprised 34% of GPP for a young P. taeda forest; and Kira (1975) reported that autotrophic respiration could approach 65% of GPP in a tropical forest.

The quantity of C allocated to respiration in conifer forests is strongly influenced by temperature. Based on C budgets for four conifer forests in contrasting climates, the percentage of net canopy photosynthesis allocated to autotrophic respiration is positively correlated to mean annual temperature (Ryan et al., in press). The amount of accumulated living biomass, which changes with stand age and environmental conditions (see Section VI), is also an important factor influencing respiration. Knyv et al. (1994) speculated that an old-growth conifer forest allocated a disproportionately greater fraction of GPP to maintenance respiration compared to younger stands (Fig. 5); however, Ryan and Waring (1992) found only a slight increase in sapwood maintenance respiration in comparing a 40- and a 245-year-old P. contorta forest. One of the most critical questions related to forest C budgets pertains to how anticipated climate change will affect net canopy photosynthesis (GPP – autotrophic respiration) versus heterotrophic respiration, because the difference reflects the capacity of the forest to store C.

B. Foliage

Carbon allocated to foliage is partitioned to chemical fractions for structure, physiologically active materials, defense, and storage. Leaf structure or specific leaf area (SLA) is affected by numerous environmental factors. The maximum net photosynthetic rate under optimal conditions is positively correlated to SLA; however, low nutrient availability, increased needle longevity, and greater water vapor deficit reduce SLA (Linder and Rook, 1984; Reich et al., 1991, 1992; Gower et al., 1993a).

Therefore, the actual SLA is a compromise between maximizing instantaneous C gain and long-term C, water, and nutrient use efficiency.

Water availability strongly influences the allometry between sapwood cross-sectional area and leaf area and the allocation of C to new foliage production. Leaf area (LA) is positively correlated to sapwood cross-sectional area (SA) for conifers (Grier and Waring, 1974), with the ratio being greater for conifers in more mesic environments (Fig. 5). Water availability also exerts a strong control on C allocation to new foliage production. Gower et al. (1992) demonstrated that for Douglas fir (Pseudotsuga menziesii), irrigated trees allocated more C to new foliage production than did similar-diameter control trees. Severe drought adversely affects the xylem water potential in the meristems at the base of needles (Zahner, 1968), which reduces needle length (Linder et al., 1987). Because nitrogen concentration is greater for foliage than for many
other tree tissues, and conifers commonly grow on nutrient limited soil, nitrogen fertilization increases the annual allocation of C to foliage (Brix and Mitchell, 1983; Grier et al., 1984; Gholz et al., 1991; Gower et al., 1992, 1995b). The greater allocation of C to new foliage production results in greater (1) needle length, (2) production of needles per shoot, and (3) production of new shoots by fertilized than by control trees (Brix and Ebell, 1969; Brix, 1981; Gower et al., 1992, 1995b). Greater nutrient availability often increases the new foliage mass ratio (Fig. 6). Because net photosynthesis is intrinsically greater for current than for older needles (Chabot and Hicks, 1982; Teskey et al., 1984; Sheriff et al., 1986), reduced needle longevity increases net canopy photosynthesis and production efficiency. Nutrient availability can also influence the allometry between total foliage mass or leaf area and stem diameter (Brix and Mitchell, 1983; Grier et al., 1984; Gower et al., 1993b); however, increased nutrient availability may not increase the total foliage mass of a tree if water or light availability is more limiting (Vose and Allen, 1988; Gower et al., 1993b).

Many of the influences of water and nutrient availability on C allocation at the tree level also occur at the stand level. Water availability also governs new foliage production at the stand level (Gower et al., 1992; Raison et al., 1992a,b; Snowdon and Benson, 1992). Grier and Running (1977) and Gholz (1982) noted that total foliage mass or area was positively correlated to water availability for different conifer species. Irrigation studies have also confirmed a similar relationship (Gower et al., 1992; Raison et al., 1992a,b; Snowdon and Benson, 1992), although the absolute increase is often smaller within than among conifer species. Extreme cold temperatures may reduce the amount of C accumulated in foliage below the physiological limit defined by water availability (Gholz, 1982). Fertilization often increases C accumulation in foliage as a result of increased new foliage production (Linder and Axelson, 1982; Vose and Allen, 1988; Gholz et al., 1991; Gower et al., 1992; Raison et al., 1992a,b; Snowdon and Benson, 1992; Passioura, 1994).

C. Fine Roots

The ability of plant roots to acquire nutrients and water affects C assimilation and allocation (Fig. 1). Plant growth is positively correlated to the availability of soil resources, therefore physical barriers that constrict root growth adversely affect plant growth (Thomson and Strain, 1991). These responses are at least partially mediated by hormonal root-shoot communication (Davies et al., 1986; Scholze, 1986; Turner, 1986; Passioura, 1988; Pereira, 1996) and can affect C allocation and accumulation. The above-mentioned effects of nutrition on C allocation involve changes in hormonal balance, but other mechanisms may be described more simply. For example, greater allocation of C to roots in nutrient-deficient soils can occur because roots are nearest to the nutrients. In nutrient-poor soils, roots use most of the limited absorbed nutrients, leaving little for translocation to aboveground tissues, thereby reducing their capacity to grow (Clarkson, 1985). This also explains the proliferation of roots at microsites of high resource availability in nutrient-poor soils (St. John, 1983; St. John et al., 1985). A second poorly understood component of forest C budgets is the
allocation of C to fine roots and mycorrhizae. A significant amount of C is allocated to fine roots annually, even though fine roots comprise a small fraction of the C content of forest trees. Based on a review of the world literature, annual allocation of C to fine root production for conifer forests ranges from 30 g C/m²/yr for a Pinus radiata forest in Ontario, Canada, to 710 g C/m²/yr for a subalpine Abies amabilis forest in Washington state (Vogt et al., 1986) (Table II). On a global scale, fine root NPP and total allocation of C to roots (i.e., root production + root respiration) are positively correlated to mean annual temperature (Fig. 7). Gower et al. (1994) also reported a strong positive correlation (r² = 0.75) between fine root NPP and mean annual temperature for pine forests. The difference between the two regression lines in Fig. 7 should approximate the quantity of C allocated to coarse root production and root respiration.

Water availability also influences belowground C allocation patterns. Annual C allocation to fine roots is greater in xeric than in mesic conifer forests (Santantonio and Hermann, 1985; Comeau and Kimmins, 1989). Gower et al. (1992) also reported that fine root production (absolute basis) was lower in irrigated and unirrigated + wood chip forests (high water availability but low nitrogen availability) than in control Douglas fir forests, suggesting that water availability directly controls C allocation to fine roots and mycorrhizae.

Another important factor influencing fine root NPP is soil nutrient availability; however, there is uncertainty surrounding both the magnitude and direction of the effect. Both comparative and experimental studies have reported greater (absolute basis) fine root NPP for infertile than fertile Pseudotsuga menziesii forests in the western United States (Keyes and Grier, 1981; Kurz, 1989; Vogt et al., 1996; Gower et al., 1992), whereas other scientists have reported only a relative decrease in the amount of C allocated to fine roots as soil nitrogen availability increases (Linder and Axelson, 1982; Comeau and Kimmins, 1989). Fertilization also decreases C allocation to mycorrhizae (Menge et al., 1977; Menge and Grand, 1978). However, Aber et al. (1985) and Nadelhoffer et al. (1985) reported that fine root NPP is positively correlated to annual N mineralization for different forest types (including conifers) in Wisconsin. The disparity in the results may be related to the different methods used to estimate fine root NPP or mycorrhizal allocation and differences in the relative importance of nutrition in controlling C allocation and allocation in different climates.

Few studies have attempted to quantify how much C is allocated to mycorrhizae or to determine if the benefits provided by mycorrhizae exceed the costs to the plant. Vogt et al. (1982) reported that 150 g C/m²/yr, or 15% of total net primary production, was allocated to mycorrhizae net production in an Abies amabilis stand. Bevege et al. (1975) found that 15 times more ¹⁵N-labeled assimilate was allocated to mycorrhizal-infecteds versus nonmycorrhizal roots. Respiration costs of mycorrhizae are largely unknown. Despite the large amount of C allocated to mycorrhizae, they are critical to the growth and survival of conifers. Growth rates are often 5- to 10-fold greater for inoculated versus nonmycorrhizal conifer seedlings (Lamb and Richards, 1971).

**D. Woody Tissue**

At the tree level, stem wood, stem bark, branch, and coarse root biomass are strongly correlated to stem diameter, although these relationships differ both within and among species. Differences in allometric relationships for stem wood and stem diameter within a species may reflect influences of environmental factors such as water and nutrient availability on tree form, whereas differences in allometric relationships between stem bark and stem diameter among species may be an adaptation to fire (Gower et al., 1987). Of all the woody components, the allometry between coarse root mass and stem diameter differs the least within and among conifer species (see Santantonio et al., 1977) and may be explained by physical principles (Coutts, 1983).

Wood NPP rates for conifer forests range from 84 to 2105 g C/m²/yr and commonly increase from cold to warm climates (Table II). When under stress, conifers allocate less C to woody tissue such as stem, branch, and coarse roots than to foliage and fine roots (Waring and Pinman, 1985; Gower et al., 1992). Relative allocation of C to woody tissue
<table>
<thead>
<tr>
<th>Species</th>
<th>Age (yr)</th>
<th>Location</th>
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<th>Source</th>
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</thead>
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<tr>
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<td>180</td>
<td>Washington, U.S.A.</td>
<td>CT 144 46 585</td>
<td>Grier et al. (1981)</td>
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<td>CT 240 121 80</td>
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</tr>
<tr>
<td>Picea contorta</td>
<td>74</td>
<td>British Columbia, Canada</td>
<td>CT 130 54 243</td>
<td>Conteau and Kimmis (1986)</td>
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<td>Pinus contorta</td>
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<td>British Columbia, Canada</td>
<td>CT 275 108 210</td>
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<td>27</td>
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<td>Ghies et al. (1986)</td>
</tr>
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<td>B 84 40 48</td>
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<tr>
<td>Pinus taeda</td>
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<th>Source</th>
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<td>Gower et al. (1992)</td>
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<td>116 (72)</td>
<td>252 (15)</td>
<td>Gower et al. (1992)</td>
</tr>
<tr>
<td></td>
<td>310 (47)</td>
<td>102 (16)</td>
<td>Gower et al. (1992)</td>
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<td></td>
<td>144 (40)</td>
<td>61 (20)</td>
<td>Gower et al. (1992)</td>
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</table>

*Biomes: ST/WT, subtropical/warm temperate; CT, cold temperate; B, boreal.
*Woody is equal to sum plus branch plus crown mass.
*Low fertility.
*High fertility.
*Control.
*Irrigated plus fertilized.
*Fertilized.
*Irrigated.
*Net NPP estimated using fine: total NPP ratio from Lindner and Axelsson (1982).
*Values in parentheses are percent of total net primary production.
is greater in subtropical/warm-temperate than in cold-temperate and boreal conifer forests. Increased nutrient availability increases the amount of C allocated to woody tissue (Keyes and Grier, 1981; Gholz et al., 1991; Gower et al., 1992; Snowdon and Benson, 1992) and can be explained by the shift in C allocation from fine roots to stem production and perhaps greater leaf area.

E. Storage

Stored C is used to construct new tissue and repair damaged tissues. The vigor of the seedling or tree is related to the amount of stored carbohydrates, suggesting that trees with depleted carbohydrate reserves are disposed to die (Sprugel, 1976; Putz, 1986). In contrast, vigorous trees store sufficient carbohydrates such that they can survive environmental stresses such as insect attack, pathogens infestations, or drought (Waring, 1991). Starch is the main storage form for carbohydrates in conifers (Adams et al., 1986; Fry and Deans, 1977). Other important storage forms include quinol and shikimic acids (Chung and Barnes, 1977; Cranswick et al., 1987) and hemicellulose (Kimura, 1969); of lesser importance are sucrose, cyclitols, and monosaccharides (Kozlowski, 1992). The importance of the storage forms varies with both tissue type and species. Interested readers are referred to Kozlowski (1992) for more detailed information on other storage forms of carbohydrates.

Carbohydrate storage patterns in conifer and deciduous tree species differ in two ways: (1) conifers store larger amounts of carbohydrates in foliage and (2) conifers tend to store less carbohydrates and accumulate them later in the season (Kozlowski, 1992). Few studies have examined seasonal patterns of starch storage for all major tissues, making the construction of stand-level storage budgets difficult; however, several patterns are consistent among conifers. The amount of carbohydrates in conifer needles varies with seasonal duration of shoot growth; maximum starch concentrations occur in pines with the shortest growing season (Kozlowski, 1992). A substantial amount of carbohydrates is stored in fine roots. Ericsson and Persson (1980) reported maximum starch concentrations of 30-50% by weight for root tissues of P. sylvestris. Although the concentration of starch in fine roots may be fixed for conifer seedlings (Marshall and Waring, 1985), data for mature P. sylvestris suggest that starch is transported into fine roots after they are formed (Gholz and Cropper, 1991). Seasonal patterns of starch storage appear to be similar for all tissues, with the maximum occurring shortly before new growth begins in the spring (Ericsson, 1979; Ericsson and Persson, 1980; Deans and Ford, 1986; Cranswick et al., 1987; Oren et al., 1988; Gholz and Cropper, 1991). The relative importance of the various tissues in terms of whole-tree C storage varies with age because biomass components change with age. Needles and fine roots are the primary storage organs for conifer seedlings (Glemm, 1980), but coarse roots and stems are the primary carbohydrate storage sites for mature trees (Cranswick et al., 1987; Gholz and Cropper, 1991).

F. Secondary Defense Compounds

Herbivores generally consume from 5 to 15% of the foliage in temperate forests during nonoutbreak years, but can consume all of the foliage in outbreak years (Schowalter et al., 1986). Although small levels of herbivory do not decrease tree growth and may increase growth (Mason and Addy, 1975), moderate to high levels of herbivory reduce photosynthetic surface area, deplete carbohydrate storage reserves, and increase the susceptibility of trees to other environmental stresses. As a result, trees allocate a portion of their annual C gain to construct and maintain defense compounds and physical barriers to deter herbivory. Clancy et al. (1994) provide a thorough discussion on herbivory and secondary defense compounds, therefore our discussion is restricted to the quantity of C allocated to defense compounds and the indirect effects of defense compounds on C assimilation and allocation.

Most evergreen conifers rely on C-based defense compounds (Swain, 1977). Little information is available on the amount of C generally allocated to defense compounds in woody plants. In general, the concentration of defense compounds appears to be inversely related to the leaf life span (Coley, 1985). Also, mild water stress increases the partitioning of C to defense compounds because cell division is adversely affected by water stress before photosynthesis. For example, Horsley (1957) reported greater lignin concentrations in control than in irrigated Douglas fir during a drought year but little difference in lignin concentration between the two treatments during a wetter year. Furthermore, increased nitrogen availability decreased the amount of C partitioned to lignin whereas decreased nitrogen availability tended to increase lignin concentration in new foliage (Fig. 8).

Partitioning of C to volatile trace gases (e.g., terpenes, isoprenes) may comprise a significant component of the leaf carbon budget; however, we have a poor understanding of the environmental and metabolic controls over their production, despite the important influence they have on the chemistry of the atmosphere (Brasseur and Chatfield, 1991). Moderate water stress and elevated temperatures increase the production of monoterpene (Hedges and Lorio, 1973; Tingey et al., 1980). Efforts to better quantify the partitioning of C to trace gases will require an understanding of how environmental factors and genetic variability affect whole-plant C allocation patterns and what factors control the partitioning of C to the various species of trace gases (Lerdau, 1991).
Defense compounds are also important because they indirectly affect C assimilation and allocation patterns. First, greater partitioning of C to defense compounds reduces stored C. Second, constitutive defenses such as lignin reduce the net photosynthetic rate, resulting in lower net C canopy gain. Third, defense compounds such as polyphenolics retard decomposition (Handley, 1961; Benoit and Starkey, 1964a,b; Davies et al., 1984; Horner et al., 1988). Foliage lignin: N ratios exert a strong control on N mineralization rates in forests (Melillo et al., 1982; Gower and Son, 1992), which in turn influence net primary primary production and C allocation patterns.

**G. Reproduction**

Reproductive structures such as flowers, fruits, strobili, and seeds are strong sinks and can consume 6–10% of the annual net canopy photosynthesis. Many trees produce more flowers than they can sustain to maturity, consequently when adverse environmental conditions restrict C assimilation, flowers are aborted (Kozlowski, 1992). The time span during which strobili are strong carbohydrate sinks for conifers ranges from one season (i.e., *Abies, Larix, Picea*, and *Pseudotsuga*) to over two growing seasons and one winter for *Pinus* (Kozlowski, 1992). The C required to construct reproductive structures is commonly derived from stored carbohydrates during the early spring when net canopy photosynthesis is very low; however, later in the spring most of the carbohydrates are obtained from current photosynthate produced largely by 1-year-old needles (Kozlowski, 1992). Few data are available on the proportion of C allocated to reproduction for conifer forests. Linder and Troeng (1981) estimated that a 14-year-old *P. sitchensis* tree allocated 6% of its canopy photosynthate to cones and Fielding (1966) estimated that the amount of C that *P. radiata* allocated to cones was about 10% of stem production. Cone production has been thought to decrease stem production (Fielding, 1966; Linder and Rook, 1984); however, more recent analyses for *P. contorta* suggest that cone production does not affect stem production (Dick et al., 1991).

**H. Leaf Leachates and Root Exudates**

Leaching of C from foliage is strongly influenced by wetting properties. Leaves with thick waxy cuticles, such as those of evergreen conifers, are not readily leached. However, damage to the epicuticular wax covering needles increases needle permeability and leaching loss of carbohydrates (Turunen and Huttunen, 1990). For example, increased needle permeability and leaching of carbohydrates have been reported for foliage subjected to artificial acidic misting (Scherbakovsky and Klein, 1983; Mengel et al., 1988). In general, C leaching losses do not appear to be a major C flux.

Root exudation sites are predominantly restricted to regions of cell elongation and the zone of meristematic activity directly behind the root tip (Rovira, 1969; Rovira and Davey, 1974; Hale et al., 1978). Although the type and amount of root exudate are influenced by species, atmospheric CO2 concentration, and other environmental conditions (Bowne, 1969; Rovira, 1969; Norby et al., 1987), the loss of C in exudates is a small flux relative to other fluxes discussed in this chapter. Rovira (1969) estimated that C contained in root exudates rarely exceeds 0.4% of the amount of C photosynthesized and Norby et al. (1987) estimated that the loss of 14C by exudation from *P. echinata* roots was about 0.5% of the total carbon allocated to roots. Despite the small amount of C lost in root exudates, root exudates play an important role in nutrient cycling because they influence nutrient availability and uptake indirectly through their effects on microbial activity in the soil (Uren and Resenauer, 1988).
VI. Changes in Carbon Dynamics during Stand Development

Carbon allocation and accumulation patterns change as trees age. Most notably, the relative allocation of C to foliage reaches a maximum early in stand development and then remains stable or declines in older stands (Gower et al., 1994). The total amount of C allocated to foliage increases as trees age (Fig. 9), while the ratio of foliage:wood decreases with stand age regardless of species or climate (Gholz et al., 1985). Aboveground NPP commonly reaches steady state or declines in older pine forests (Gower et al., 1994). The imbalance in C accumulation of foliage versus respiring tissue is the basis for the often-cited (but not rigorously tested) hypothesis that NPP decreases with stand age due to an imbalance between the accumulation of photosynthetic and respiring tissue (Kira and Shellet, 1967). However, this explanation for decreased NPP has been questioned (Sprugel, 1984; Ryan and Waring, 1992). Other explanations for decreased aboveground NPP in older conifer forests include increased nutrient availability in older stands (Van Cleve et al., 1981; Gholz et al., 1985) and reduced stomatal conductance in mature trees (Ryan and Waring, 1992).

Few studies have compared belowground carbon accumulation and production patterns across a conifer forest age chronosequence. Vogt et al. (1987) found that maximum fine root NPP occurs earlier in high versus low site quality coastal Pseudotsuga menziesii forests. However, irrespective of site quality, fine root production and growth efficiency often peak simultaneously. This pattern suggests that maximum fine root and mycorrhizal NPP may occur during stand development when the ratio of the mass of photosynthetically respiring tissue is greatest, although additional data are needed to test this hypothesis rigorously.

VII. Multiple Resource Limitations

Thus far, we have largely focused on the effect of a single resource limitation on C assimilation and allocation; however, conifer forests routinely experience more than one environmental constraint concurrently. Unfortunately, little is known about the effects of concurrent biotic and abiotic stresses on carbon allocation in plants (Dickson and Isbrands, 1991). Below, we provide several examples illustrating the nonlinear response of physiological processes controlling C budgets due to multiple resource limitations.

Fertilization commonly increases new foliage production by conifers (Fig. 10a), but the vertical distribution of increased foliage production varies depending on the light environment of the canopy (Fig. 10b). However, the increased new foliage production resulting from fertilization may not increase total foliage mass (Fig. 10c) if water is the primary resource limiting the amount of foliage or leaf area a site can support. Therefore, it is not surprising that the greatest increase in foliage mass (+40%) occurs for the nutrient-poor P. resinosa forests in a cool, moist climate, whereas little or no increase in total foliage mass occurs for fertilized P. ponderosa forests in an extremely dry climate. Other studies have also noted the combined effect of fertilization and irrigation on foliage production and accumulation exceeded the additive effect of
each resource when applied by itself (Linder, 1987; Raison et al., 1992; Snowden and Benson, 1992).

Air pollutants also influence C assimilation, but much less information is available on the effects on C partitioning and allocation (Kozlowski and Constantiniou, 1986). There have been numerous studies of air pollutants on carbon assimilation in conifers (Kozlowski and Constantiniou, 1986). Potential effects of elevated atmospheric CO$_2$ concentrations on C assimilation, allocation, partitioning, and accumulation are reviewed by Eamus and Jarvis (1989), Bazzaz (1990), Farrier and Williams (1991), and Woodward et al. (1991). Most of what is known is from studies on seedlings with a single pollutant such as sulfur dioxide, ozone, acid precipitation, and CO$_2$ (Table III). Air pollutants, however, are more likely to act simultaneously (i.e., ozone and CO$_2$) or with other environmental stresses, to influence C budgets of conifers (Peterson et al., 1989; McLaughlin and Kohut, 1992). For example, the magnitude of seedling or tree growth in response to elevated CO$_2$ varies depending on successional status, light environment, and soil nutrient availability (Eamus and Jarvis, 1989; Bazzaz et al., 1990). Ecosystem responses to elevated CO$_2$ are also likely to vary depending on the availability of other resources. Using a forest ecosystem model, FOREST-BGC (Running and Coughlan, 1988; Running and Gower, 1991; Running and Nemani, 1991) simulated gross net primary production, net primary production, and respiration for two conifer forests in contrasting climates (short growing season/dry summer and long growing season/moist summer). Increased temperature (+4°C) and precipitation (+10%) decreased net canopy photosynthesis at both sites, although the decrease was substantially greater for the conifer forest in the subtropical environment due to excessive respiration costs throughout the year (Fig. 11). Assuming elevated CO$_2$ will increase water use efficiency (see Woodward et al., 1991), NPP may increase for conifer forests that experience water stress whereas increased water use efficiency may have little or no effect on NPP for subtropical forests due to the greater respiration costs. Moreover, the effects of pollutants on C processes can vary with respect to genetics (Sasek et al., 1991). These examples illustrate the non-
VIII. Future Research

Ecophysiological research during the last decade has contributed to a better understanding of C allocation and forest productivity. Yet, to answer scientific questions (Will fertilization increase forest net primary production? Are northern latitude forests a C sink?) requires a unified theory for understanding and predicting the effect of multiple environmental stresses on C assimilation and allocation. Knowledge of C assimilation, partitioning, and allocation patterns has greatly increased for a few well-studied conifers (P. elliottii, Pseudotsuga menziesii, P. radiata, and P. sylvestris), but still too often the “first principles” derived from these species do not completely apply to other conifers. This problem may be due to differences in methodology or an incomplete understanding of multiple stress interactions and their interactions on C allocation.

What approaches may be useful in developing a mechanistic understanding of C partitioning and allocation for conifers? Controlled-environment chamber experiments using seedlings will help elucidate basic controls on C partitioning and allocation and can be used to manipulate the availability of a number of resources. However, the results may have limited application to forests because seedlings have inherently different C partitioning and allocation patterns compared to mature trees (Cregg et al., 1989; Woodward et al., 1991). Stand-level, multiple resource manipulation experiments are expensive and difficult to design, especially for forests. One useful approach to increasing our understanding is through the use of physiological process models in conjunction with experimentation (Isbrandtsen and Burkh, 1992). Simple, process-based models can be used to determine if field measurements of C fluxes are “realistic” and to design the necessary measurements to test hypotheses related to controls on C allocation. Coupling physiologically based models of different temporal and spatial scale will likely play an important role in the future, although implementation of such models is in its infancy (Ehlertinger and Field, 1993). Studies involving modelers, physiological ecologists, and micrometeorologists will provide the best opportunity to develop and test unifying theories on C partitioning and allocation. Eddy correlation, a technique traditionally used by micrometeorologists to measure net CO2 uptake, and energy flux from an ecosystem, should help resolve uncertainties related to scaling instantaneous CO2 fluxes from chamber measurements to annual stand-level CO2 fluxes and allow scientists to partition net CO2 flux into C sinks and sources (Schimel, 1993). This decomposition is important because soil respiration and photosynthesis are controlled by different processes and differ in sensitivity to environmental stresses. Furthermore, such experiments provide physiological ecologists and modelers an opportunity to determine if the scaling approaches used to develop stand-level C budgets are valid, and if not, why.

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Hoes, New York.


Respiration from the Organ  
Level to the Stand

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I. Introduction

As several reviews have emphasized, respiration is a major factor in plant, stand, or ecosystem energy budgets, estimated to consume anywhere from 50 to 70% of total carbon fixed (Sprayg and Besecke, 1991; Hagihara and Horami, 1991; Ryan, 1991a). Respiration has been an area of particular interest and concern recently because of the possibility that CO₂-induced global warming might lead to substantial increases in respiration in temperate and boreal ecosystems, which could decrease net primary productivity (Ryan, 1991a). This concern, coupled with a general interest in scaling of physiological processes (e.g., Ehleringer and Field, 1993), has led to a resurgence of interest in respiration and in techniques for estimating respiration of stands and ecosystems. Before we begin our discussion of respiration, a few definitions are in order. This chapter will deal with dark respiration (beneath the simple respiration), the process by which glucose is enzymatically combined with oxygen to liberate chemical energy and CO₂. It is generally assumed that most respiration in trees is through the "normal" cytochrome-mediated pathway, but there is an alternative: cyanide-resistant or salicylyhydroxamic acid-sensitive respiration is a nonphosphorylating respiration pathway that generates only 40-50% as much chemical energy per glucose oxidized (Lambers, 1980). In most ecophysiological


