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Interpreting foliar analyses from Douglas-fir as weight per unit of leaf area[1]

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To evaluate whether changes in leaf weight might affect the interpretation of foliar analyses, seasonal samples of current and older Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) needles were compared from contrasting environments in the Coast Range and Cascade Mountains of western Oregon, U.S.A. Foliage from trees grown in the climatically mild and moist Coast Range maintained nearly constant weight and nitrogen content per unit of leaf area throughout the year, regardless of whether stands were thinned or left unthinned. In contrast, foliage from trees growing in the harsher environment of the Cascade Mountains averaged only half the weight per unit of leaf area of samples from the Coast Range during the dormant season. During the summer, foliage weight and nitrogen content per unit of leaf area increased by more than 50% in the Cascades. These values were 20–40% less, respectively, than those observed in the foliage of Coast Range trees. In the Cascades, thinning significantly increased both foliage weight and nitrogen content. Implications of these findings are discussed in regard to interpreting foliar analyses.

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Afin d'évaluer si les changements dans le poids des feuilles peuvent affecter l'interprétation des analyses foliaires, des échantillons saisonniers d'aiguilles de l'année courante et celles plus âgées du sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) ont été comparés pour des milieux contrastants de la Chaîne Côtière et des Cascades de l'ouest de l'Oregon, U.S.A. Le feuillage des arbres croissant en climat doux et humide de la Chaîne Côtière a maintenu un poids et un contenu en azote par unité de surface de feuillage presque constant durant l'année, tant dans les peuplements éclaircis que non éclaircis. En contraste, le feuillage des arbres croissant dans un environnement plus rude des Cascades a, en moyenne, seulement la moitié du poids par unité de surface de feuillage comparé à la Chaîne Côtière durant la saison de dormance. Durant l'été, le poids et le contenu en azote par unité de surface de feuillage augmentent de plus de 50% dans les Cascades. Ces valeurs étaient respectivement de 20–40% inférieures de celles observées dans le feuillage des arbres de la Chaîne Côtière. Dans les Cascades, l'éclaircie accroît significativement le poids du feuillage et le contenu en azote. Les implications de ces observations sont discutées au plan de l'interprétation des analyses foliaires.

[Traduit par le journal]

Introduction

In studies of mineral cycling, the importance of mineral storage and remobilization from twigs and older foliage has been noted (Bormann et al. 1977; Ryan 1978; Waring and Franklin 1979; Fagerström and Lohm 1977; Miller et al. 1979). At the same time, there is increasing evidence that major changes in tissue dry weight may result from fluctuations in stored carbohydrates (Bradbury and Malcolm 1978; Lewandowska and Jarvis 1977). Because mineral composition is usually expressed as a percentage of dry weight of the tissue, major changes in carbohydrate reserves could confound interpretations.

As an alternative, Stachurski and Zimka (1975) have suggested expressing mineral composition in terms of content per unit of leaf area. This seems reasonable and follows recent standardization of expressions for water vapor and carbon dioxide flux from canopies (Sestak et al. 1971; Campbell 1977; Monteith 1975). Leaf (1973) reviewed a number of studies where mineral analysis were reported as content per leaf. To date, however, we have found only a single study by Gholz (1978) that reported changes in foliar composition as content per unit of leaf area. Gholz found significantly less variation when results were so reported, but his work, like that of Stachurski and Zimka (1975), was restricted to broadleaf species.

In this paper we report a comparison of foliar analyses for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), an evergreen conifer, growing under contrasting environments. We selected nitrogen as a mineral for comparison because it is most likely to be limiting growth in the Pacific Northwest (Gessel et al. 1973). By comparing changes in nitrogen content per unit of leaf area throughout the year, we can assess the relative error occurring in conventional analyses that express composition as a percentage of dry foliage weight.

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Study areas

Two Douglas-fir forests were the subject of study. One was located in the Oregon Coast Range at 45° N latitude and 123.5° W longitude at an elevation of 90 m on a southwest-facing slope of 35%. The other site was situated in the western Cascade Mountains at 45° N latitude and 122.5° W longitude at an elevation of 670 m on a southeast slope of 30%. Both environments average more than 2000 mm of precipitation annually, but only 4–7% falls during the summer months. Although similar in the amount and distribution of rainfall, the Cascade site has much less cloud cover and fog during the growing season than the Coast Range site. Correspondingly, the summer temperatures, as reflected by the warmest month of July, average 22°C in the Cascades and 16°C in the Coast Range (Franklin and Dyrness 1973).

Winters are relatively mild at both sites with January temperatures averaging about 2°C in the Cascades and 5°C in the Coast Range. Snow does not generally accumulate at either place, but the Cascade site usually has short periods with snow each winter. Thus, the climatic environment for sustained photosynthesis is much more consistent in the Coast Range than in the Cascades (Emmingham and Waring 1977), but both sites are comparable in regard to tree growth (site class III). The deep soils derived from andesitic colluvial materials in the Cascades and from sedimentary sandstones in the Coast Range provide ample water throughout the summer months (Grier and Running 1977; Zobel et al. 1976).

The vegetation differed slightly at the two sites, with Oregon grape (*Berberis nervosa* (L.) Pursh) dominating the understory in the Coast Range and bracken fern (*Pteridium aquilinum* (L.) Kuhn) more common on the Cascade site. Both forests were composed of young, even-aged trees. At the time of the study, those in the Coast Range were 40 years old while those in the Cascades were 25.

Both forests had thinned and unthinned portions for comparison. The Coast Range stands had basal areas of 52 m^2/ha when unthinned and 35 m^2/ha after thinning. Leaf area indices, estimated from correlations with sapwood basal area (Grier and Waring 1974), averaged 9.0 m^2 of projected foliage area per square metre of ground surface in the unthinned portion and 5.5 m^2 in the thinned portion. Mean tree diameters at breast height (dbh) were essentially the same, 44.3 compared with 44.1 cm, because measurements were taken just following the thinning in the fall of 1978.

The Cascade stands had basal areas of 9.0 and 5.6 m^2/ha in the unthinned and thinned portions, respectively. Corresponding estimates of leaf area indices were 2.9 and 1.7 m^2 of foliage surface per square metre of ground surface. Thinning was accomplished during the summer of 1977; consequently, tree diameters differed significantly when measured in the fall of 1978. Trees in the unthinned forest averaged 13.5 cm, whereas those in the thinned portion averaged 14.4 cm in diameter.

Materials and methods

Samples of foliage were collected with the aid of a shotgun at approximately monthly intervals from October 1978 to September 1979. Separate samples were collected from five trees in each of the four stands. From each tree, two branches from the midcrown were collected, placed in plastic bags, and transported to the laboratory for further processing.

Within 24 h of collection, foliage was removed from the sampled branches and separated into two categories: the current or new foliage, less than a year old, and all the foliage greater than a year old. All foliage was then resealed in plastic bags and stored at −15°C until analysis. Separate subsamples were taken for determining weight and nitrogen content. Because we shall compare mineral composition of forest floor litter with live foliage in another paper, we choose to present results on needles oven-dried at 70°C for 24 h. From comparison with fresh foliage, we know that the surface area of fresh Douglas-fir needles is decreased 20 ± 2% by drying.

The projected surface area of dried needles was consistently underestimated an additional 7−10% because the instrument used, a Li-Cor model LI-3000 area meter, was unable to fully account for the surface area of narrow objects such as needles. Thus, although the absolute precision of area determinations was within 2%, the correct values for fresh foliage would be approximately 30% more. Such an increase would reduce weight and nitrogen content values by 23% (reciprocal of 1.3 = 0.77) when expressed on the basis of fresh rather than dried surface area.

Needles selected for surface area measurements were later weighed to the nearest milligram and the results expressed as grams per square metre of projected leaf surface. A separate subsample of dried needles was passed through a 40-mesh screen in a Wiley mill and weighed for micro-Kjeldahl analysis of nitrogen (Schuman et al. 1973). Results were expressed as both a percentage of needle dry weight and as grams of N per square metre.

The data were subjected to an analysis of variance. Weight and nitrogen content per unit area were variables dependent upon site, treatment, foliage age, and sampling data. Diameter of the sampled trees at breast height was analyzed by covariance to remove this possible source of variation. A Student–Newman–Keuls (SNK) test (Steel and Torrie 1980) showed the main effects of treatment and date of sampling upon the dependent variables.

Preliminary analyses showed that the nitrogen content (grams per square metre) was influenced by a significant interaction between sampling date and foliage age, necessitating comparisons of individual means (Neter and Wasserman 1974). A *t*-test was employed to compare differences between foliage ages while holding sampling dates constant, and the SNK test was used to compare sampling dates while holding foliage age constant. Only results significant at the 0.05 level are reported.

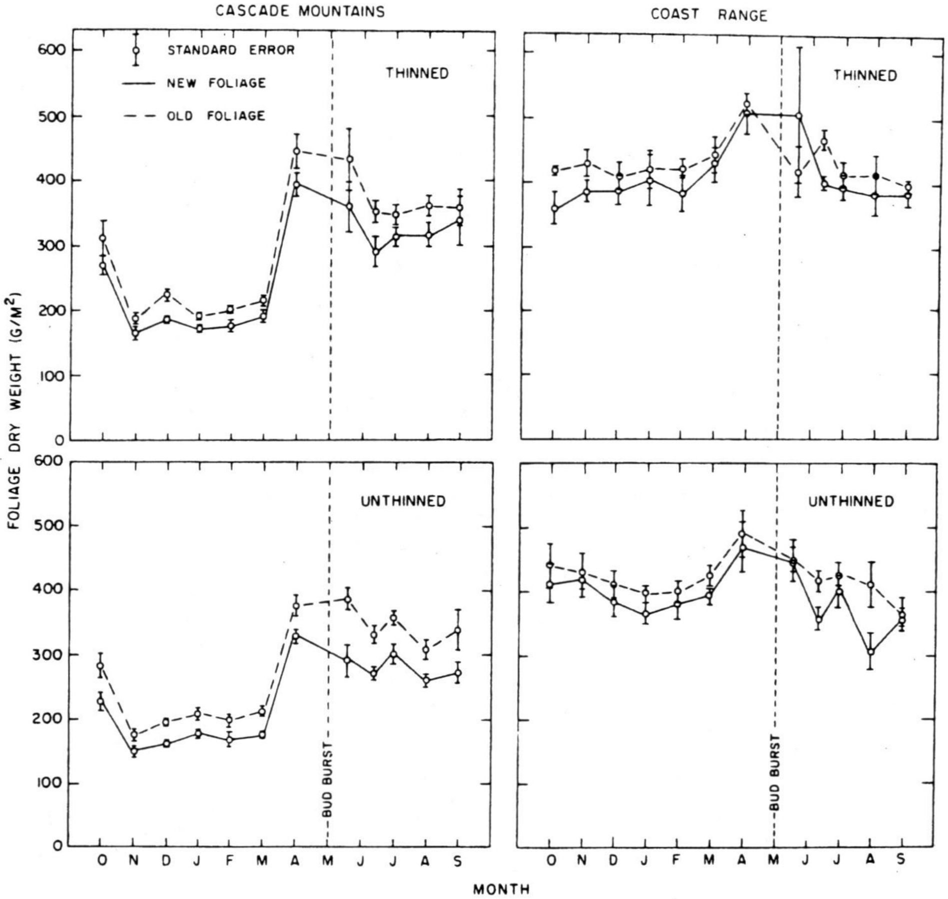

FIG. 1. Seasonal variation in foliage dry weight (projected area basis) of thinned and unthinned portions of Cascade Mountain and Coast Range stands.

Results

Changes in foliage weight

Large seasonal differences in leaf weight were evident from trees in the Cascade Mountain stands (Fig. 1). From November through March, values averaged 190 g/m^2 with negligible variation among trees. In April, however, leaf weight increased abruptly, exceeding the winter values by about 90% in the unthinned and by 125% in the thinned stand. By late June, values had declined to an average of 320 g/m^2, which was maintained through September. In October, values began to drop again, averaging 270 g/m^2.

Foliage from trees in the thinned stand had significantly higher weight per unit of leaf area than foliage from the unthinned stand. The older foliage, averaging 290 g/m^2, was heavier than new foliage in both the unthinned (average 230 g/m^2) and thinned stand (average 270 g/m^2).

Seasonal changes in leaf weight were much less pronounced in the Coast Range than in the Cascade Mountains (Fig. 1). From October to March, leaf weight averaged 400 g/m^2, increasing in April to an average of 500 g/m^2, or 25% above winter levels. In early June, values decreased to 460 g/m^2, and continued to decline slowly until August and September, when they reached 380 g/m^2.

In the Coast Range, differences between thinned and unthinned stands were not apparent, but the older foliage in both stands averaged about 8% more weight per unit of area than new foliage.

Changes in foliar nitrogen

In Figs. 2 and 3, the seasonal variations in foliar nitrogen at both sites are contrasted when composition is expressed per unit of leaf area or as a percentage of dry weight. In general, error estimates are smaller when results are expressed per unit of leaf area. In the Coast Range environment, interpretation of data would be similar, regardless of how it were expressed, because foliage weight remains relatively constant throughout the year (Fig. 1).

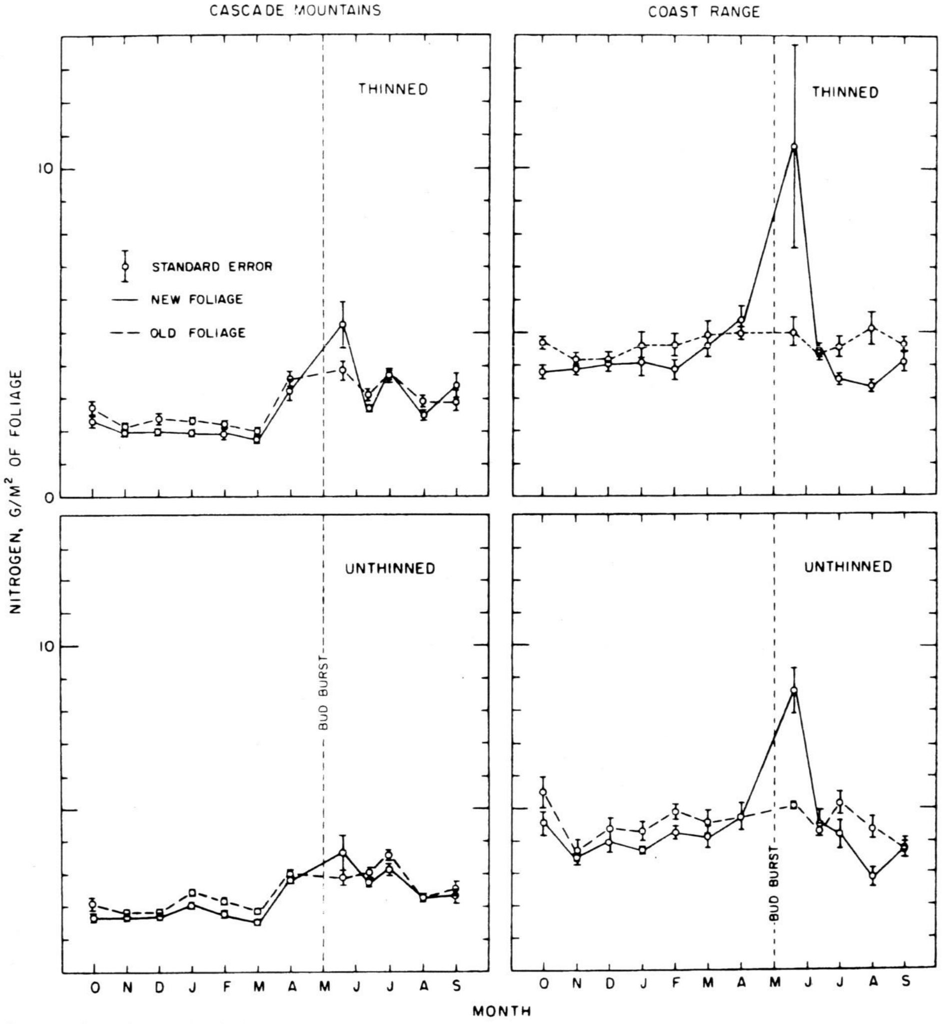

FIG. 2. Seasonal variation in foliage nitrogen, expressed in grams per square metre, of thinned and unthinned portions of Cascade Mountain and Coast Range stands.

In the Cascades, where foliage weight changes abruptly before and after the growing season, major errors in interpretation are likely if analyses are expressed as a percentage of dry weight. For example, from October to November, nitrogen composition appears to increase about 50%, from approximately 0.8 to 1.2% of dry weight (Fig. 3). In actuality, however, the amount of nitrogen in the needles remains essentially constant at approximately 2 g of N/m^2 (Fig. 2) because the foliage weight has decreased from one month to the next by approximately 50% (Fig. 1). Thus, because the two sites differ so much in foliar weight, a very misleading interpretation could result if nitrogen composition is expressed as a percentage of dry weight. For example, during the period from November through February (Fig. 3), one could assume the foliage at both sites had similar nitrogen composition of approximately 1%. Yet, when results were expressed as nitrogen content per unit of leaf area (Fig. 2), the Coast Range site had values twice those of the Cascades.

We performed detailed comparisons only on those data presented in Fig. 2. In the Cascade Mountains, total foliar nitrogen varied seasonally and was higher in the thinned than in the unthinned stand. Nitrogen levels from October through March were 40% lower than from April through September. Both stands averaged 2 g of N/m^2 from January through March when leaf weights were low. Foliar nitrogen increased in April to an average of 2.9 g/m^2 in the unthinned and 3.4 g/m^2 in the thinned stand. In early June, the highest nitrogen levels of the year were recorded in newly expanding foliage while older foliage maintained levels comparable to those in April. During the summer, nitrogen levels fluctuated and then fell significantly in August

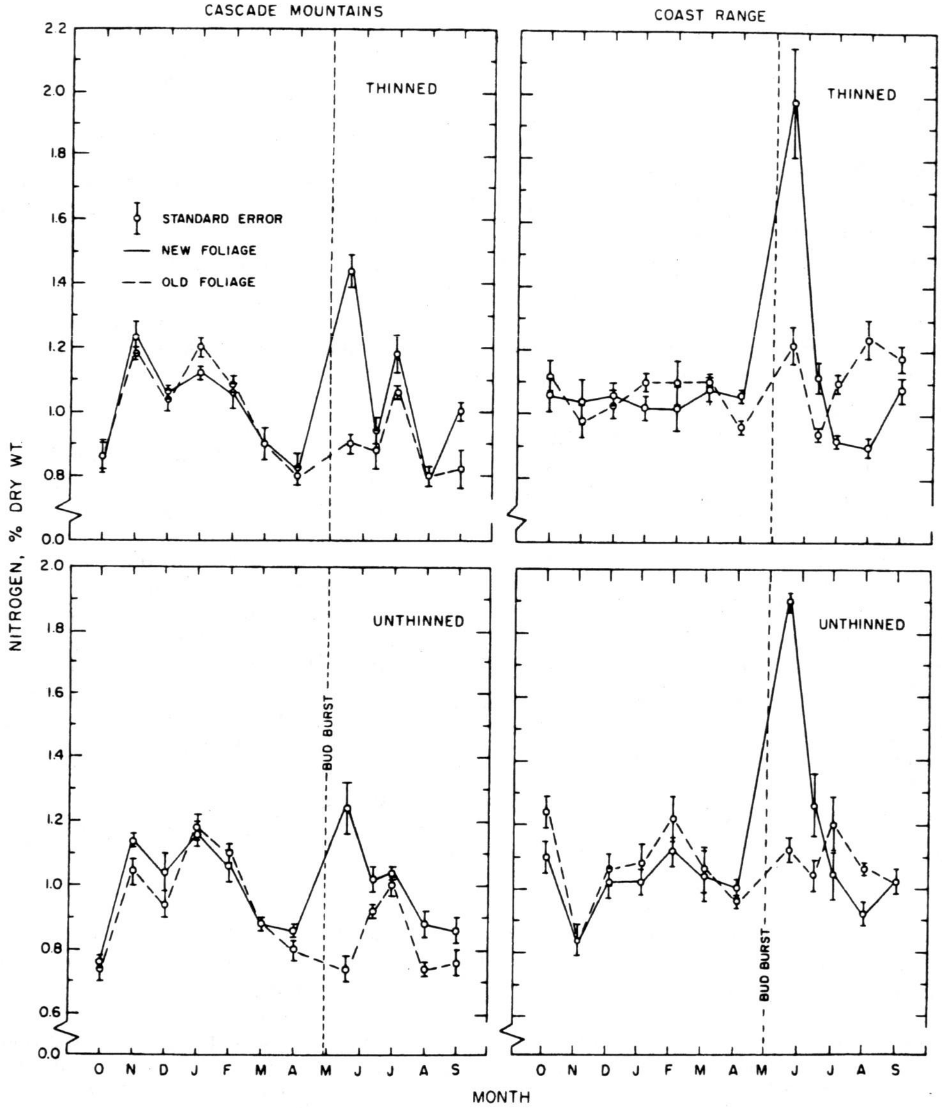

FIG. 3. Seasonal variation in foliage nitrogen, expressed in percent dry weight, of thinned and unthinned portions of Cascade Mountain and Coast Range stands.

and September.

In the Coast Range, nitrogen in the older foliage from the unthinned and thinned stands differed little, maintaining values between 4 and 5 g/m^2 for most of the year (Fig. 2). These values were significantly higher than those reported for the Cascade stands. Nitrogen content in newly emerging foliage was higher than in older foliage, reaching 8.5 g/m^2 in the unthinned and 10.7 g/m^2 in the thinned stand. During August, nitrogen levels in new foliage in the unthinned area dropped to 2.8 g/m^2, significantly less than the April value of 4.7 g/m^2 and one-third that recorded during expansion in early June.

Discussion

Seasonal changes in leaf weight reflect a balance between photosynthate production, respiration, and export of carbohydrates and other materials from the leaves. A possible explanation for consistently heavy leaves from the Coast Range site is that photosynthesis continues at a relatively high level throughout the year and that the growth of above- and below-ground organs also proceeds throughout the year (Harris et al. 1980). Relatively high rates of photosynthesis have been recorded during winter months in the Coast Range of Washington (Salo 1974; Helms 1965), and Emmingham and Waring (1977) developed a model for

Douglas-fir which simulates relatively constant photosynthetic activity year round in the Oregon Coast Range.

Although photosynthesis is also possible almost year round at the Cascade site, the rates predicted are much more variable (Emmingham and Waring 1977). Because of the shorter and warmer growing season, the likely result is a more varied demand for carbohydrates. These factors may account for the greater seasonal fluctuations and generally lower leaf weights of Douglas-fir growing in the Cascades.

From our data alone, we cannot completely evaluate the nitrogen status of the two sites. Clearly, the Coast Range stands have more nitrogen in their foliage at all times of the year. The fact that the older foliage is not depleted of nitrogen at the time of leaf expansion suggests that nitrogen is in adequate supply to meet demand (Waring and Youngberg 1972).

Additional insight may be gained by evaluating how much nitrogen is mobilized before leaves are shed. We have such a study in progress. This will require comparing nitrogen levels in older foliage and in fresh needle litter, as suggested by Stachurski and Zimka (1975). Because both fresh foliage and leaf litter shrink as they dry, care should be taken to assure that foliage is dried before determining surface area.

Even without those data, the present study shows that the base on which percentage calculations are made changes seasonally and differs between sites during the same season by more than 100%. Clearly, such analyses are inappropriate for interpreting either physiological status or ecosystem cycling. As an alternative, expressing results in terms of content per unit of leaf area is superior and is recommended.

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