United States
Department
of Agriculture

Forest Service

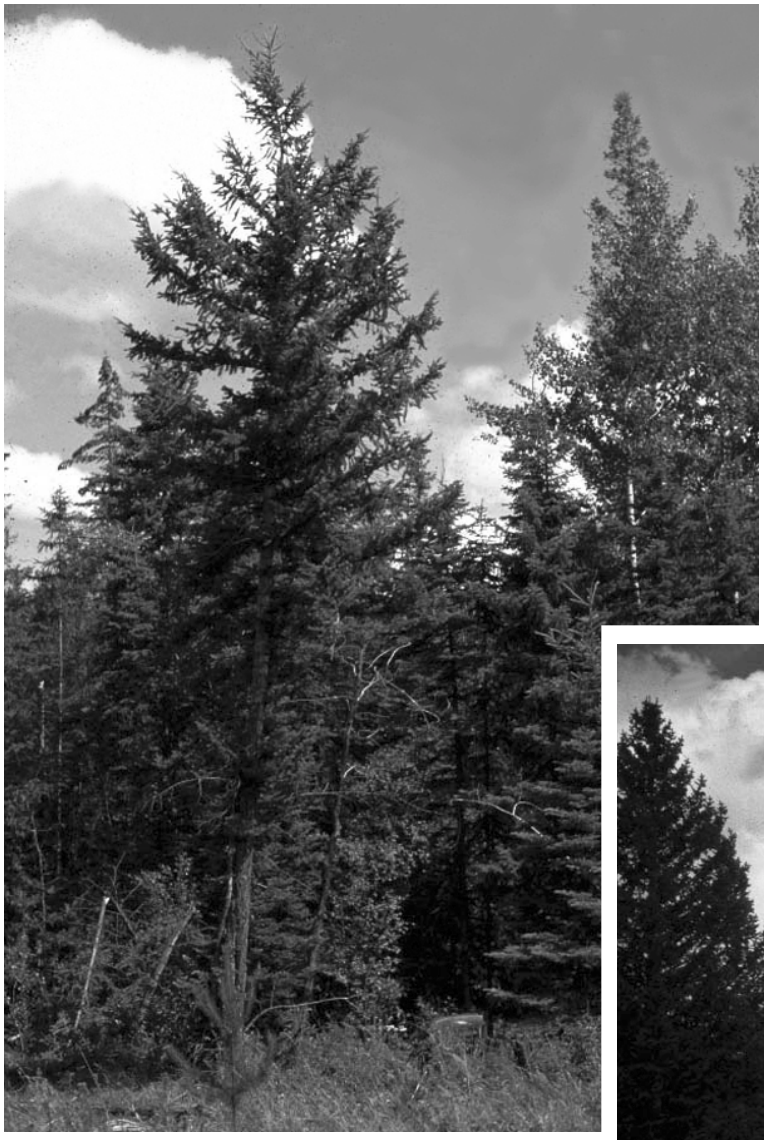
**Rocky Mountain
Research Station**

General Technical
Report RMRS-GTR-73

June 2001

# Physiological Attributes of 11 Northwest Conifer Species

**Ronni L. Korol**



## Abstract

Korol, Ronni L. 2001. **Physiological attributes of 11 Northwest conifer species**. Gen. Tech. Rep. RMRS-GTR-73. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 9 p.

The quantitative description and simulation of the fundamental processes that characterize forest growth are increasing in importance in forestry research. Predicting future forest growth, however, is compounded by the various combinations of temperature, humidity, precipitation, and atmospheric carbon dioxide concentration that may occur. One method of integrating new management objectives and potential climate scenarios is to model ecosystems mechanistically. General application of ecosystem process models has been difficult. In particular, obtaining initial physiological parameters from current techniques that rely on instantaneous gas exchange measurements can be both expensive and challenging. Frequently, data necessary to parameterize ecosystem process models are not readily available. This report provides model parameters for 11 conifer species of the Inland Northwest. Field measurements of A, $A_{max}$, g, $g_{max}$, $c_i$, predawn water potentials, analysis of leaf nitrogen concentration, carbon isotope discrimination ($\Delta$), and values of $c_{i,}$ and intrinsic water use efficiency (A/g) inferred from the carbon composition ($\delta^{13}C$) are presented. The relationship of wet leaf weight to dry leaf weight is also presented. The data in this report can be used to calibrate and constrain physiological parameters for modeling physiological processes of 11 conifer species in the Inland Northwest.



**Keywords:** photosynthesis, stomatal conductance, gas exchange, model parameterization, conifer, process models.


## The Author

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# Physiological Attributes of 11 Northwest Conifer Species

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## Introduction

The biggest challenge facing ecophysiologists today is predicting the ecosystems of the future. As forest management objectives change from maximizing forest growth and yield to ecosystem management, the tools used by management must broaden. Predictors that incorporate multiple aspects of the ecosystem are necessary (such as hydrology, pests, wildlife, climate, and vegetation) to develop optimal management plans and forecast forest growth. Overall, the quantitative description and simulation of the fundamental processes that characterize forest growth are increasing in importance in forestry research (Blake and others 1990), but predicting future forest growth is compounded by the various combinations of temperature, humidity, precipitation, and atmospheric carbon dioxide concentration that may occur.

One method of integrating new management objectives and potential climate scenarios is to model ecosystems mechanistically (Fosberg 1990; Schimel 1993). Ecosystem process models have been used to predict the growth of forests under different climate regimes and at various scales (tree to stand to landscape). These models generally rely on estimating net photosynthesis, which quantifies the carbon available for respiration and biomass production. Net photosynthetic rates depend both on the diffusion of $CO_2$ into the leaf and on the biochemical capacity for photosynthesis (see also Kirschbaum 1993; Running and Coughlan 1988; Vasala and others 1996).

General application of ecosystem process models, however, has been difficult. In particular, obtaining initial physiological parameters from current techniques that rely on instantaneous gas exchange measurements can be both expensive and challenging. Quite frequently, data necessary to parameterize ecosystem process models are not readily available.

In either case, species-specific knowledge of the relationship between net photosynthetic rate (A), internal carbon concentration ($c_i$), and conductance (g) is integral to ecosystem process models. In particular, maximum rates of net photosynthesis ($A_{max}$) and conductance ($g_{max}$) are valuable in constraining process models because these values can represent optimum environmental conditions. Unfortunately, many environmental factors make it difficult to obtain these variables (Yoder 1992). This report provides model parameters for 11 conifer species of the Inland Northwest.

## Objective

This report presents field measurements of A, $A_{max}$, g, $g_{max}$, $c_i$, predawn water potentials, analysis of leaf nitrogen concentration, carbon isotope discrimination ($\Delta$), values of $c_{i,}$ and intrinsic water use efficiency (A/g) inferred from the carbon composition ($\delta^{13}C$). The relationship of wet leaf weight to dry leaf weight is also presented. These data, which were collected on 11 coniferous tree species located in the Inland Northwest, can be used to calibrate or parameterize process models for application in that region.

## Methods

### Theory

Several process models describe the photosynthetic carbon assimilation rate as:

$$A = g_c(c_a - c_i) \qquad (1)$$

where A ($\mu$mol $m^{-2}s^{-1}$) is net photosynthetic rate, $g_c$ (mol $m^{-2}s^{-1}$) is leaf diffusive conductance to $CO_2$, $c_a$ (ppm) is $CO_2$ concentration of the air surrounding the leaf, and $c_i$ (ppm) is intercellular $CO_2$ concentration of the leaves. Whereas $c_a$ values are readily available, both $c_i$ and $g_c$ can be difficult to obtain.

Farquhar and others (1982) developed a theoretical relationship between isotopic composition of leaves of a $C_3$ plant ($\delta^{13}C_p$) and the ratio of intercellular and atmospheric $CO_2$ concentrations. The carbon isotope composition also depends on $\delta^{13}C_a$, the isotopic composition of $CO_2$ in the atmosphere, so that the relationship is now conventionally expressed as one between carbon isotope discrimination, $\Delta$, and $c_i/c_a$:

$$\Delta = a + (b\text{-}a)\, c_i/c_a \qquad (2)$$

where $\Delta$ is calculated as:

$$\Delta = \frac{^{13}\delta C_a - ^{13}\delta C_p}{1 + ^{13}\delta Cp} \quad (3)$$

Current atmospheric conditions ($\delta^{13}C_a$) were assumed to be –8‰; '*a*' is the discrimination associated with diffusion (4.4‰), and '*b*' is a fitted parameter with a value determined primarily by the discrimination of the enzyme Ribulose bisphosphate carboxylase/oxygenase (27‰) (Farquhar and others 1989).

The $c_i/c_a$ ratio can been calculated from measurements of D by substituting the parameter values and rearranging equation (2) as:

$$c_i/c_a = (\Delta - 4.4‰) / 22.6 \quad (4)$$

Once carbon has been fixed, the ratio of the stable carbon isotopes $^{13}C$ and $^{12}C$ remains constant unless the carbon is subsequently used for further biological reactions, which may further discriminate between the different carbon isotopes.

Using equation (1), A can be calculated directly from gas exchange measurements and measured values of $g_c$, $c_a$ and $c_i$, or inferred from measurements of $\Delta$ using equation (4) and *a priori* knowledge of $c_a$. Intrinsic water use efficiency (TE) can also be calculated using estimates of $c_i$ inferred from $\Delta$:

$$TE = ( c_a - c_i) / (1.6v) \quad (5)$$

where the term 1.6*v* is largely determined by climatic conditions, and the term ($c_a - c_i$) is primarily determined by plant physiological adjustments (Korol and others 1999).

## Study Sites

Trees were sampled from the Flathead Indian Reservation and the Coram Experimental Forest in northern Montana, and the Priest River Experimental Forest in northern Idaho. Species sampled include Douglas-fir (*Pseudotsuga menziesii* var *glauca* [Bessin] Franco), ponderosa pine (*Pinus ponderosa*s Laws), lodgepole pine (*Pinus contorta* spp. *latifolia* Dougl.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), grand fir (*Abies grandis* (Dougl.) Lindl.), Engelman spruce (*Picea engelmannii* Parry), western red cedar (*Thuja plicata* Donn), western larch (*Larix occidentalis* Nutt.), western white pine (*Pinus monticola* Dougl.), whitebark pine (*Pinus albicaulis* Engelm), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). For all 11 species, gas exchange data (including the maximum rates of photosynthesis, $A_{max}$, and stomatal conductance, $g_{max}$) were obtained on leaves that had fully elongated using a Licor-6200 portable photosynthesis system. To obtain A and g, the same trees were sampled diurnally and every 4 weeks over the growing season. Leaf samples were obtained using a shotgun to detach samples from the upper one-fourth of the canopy. Previous work suggests that there is no immediate influence of detachment on gas exchange (Zhang and others 1993), except perhaps in western larch.

Canopy profiles were obtained on four species (Douglas-fir, western white pine, western larch, and grand fir) at the Priest River Experimental Forest. Measurements included leaf nitrogen, $\Delta$, and gas exchange obtained at intervals of one-fourth the canopy length of each tree. The measurements were collected from intact samples using a cherry picker to reach the samples. Branches were flagged so that the same branch was measured repeatedly, both diurnally and seasonally.

In addition, predawn water potentials were measured using standard pressure bomb techniques at the Flathead Reservation site and at two sites in the Priest River Experimental Forest. These measurements were taken in July 1996 on ponderosa pine, western larch, grand-fir, and western white pine.

All leaf samples used for gas exchange measurements obtained were brought back to the laboratory, and projected leaf area was determined with JAVA video analysis software (Jandel Scientific), using a Coho 4819-5000 high-resolution monochrome video camera. Photosynthesis rates were expressed per unit weight, and per unit leaf area (determined by analysis of the perimeter of leaf cross-sections divided by their width using photomicrographs and the image analysis system), and the specific leaf area calculated. Regression equations were developed to predict leaf area from dry leaf weight for the seven species (subalpine fir, ponderosa pine, Douglas-fir, lodgepole pine, western hemlock, western red cedar, and spruce) that had a large enough sample size (>15) to adequately develop the relationships. Leaf samples were sent to the University of Waikato stable isotope facility in New Zealand for analysis of $\partial^{13}C$. A subsample of the leaves had carbon, hydrogen, and leaf nitrogen concentrations analyzed at the Analytical Sciences Laboratory, University of Idaho.

# Results and Discussion

## Gas Exchange Measurements

Species estimates of the maximum rates of photosynthesis ($A_{max}$) ranged from 3.1 µmol $m^{-2}s^{-1}$ for western hemlock to 14.1 µmol $m^{-2}s^{-1}$ for ponderosa pine (fig. 1). Douglas-fir and the pine species, which tend to be less shade tolerant, had higher rates of $A_{max}$ than the more shade-tolerant species. The measured rates of $g_{max}$ had a slightly different trend and ranged from a low 0.045 mol $m^{-2}s^{-1}$ for western hemlock to a high of 0.37 mol $m^{-2}s^{-1}$ for lodgepole pine (fig. 2). Whitebark pine had one of the higher rates of $A_{max}$ yet had one of the lower rates of $g_{max}$ (close to the rate measured for

## Key for Species Abbreviations

| | | | |
|---|---|---|---|
| DF | - | Douglas-fir | (*Pseudotsuga menziesii* var *glauca* [Bessin] Franco) |
| PP | - | ponderosa pine | (*Pinus ponderosas* Laws) |
| LL | - | lodgepole pine | (*Pinus contorta* spp. *latifolia* Dougl.) |
| AF | - | subalpine fir | (*Abies lasiocarpa* (Hook.) Nutt.) |
| GF | - | grand fir | (*Abies grandis* (Dougl.) Lindl.) |
| ES | - | Engleman spruce | (*Picea englemannii* Parry) |
| WRC | - | western red cedar | (*Thuja plicata* Donn) |
| WL | - | western larch | (*Larix occidentalis* Nutt.) |
| WWP | - | western white pine | (*Pinus monticola* Dougl.) |
| WBP | - | whitebark pine | (*Pinus albicaulis* Engelm) |
| WH | - | western hemlock | (*Tsuga heterophylla* (Raf.) Sarg. |

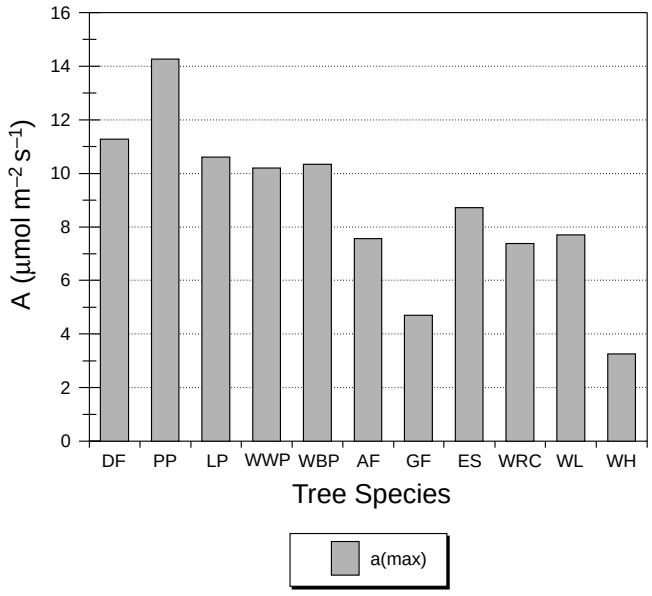



**Figure 1**—Mean maximum assimilation rates (µmol $m^{-2}$ $s^{-1}$) for different tree species measured every 4 weeks from May through October between 10:00 am and 1:00 pm, using gas exchange techniques.

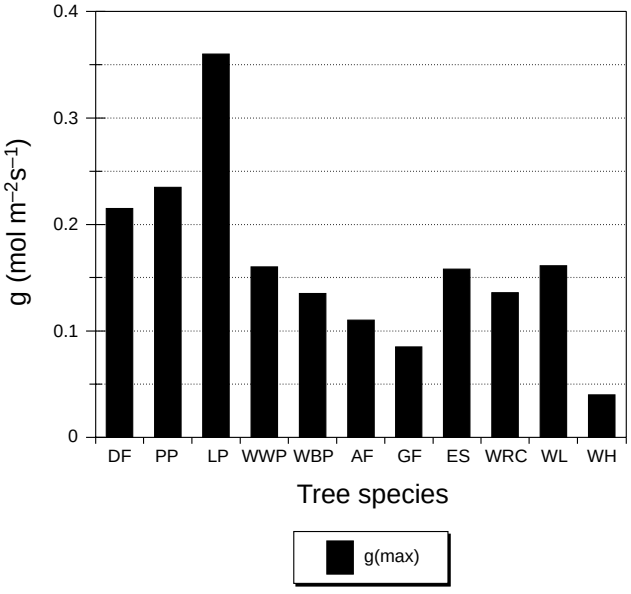



**Figure 2**—Maximum stomatal conductances (mol $m^{-2}s^{-1}$) for different tree species measured every 4 weeks from May through October between 10:00 am and 1:00 pm, using gas exchange techniques.

western red cedar). Figure 3 shows the relationship between $A_{max}$ and $g_{max}$.

Sensitivity of the assimilation rate to the ratio of $c_i/c_a$, measured with LI-6200, varied considerably by species (fig. 4a and 4b). Western white pine had large changes in assimilation rates over a small range of the $c_i/c_a$ ratio (0.58 to 0.78). All other species had a wide range (0.35 to 0.95) of measured $c_i/c_a$. Grand fir showed little sensitivity of A to the ratio. Generally, rates of A were higher when the $c_i/c_a$ ratio was less then 0.65, and significantly lower as the ratio increased above 0.65. Ponderosa pine had the highest rates of A for a given ratio, while Douglas-fir had the lowest rates. The lack of a strong relationship between A and the $c_i/c_a$ ratio suggests that the trees are keeping $c_i/c_a$ relatively constant by adjusting g.

Generally, for all species the greater the difference between $c_a$ and $c_i$, the lower the measured rates of g (fig. 5), which supports the assumption that there was no immediate influence on gas exchange. This response appeared to be more species specific, however, with Douglas-fir and western hemlock exhibiting lower rates of g, and lodgepole pine and whitebark pine exhibiting higher rates of g for a given $(c_a–c_i)$. Subalpine fir appeared to be the most sensitive to changes in $(c_a–c_i)$.

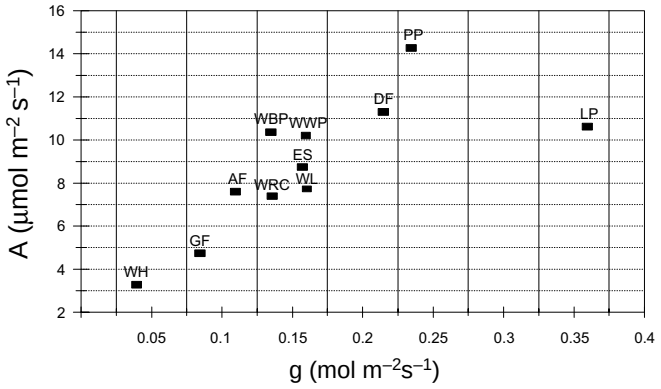
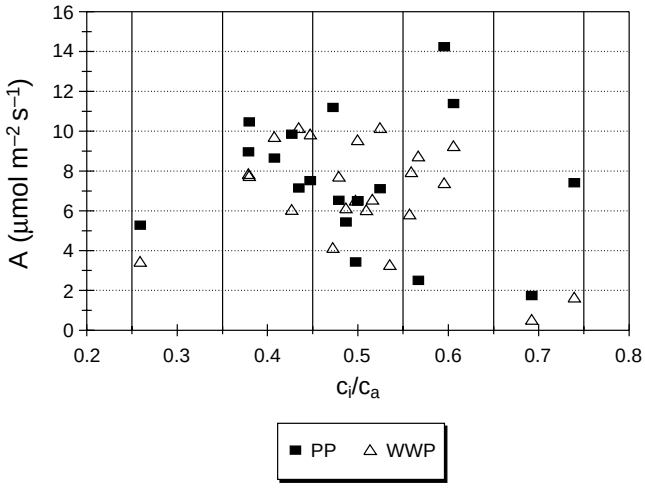
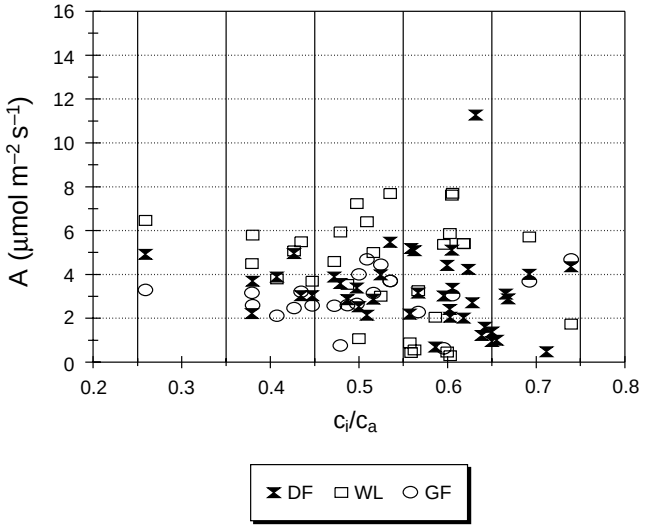



**Figure 3**—The relationship between maximum assimilation rate (A: µmol $m^{-2}$ $s^{-1}$) and maximum stomatal conductances (g: mol $m^{-2}s^{-1}$) for different tree species measured every 4 weeks from May through October between 10:00 am and 1:00 pm, using gas exchange techniques.




**Figures 4a and 4b**—The relationship between assimilation rate (A: µmol $m^{-2}$ $s^{-1}$) and the $c_i/c_a$ ratio for different tree species measured using gas exchange techniques. Each data point shown represents one sample.

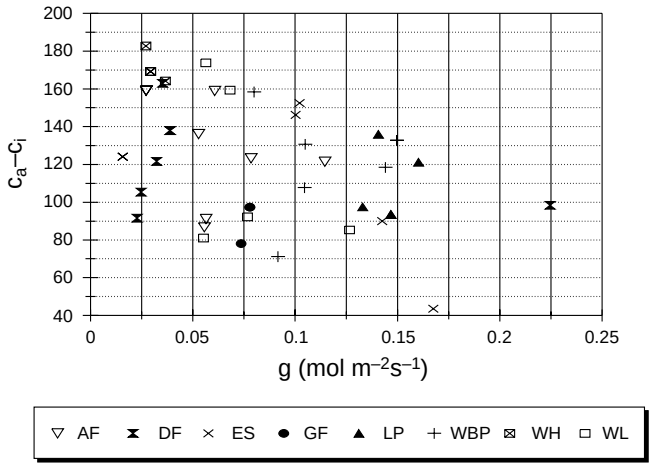
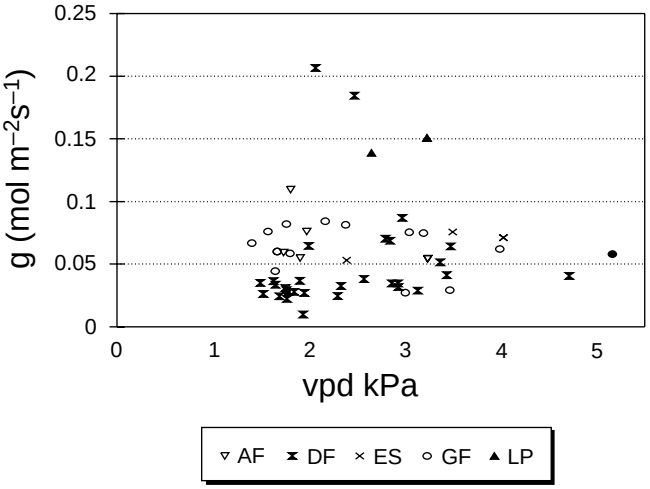


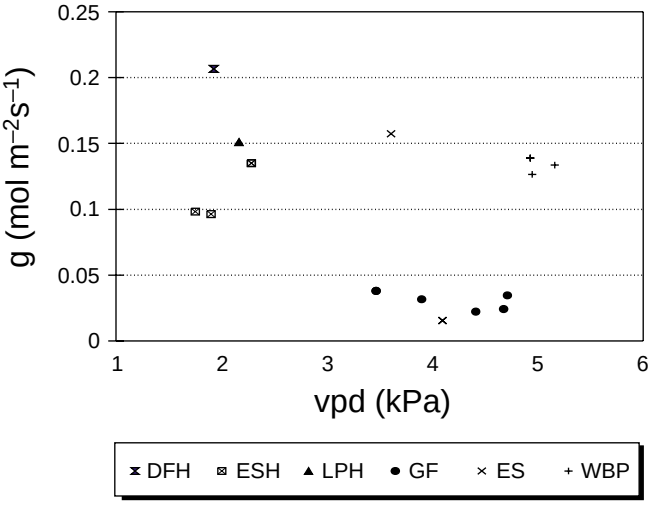

**Figure 5**—The relationship between the difference of $c_a$ and $c_i$ and stomatal conductances (g: mol $m^{-2}s^{-1}$) for different tree species measured using gas exchange techniques. Each data point shown represents one sample.

Studies have shown correlations between conductance and hours since sunrise, vapor pressure deficit (Jarvis and McNoughton 1986), low night temperatures, and relative humidity (Ball and others 1987). Figures 6a and 6b show measured rates of stomatal conductance for the vapor pressure deficits (vpd) as measured in the cuvette. The vpd inside the cuvette was maintained such that it was similar to the vpd outside the cuvette. The data showed no discernible relationship between stomatal conductance and photosynthetically active radiation (PAR), probably because the PAR recorded in the cuvette differed from the PAR influencing the leaf before detachment. The leaves were measured in the cuvette as soon as possible after detachment, possibly before the conductance was able to acclimatize to the new levels of PAR.

## Carbon Isotope Analysis

The average carbon isotope discrimination (Δ‰) for conifer leaves is shown by species in figure 7. Western red cedar had the lowest average value of Δ at 17.5‰, while grand fir had the highest at 22‰. A 1‰ change in Δ corresponds to approximately a 16 µmol $mol^{-1}$ in $c_i$ or a 12% change in transpiration efficiency (if initially $c_i$ = 200 µmol $mol^{-1}$). This implies that western red cedar would have a significantly higher transpiration efficiency than grand fir. However, figure 8 shows that the average intrinsic transpiration efficiencies of western red cedar and grand fir are similar, which illustrates the difficulty in comparing the average instantaneous (30 sec) point measurements of gas




**Figures 6a and 6b**—The relationship between stomatal conductances (g: mol $m^{-2}s^{-1}$) and vapor pressure deficits (vpd: kPa) for different tree species measured using gas exchange techniques.

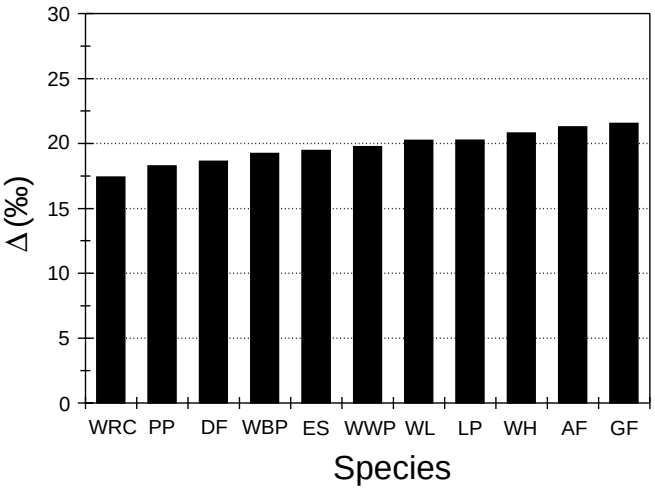



**Figure 7**—The average carbon isotope discrimination (Δ‰) for different coniferous tree species.

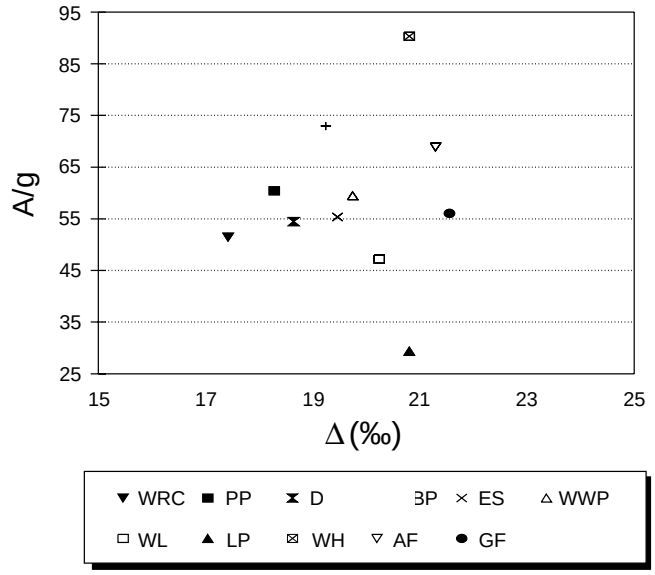



**Figure 8**—The relationship between A/g and average carbon isotope discrimination (Δ‰) for different tree species.

exchange data to the more integrated measurements of A/g, inferred from leaf samples. The carbon isotope discrimination of the leaf reflects the environmental conditions surrounding the leaf for the growing season (minus any translocated carbon) and is therefore an integrated measure. Figure 9 illustrates the wide range of intrinsic transpiration water efficiencies (point measurements) that correspond to the different values of Δ (integrated measurement). It is apparent that western red cedar does tend to have higher intrinsic transpiration efficiencies than grand fir. This is further illustrated in figure 10, which shows the relationship between Δ and g.

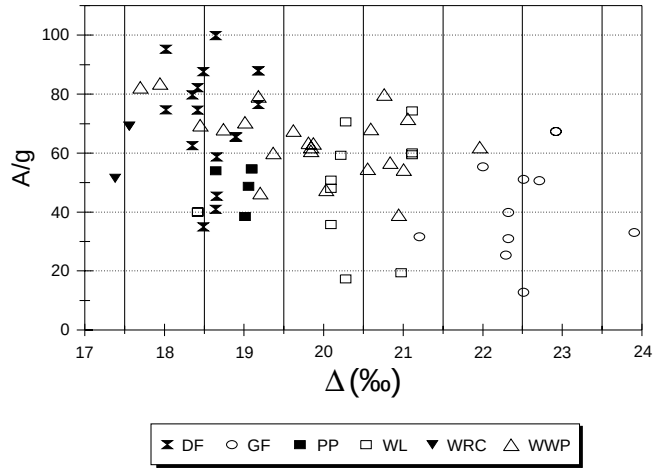



**Figure 9**—The range of carbon isotope discrimination (Δ‰) for different values of A/g measured using gas exchange techniques for various tree species. Each point represents the A/g ratio measured for a given leaf tissue that was then analyzed for Δ.

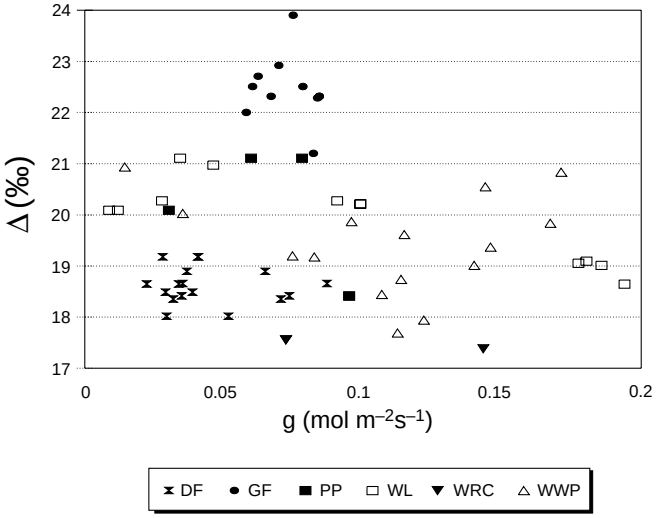



**Figure 10**—The range of carbon isotope discrimination (Δ‰) for different values of g measured using gas exchange techniques for various tree species.

## Canopy Profiles

The canopy profile data for the four species sampled at the Priest River Experimental Forest support the findings of Ehleringer and others (1986) and Broadmeadow and Griffiths (1993), who indicate that Δ varies within a canopy of coniferous trees. The influence of canopy position was such that Δ tended to be higher for foliage taken from the upper crown than for foliage samples obtained from lower in the canopy (fig. 11). Upper foliage was also found to have a lower Δ for a given stomatal conductance (fig. 12) and, correspondingly, for a given vapor pressure deficit (fig. 13).

The within-canopy vpd differed significantly between foliage samples obtained from the top quarter of the canopy and those obtained from the lower quarter of the canopy (fig. 14). The top quarter of the canopy had vpds of less than 3 kPa, while the lower quarter had vpds of greater than 3 kPa. When comparing the relationship of stomatal conductance with vpd, there were two distinct data clusters, depending on the canopy position (fig. 14). The range of stomatal conductances was only slightly higher for the upper canopy, varying little from the range found for the lower canopy. This result suggests that within-canopy stomatal conductance is not sensitive to within canopy changes in vpd.

## Predawn Water Potentials

Average predawn water potentials of selected species during the period of July 10 through 15, 1996, are shown in figure 15. Ponderosa pine had the lowest water potentials (ψ) at 3.4 kPa, while western white pine had the highest ψ at 6 kPa. These data indicate the type of water stress and the overnight recovery that tree species experience in the Inland Northwest and provide an insight into the site soil water balance.

## Leaf Nitrogen Concentrations

The average leaf nitrogen concentrations ranged from 1.09% for grand fir to 1.62% for western red cedar (fig. 16). Farquhar and Von Caemmerer (1982) have shown a strong correlation between photosynthesis and the nitrogen held in rubisco. We found that assimilation, measured using gas exchange (point measurement), tended to increase with leaf nitrogen (fig. 17), as did stomatal conductance. The Δ also tended to increase with leaf nitrogen concentration for each species (fig. 18).

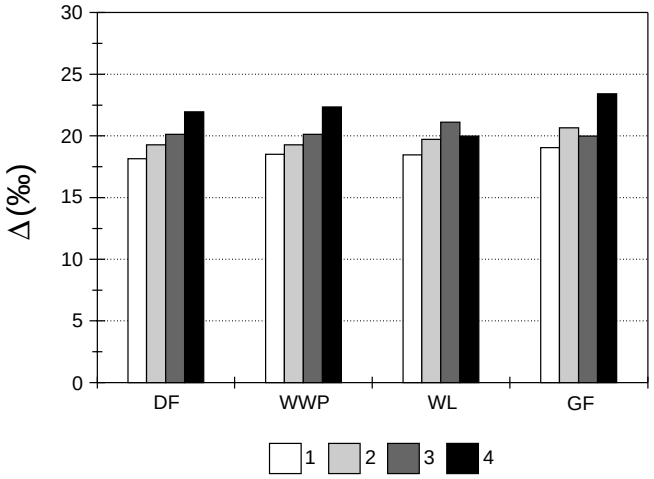



**Figure 11**—The range of average carbon isotope discrimination (Δ‰) measured throughout the crowns of four coniferous species. Position 1 refers to the lower one-fourth of the crown while position 4 refers to the top one-fourth of the crown.

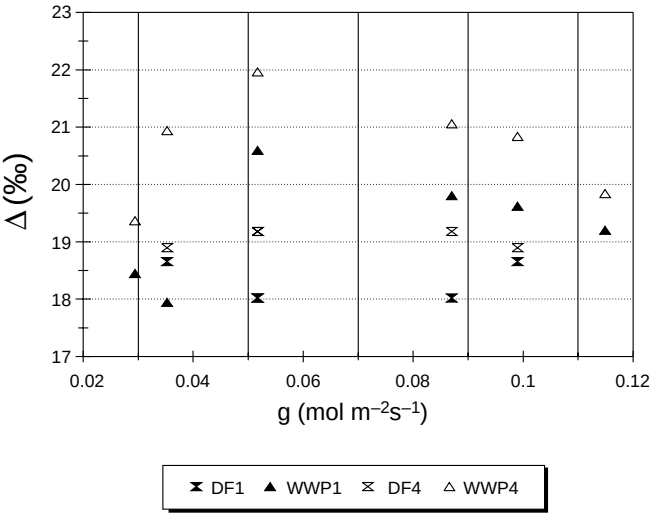



**Figure 12**—The relationship between carbon isotope discrimination (Δ‰) and stomatal conductances (g: mol $m^{-2}s^{-1}$) in the bottom one-fourth of the crown (Position 1) and top one-fourth of the crown (Position 4).

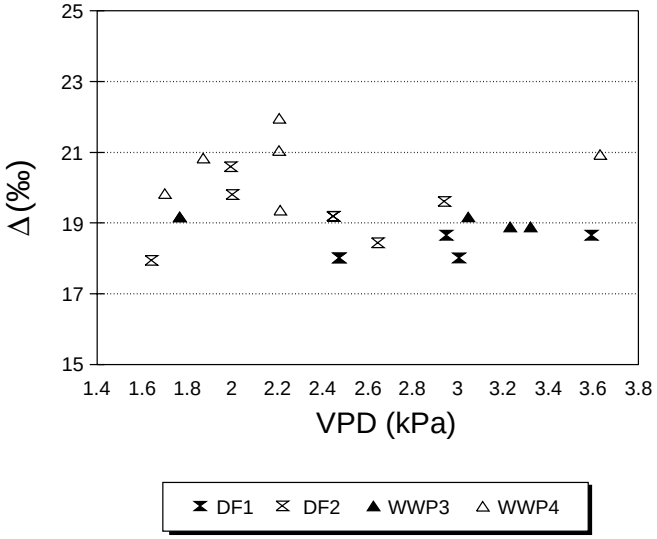



**Figure 13**—The relationship between carbon isotope discrimination (Δ‰) and vapor pressure deficit (vpd; kPa) in the bottom one-fourth of the crown (low) and top one-fourth of the crown (high).

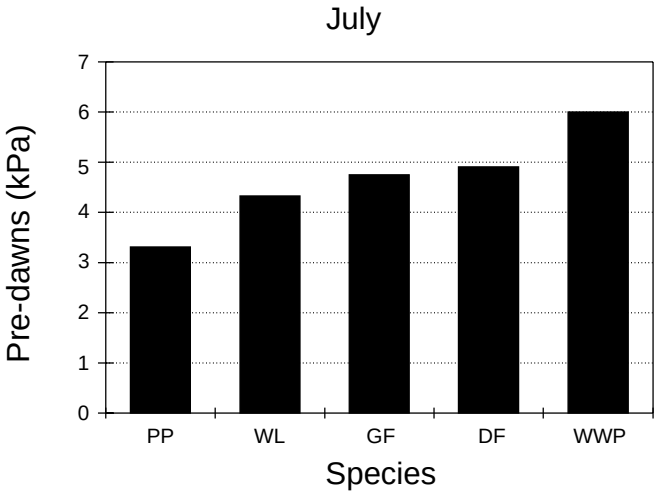



**Figure 14**—The relationship stomatal conductances (g: mol $m^{-2}s^{-1}$) and vapor pressure deficit (vpd; kPa) in the bottom one-fourth of the crown (low) and top one-fourth of the crown (high).

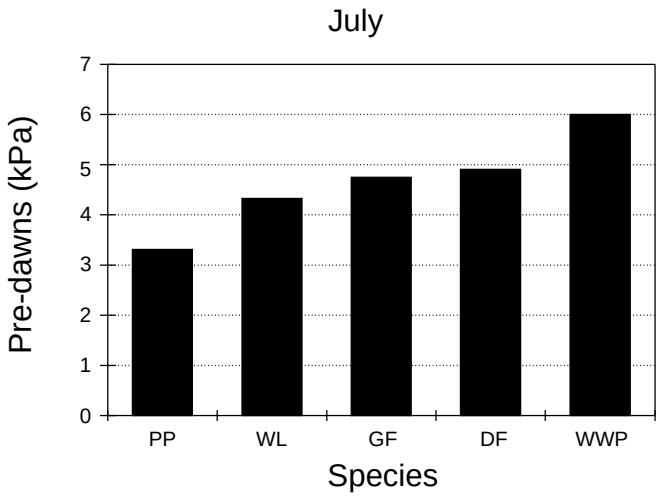



**Figure 15**—Average predawn water potentials (kPa) for different coniferous tree species taken in July 1996.

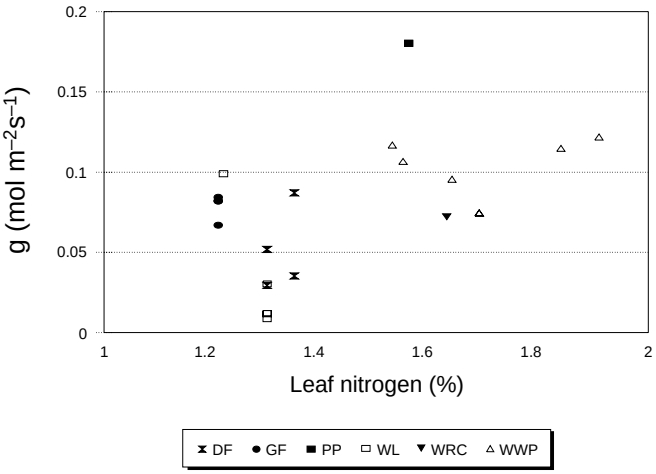



**Figure 17**—The relationship between stomatal conductances (g: mol $m^{-2}s^{-1}$) and leaf nitrogen concentration (%) for different coniferous tree species.

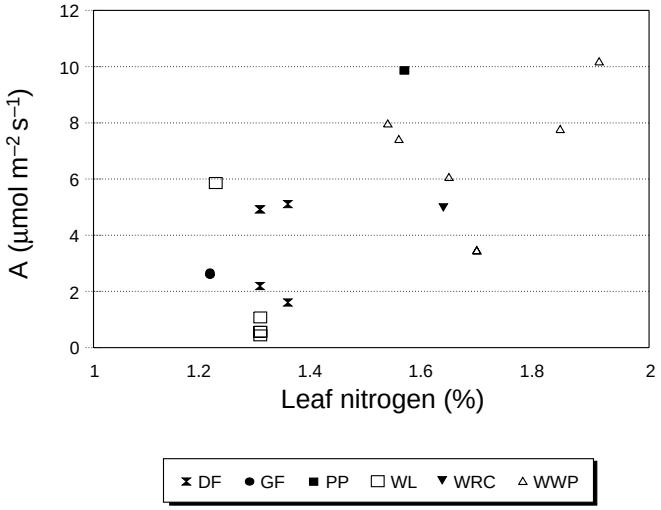



**Figure 16**—Average leaf nitrogen concentrations (%) for different coniferous tree species.

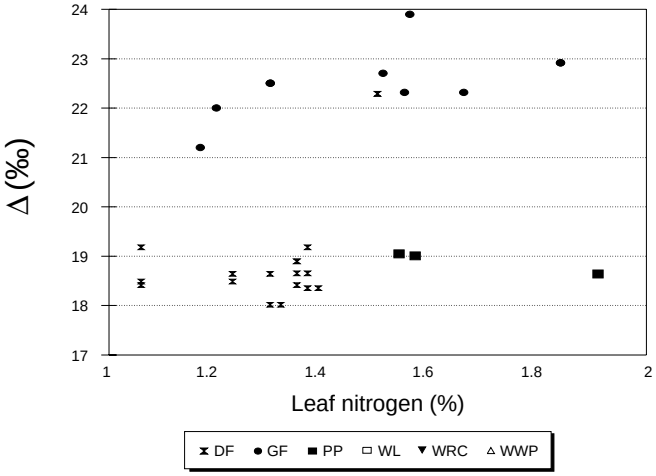



**Figure 18**—The relationship between carbon isotope discrimination (Δ‰) and leaf nitrogen concentration (%) for different coniferous tree species.

## Leaf Area/Leaf Weight Relationships

Table 1 lists the regression equations for predicting leaf area from dry leaf weight. The highest correlation coefficients calculated ($r^2$) were for western hemlock ($r^2 = 0.88$), western red cedar ($r^2 = 0.90$), and spruce ($r^2 = 0.81$). Separating the data by aspect (north and south) increased the correlation coefficients for subalpine fir, Douglas-fir, and lodgepole pine.

# Conclusion

Several models of stand and tree growth currently exist and more are being developed. A large number of these models rely on relationships developed at the leaf level (for example, Farquhar and von Caemmerer 1982) to predict growth at the stand level. As the use of such models to predict carbon uptake and sequestration or stand growth increases, the need for

**Table 1**—Leaf area equations (leaf area (cm/cm) = a + (leaf weight * b)). Species with large samples in different aspects were stratified by aspect.

| Species | n | $r^2$ | see | a (se) | b (se) leaf wt (gr) |
|---|---|---|---|---|---|
| **Subalpine fir** | 68 | 0.58 | 3.224 | 3.41 (0.991) | 33.54 (3.545) |
| north | 49 | 0.69 | 1.935 | 3.53 (0.656) | 26.26 (2.575) |
| south | 19 | 0.73 | 1.726 | 9.31 (1.256) | 27.29 (4.042) |
| **Ponderosa pine** | 24 | 0.67 | 3.167 | 5.72 (2.676) | 33.12 (5.123) |
| **Douglas-fir** | 46 | 0.64 | 1.895 | 2.46 (1.028) | 34.539 (3.920) |
| north | 18 | 0.89 | 1.212 | 4.96 (0.924) | 30.007 (2.926) |
| south | 28 | 0.70 | 1.321 | 1.05 (1.662) | 39.639 (4.277) |
| **Lodgepole pine** | 23 | 0.67 | 2.544 | 6.10 (1.754) | 24.46 (3.737) |
| north | 12 | 0.93 | 1.008 | 0.40 (1.419) | 30.08 (2.926) |
| south | 11 | 0.85 | 1.543 | 0.87 (2.292) | 39.64 (4.277) |
| **Western hemlock** | 8 | 0.88 | 0.145 | 4.55 (0.503) | 43.44 (6.379) |
| **Western red cedar** | 15 | 0.90 | 3.154 | 1.82 (1.989) | 41.84 (3.786) |
| **Spruce** | 43 | 0.81 | 2.105 | 0.21 (0.844) | 39.25 (2.990) |
| north | 30 | 0.82 | 1.4329 | 1.63 (1.027) | 32.03 (2.872) |
| south | 13 | 0.85 | 1.4687 | 1.23 (0.987) | 35.87 (2.910) |
| **Whitebark pine** | 15 | 0.87 | 1.077 | 2.88 (0.859) | 22.13 (2.330) |
| **Grand-fir** | 36 | 0.76 | 2.355 | 5.01 (1.061) | 31.20 (2.998) |

physiological data to calibrate the models becomes increasingly important. Leaf-level physiological data are both difficult and expensive to obtain, and the results can be quite variable due to the multitude of environmental effects. The real data presented in this report can be used to calibrate and constrain physiological parameters for 11 conifer species in the Inland Northwest.

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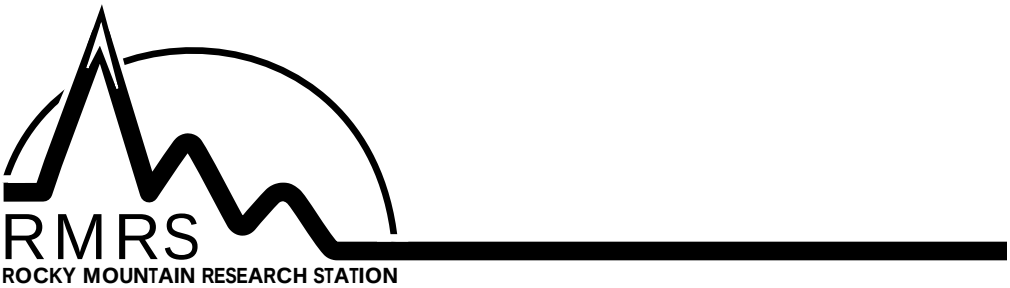


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