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Specific leaf area and nitrogen distribution in New Zealand forests: Species independently respond to intercepted light

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Abstract

The foliage of five forested sites across a climatic gradient on the South Island of New Zealand were studied to assess whether the distribution of specific leaf area (SLA) and leaf nitrogen (N) were due to the light environment or intrinsic species characteristics. Within both mixed and single species stands, SLA and N were correlated with relative light interception (τ) but varied greatly. For N, this variation was reduced by expressing N values as relative site N (N/maximum site N) that increased correspondence between N and ln(τ) across sites ($r^2 = 0.79$). However, comparison of mixed species composition to a monoculture stands showed difference in the N-τ especially in stands with high species richness. The nitrogen extinction coefficient (k_N) was estimated for canopies based on profiles of measured projected leaf area indices (PLAI) and leaf N, with an average value of 0.17 ± 0.06 indicating a conservative relationship between N and τ in these forests. Site maximum leaf N is correlated positively with annual incident irradiance further corroborating the N and light relationship as well as providing a potential mechanism for estimating canopy N over larger areas.

Keywords: Leaf nitrogen; Specific leaf area; Nitrogen extinction coefficient; Light interception; Productivity modeling

1. Introduction

Leaf morphology and nitrogen (N) content change predictably through vegetation canopies as leaf area distribution in the canopy affects incident light transmittance. Specific leaf area (SLA), the ratio of the area to mass for an individual leaf, is related to species, water availability, canopy position, and site irradiance levels (Hirose and Werger, 1995; Niinemets, 1995; Hollinger, 1996; Sellin, 2001). Canopy interception of light affects SLA as leaf surface area increases with canopy depth associated with radiation transmittance. While genetic features constrain the limits of SLA for individual species, the incident light regime dictated by climate is highly associated with SLA gradients within most canopies (Aerts et al., 1992; Reich and Walters, 1994; Donovan and Pappert, 1998). For example, forests in areas with high intensity, direct beam radiation have lower SLA than forests with low intensity diffuse radiation (Specht and Specht, 1989; Pierce et al., 1994). The evolution of different SLA values among species is, therefore, derived from plant species competition for light balanced with the efficiency of leaves to convert light to dry matter (Hirose and Bazzaz, 1998; Cunningham et al., 1999).

Leaf morphology is also associated with nitrogen where higher SLA values result in tighter coupling between leaf N and photosynthesis, as potential productivity increases directly with N per unit leaf area (Reich et al., 1998; Meziane and Shipley, 1999). Nitrogen allocation within layers of the canopy are positively related to intercepted light, especially when N is expressed on a per unit leaf area basis (N_A) (Aerts et al., 1992; Kull et al., 1995; Anten et al., 1998; Milroy et al., 2001). This is primarily due to the inverse relationship between SLA and light (Niinemets, 1995; Rosati et al., 2000). Leaf N when expressed on a mass basis (N_M), is generally constant through the canopy, unrelated to the light interception (Reich et al., 1994). However, sites with larger leaf area index values tend to have higher average N_M when observed across a precipitation gradient (Pierce et al., 1994; Hebert and Jack, 1998). Mechanistically, the relationship between leaf N allocation with regard to light may be

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an optimization strategy given that photosynthesis also correlates with N_A (Hollinger, 1989). Process-based modeling of canopy photosynthesis confirms observations that N_A determines carbon uptake under varying environmental factors such as diffuse and direct radiation environments (Leuning et al., 1995) leading to a hypothetical N distribution optimization under differing environmental conditions (Dewar, 1996). Under different climate regimes, SLA varies changing the photosynthesis–N_A relationship (Reich and Walters, 1994). However, C fixation as a function of N is species dependent, because N incorporation into functional proteins such as photosynthetic enzymes differs among species (Niinemets et al., 1998). Because of potential variability of both SLA and N allocation by species, species composition affects canopy N distribution.

Understanding the predictability of SLA and N distribution in canopies is important for modeling growth and production in forests. Most canopy parameter values for forest productivity models are derived from a limited set of experimental data on canopy structure and nutrient distribution. As a simplification, models may assume an ‘‘average’’ leaf N_A that significantly underestimates the ‘‘true’’ value of total canopy nitrogen due to exponential changes in N_A with canopy intercepted radiation (Hollinger, 1996) leading to potential errors in photosynthesis and respiration calculations (Reynolds et al., 1992). Canopy radiation can be expressed as the ratio of light intercepted by canopies to site irradiance (τ) with values ranging from 0.0 to 1.0. To avoid log-linear biases, canopy N_A distribution can be represented by a modified Beer–Lambert law:

$$N_{A_i} = N_{A_t}\, e^{(-k_N \xi)} \qquad (1)$$

where N_{A_i} is the leaf nitrogen at level i in the canopy, N_{A_t} the maximum site N_A, and k_N is a coefficient that represents the change in N_A with cumulative leaf area (ξ) (Hirose and Werger, 1987a; Leuning et al., 1995; Dewar, 1996; Hollinger, 1996; Anten, 2002) applicable to closed canopies. Literature values of k_N for forested canopies are mostly theoretical with little information on what influence mixed species have on the k_N coefficient value.

In this study, we examine how light penetration affects leaf SLA and N distribution in New Zealand forest canopies and utilize this information to derive values of k_N. The influence of species-effects on the relationship between light attenuation, k_N, and N_A are also compared between monoculture and mixed species forests. Because of the importance of leaf N to production modeling, generalized relationships between N, radiation, and projected leaf area index are also examined as a method to determine if large-scale mapping of total canopy N is feasible from general climate and stand characteristics.

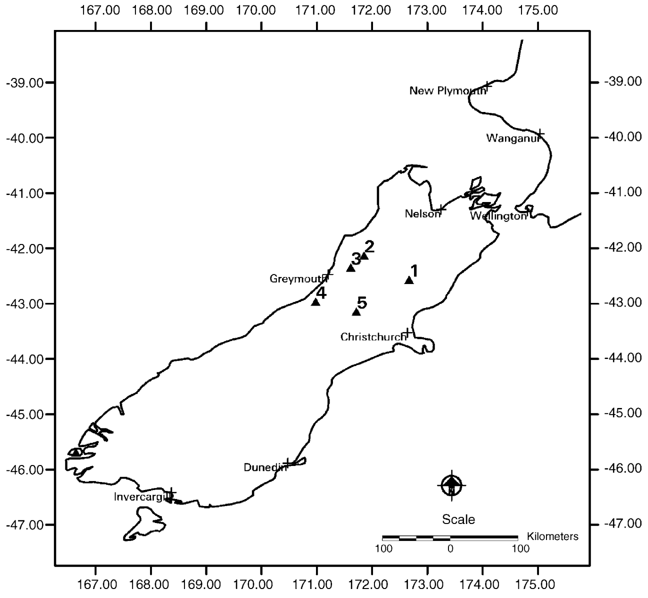

Fig. 1. Map of the South Island of New Zealand with sampling locations. Numbers correspond to site descriptions found in Table 1.

2. Methods

Five forested sites across the central portion of the South Island of New Zealand were selected to span a broad gradient of climate, soil, and vegetation. At each site, leaf samples were collected at different heights in the canopy that were later analyzed to determine SLA and leaf N concentration. In addition, optical measurements of light interception were acquired through the canopy to determine τ and PLAI. Sites generally varied in species composition, annual temperature, precipitation and annual photosynthetic active radiation (PAR) (Fig. 1; Table 1).

2.1. Site description

During November 1997, up to three 150 m transects were randomly established in continuous forest patches at each site for

Table 1
Sample site characteristics. Climate information is derived from extrapolated data (J.R. Leathwick and R.T.T. Stephens, unpublished data)

Site	Dominant species	Latitude (°)	Longitude (°)	Average temperature (°C)	Annual precipitation (mm)	Annual PAR (MJ m^{-2} yr^{-1})	$PLAI_{MAX}$ (m^2 m^{-2})	Species	No. of transects
1	*K. ericoides*	−42.560	172.663	9.4	1064	2230	3.8	7	2
2	*W. racemosa, N. menziesii*	−42.227	171.885	9.7	2323	2209	5.8	13	3
3	*N. truncata, W. racemosa*	−42.120	171.851	10.9	2600	2225	6.4	10	2
4	*W. racemosa, D. cupressinum*	−42.945	170.729	11.3	3320	2157	9.5	20	2
5	*N. solandri* var. *cliffortioides*	−43.142	171.718	5.7	2038	2289	3.8	1	3

The PLAI values are the maximum values measured from the LAI-2000 for each site. The total number of species encountered per site is provided as an indication of the species richness.