

Differences in nitrogen economy of temperate trees

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Summary Twenty-four temperate tree species were classified into three groups based on cluster analysis of relative growth rate, nitrogen concentration, nitrogen-production efficiency, nitrogen-distribution ratio and nitrogen-use efficiency as follows: Group I (Asteridae and Rosidae), Group II (Dilleniidae and Hamamelidae) and Group III (Coniferopsidae). Relative growth rate (RGR) was high in Group II, moderate in Group I and low in Group III. The regression coefficient for the relationship between RGR and leaf nitrogen concentration was higher in Group II than in Group I, and no relationship was observed in Group III. Parameter analysis of RGR indicated that RGR per unit leaf nitrogen was important for all three groups, but that the allocation of nitrogen to leaves was particularly important in Groups I and II. The ratio of dark respiratory rate (R) to net photosynthetic rate (A) was higher in Group I than in Group II. Neither A nor R was measured in the Group III species. A linear relationship was observed between leaf nitrogen concentration and A in Group II, but this relationship was not evident in Group I.

Keywords: nitrogen-distribution ratio, nitrogen-production efficiency, nitrogen-use efficiency, photosynthesis, relative growth rate, respiration.

Introduction

Relative growth rate (RGR) is closely related to whole-plant nitrogen concentration (N_{total}) (Ingstad 1977). Although the RGR– N_{total} relationship has been widely studied (e.g., Greenwood et al. 1991, Ingstad and Ågren 1992), it has proved difficult to apply to different growth stages because it changes with RGR, particularly during the later stages of growth (Greenwood et al. 1991). Many studies have shown a positive correlation between leaf nitrogen concentration (N_{leaf}) and leaf net photosynthetic rate (A) (e.g., Gulmon and Chu 1981, Field and Mooney 1986, Hirose and Kitajima 1986, Evans 1989). However, the A – N_{leaf} relationship, like the RGR– N_{total} relationship, differs with growth stage (Murata 1961, Hayami 1982), and among species (Evans and Seemann 1989). Variation in the A – N_{leaf} relationship among different species is often correlated with differences in specific leaf area (SLA) (Reich and Walters 1994, Reich et al. 1997, Poorter and Evans 1998). Changes in the A – N_{leaf} relationship can also be explained by variation in the allocation ratio of nitrogen to ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) in leaves (Ev-

ans and Seemann 1989).

Respiration is regulated by demand for synthesis of plant components and the requirement for energy (Penning de Vries 1975). Respiratory rate (R) has been related to N_{leaf} (Ryan 1995, Reich 1996, Reich et al. 1998b, 1998c), because N_{leaf} is the main component of protein, and the synthesis and maintenance of protein is costly (but see Byrd et al. 1992). However, based on the observation that, in several species, large amounts of primary photosynthate and storage compounds are respired regardless of the growth or maintenance process, Shinano et al. (1996) hypothesized that R is not regulated solely by N_{leaf} .

Although it is well established that nitrogen and carbon are essential elements for growth, it is still unclear whether the interrelationships between plant growth and nitrogen differ among phylogenetic groups of trees. We have studied the interrelationship between plant growth (carbon assimilation) and nitrogen in 24 tree species growing in fertile soil under similar growth conditions without mutual shading for 3 years. The tree species were classified into three groups based on cluster analysis of various parameters of carbon and nitrogen: Group I (Asteridae and Rosidae), Group II (Dilleniidae and Hamamelidae) and Group III (Coniferopsidae). From an evolutionary perspective, the Coniferopsidae belongs to the oldest class in the current study, followed by the Hamamelidae and Dilleniidae (Cronquist 1988). The Rosidae and Asteridae have evolved relatively recently. The species studied in each group are listed in Table 1.

Materials and methods

On May 8, 1992, seedlings of 24 tree species were transplanted in a field at Hokkaido University. At the time of transplanting, seedlings of the Pinaceae species were 5 years old, whereas seedlings of all of the other species were 3 years old except for the Salicaceae species, for which saplings grown from a cutting were used. Phosphorus and potassium were applied as 100 kg P_2O_5 ha⁻¹ and 100 kg K_2O ha⁻¹, respectively. Nitrogen (N) was applied as ammonium sulfate at 0 and 300 kg N ha⁻¹. Because the effect of N application on leaf N concentration was not significant except for the *Prunus* spp. (Table 2), data were expressed as the mean of both N treatments. Planting density was 1 × 1 m to avoid mutual shading. Plants were sampled on May 8, June 20–27, September 11 and

Table 1. List of species used in the experiment. According to Cronquist et al. (1988), Groups I, II and III are ordered on the basis of evolutionary age, with Group I comprising the most recently evolved classes.

Class	Order	Family	Species	Symbol	Grouping ¹	
<i>Anthophyta</i>						
Asteridae	Scrophulariales	Oleaceae	<i>Fraxinus mandshurica</i> Rupr. var. <i>japonica</i> Maxim.	Fm	I	
Rosidae	Sapindales	Aceraceae	<i>Acer mono</i> Maxim.	Am	I	
			<i>Acer saccharum</i> Marsh.	As	I	
	Rosales	Rosales	<i>Prunus sargentii</i> Rehd.	Ps	I	
			<i>Prunus nipponica</i> Matsum. var. <i>kurilensis</i> (Mayibe) E. H. Wils	Pn	I	
			<i>Sorbus commixta</i> Hedl.	Sc	I	
	Fabales	Fabaceae	<i>Maackia amurensis</i> Rupr. & Maxim. var. <i>buergeri</i> (Maxim.) C.K. Schneid.	Ma	I	
			<i>Robinia pseudoacacia</i> L.	Rp	I	
<i>Cornus controversa</i> Hemsl.			Cc	I		
Dilleniidae	Salicales	Salicaceae	<i>Populus maximowiczii</i> A. Henry	Pm	II	
			<i>Populus euroamericana</i> Rehd.	Pe	II	
			<i>Salix babylonica</i> L.	Sb	II	
Hamamelidae	Fagales	Fagaceae	<i>Fagus crenata</i> Blume	Fc	II	
			<i>Quercus mongolica</i> Fisch ex Turcz. var. <i>grosseserrata</i> (Blume) Rehd. & E. H. Wils.	Qm	II	
			Betulaceae	<i>Betula maximowicziana</i> Regel.	Bm	II
				<i>Betula ermanii</i> Cham.	Be	II
				<i>Alnus hirsuta</i> Turcz.	Ah	II
	Juglandales	Juglandaceae	<i>Juglans ailantifolia</i> Carrière	Ja	II	
	Urticales	Ulmaceae	<i>Ulmus davidiana</i> Planch. var. <i>japonica</i> (Rehd.) Nakai	Ud	II	
<i>Progymnospermophyta</i>						
Coniferopsidae	Taxodiaceae	Pinaceae	<i>Abies sachalinensis</i> (Friedr. Schmidt) M. T. Mast.	Abs	III	
			<i>Picea glehnii</i> (Friedr. Schmidt) M. T. Mast.	Pg	III	
			<i>Picea jezoensis</i> (Siebold & Zucc.) Carrière	Pj	III	

¹ See text for parameter analysis grouping method.

October 1–14, 1992; May 15–20 and October 1–14, 1993; and April 18–28, July 6 to August 1, and September 21 to October 20, 1994. Shoots and roots were collected except for the October 1–14, 1993 sampling when only shoots were sampled. Coarse roots were collected by excavating around each tree, but fine roots (< 2 mm diameter) were not collected. Although fine roots comprise only a small proportion of total root dry weight, they make a substantial contribution to root length. However, because N uptake by roots is similar whether expressed on the basis of root length or dry weight (Shinano et al. 1994), we used root dry weight as the root parameter.

Each sample was cut into pieces (about 8 cm³), air-dried at 80 °C for 96 h, and ground for subsequent analysis. A portion of leaf sample was weighed and leaf area was determined with an automatic leaf area meter (Hayashi Denko, Ltd., Tokyo, Japan). Nitrogen concentration was determined by the semi-micro Kjeldahl method.

Net photosynthetic rate (*A*) was measured by placing the intact leaf in various sized transparent plastic chambers that were connected to a differential-type infrared gas analyzer (Model ADC-3, Shimadzu, Kyoto, Japan). Net photosynthetic rate was measured at light saturation (i.e., at 1000–1500 μmol m⁻² s⁻¹ supplied by a halogen lamp (KTS-100R, Kenko Co. Ltd., Tokyo, Japan)). Air temperature, relative humidity, and

CO₂ concentration in the chamber were 20–25 °C, 40–50%, and 350–370 ppm, respectively, and the flow rate was 0.5 l min⁻¹ for the measurement of *A* and respiratory rate (*R*). Respiratory rate was measured by covering the leaf with aluminum foil after *A* was measured. Values of *R* were adjusted to 25 °C, assuming *Q*₁₀ = 2.

Relative growth rate (RGR) was calculated based on the mean value of whole-plant dry weight at each sampling. To further analyze the characteristics of RGR, it was parameterized as follows:

$$\text{RGR} = \left(\frac{\Delta \text{DM} / \Delta t}{N_{(\text{leaf})}} \right) \left(\frac{N_{(\text{leaf})}}{N_{(\text{total})}} \right) \left(\frac{N_{(\text{total})}}{\text{DM}} \right), \quad (1)$$

where ΔDM is amount of dry matter accumulated over the period between day of planting and the last sampling, *N*_(leaf) is amount of N accumulated in the leaf, *N*_(total) is amount of N accumulated in the whole plant, DM is mean amount of dry matter accumulated in the plant and Δ*t* is days of the period. We refer to ΔDM/Δ*t*/*N*_(leaf) as N-production efficiency, *N*_(leaf)/*N*_(total) as N-distribution ratio to leaf and DM/*N*_(total) as N-use efficiency.

Table 2. Mean (\pm SE) N concentrations (mg g^{-1}) in leaves, stem and roots of the studied tree species. Within a row, Class means followed by different letters are significantly different at 5% (LSD).

Class	Species	Leaves ¹		Leaves ²	Stem ²	Roots ²	Whole plant ²
		0 N	300 N				
Asteridae	<i>Fraxinus mandshurica</i>	35.0 \pm 2.17 a	36.7 \pm 4.47 a	35.8 \pm 2.27 c	8.9 \pm 0.67 ab	10.4 \pm 0.61 ab	13.6 \pm 0.95 abc
Rosidae	<i>Acer mono</i>	24.7 \pm 1.20 a	26.1 \pm 1.54 a	25.4 \pm 0.96	8.3 \pm 1.16	14.9 \pm 1.75	13.0 \pm 1.07
	<i>Acer saccharum</i>	25.6 \pm 2.52 a	29.1 \pm 4.14 a	27.5 \pm 2.48	9.8 \pm 0.75	12.4 \pm 1.59	14.1 \pm 1.15
	<i>Prunus sargentii</i>	22.9 \pm 3.69 a	33.8 \pm 4.19 a	28.3 \pm 3.08	8.5 \pm 0.63	11.5 \pm 0.95	13.1 \pm 0.78
	<i>Prunus nipponica</i>	18.3 \pm 2.95 a	28.3 \pm 3.33 b	23.7 \pm 2.59	8.4 \pm 1.30	11.8 \pm 1.45	13.1 \pm 1.21
	<i>Sorbus commixta</i>	21.4 \pm 3.90 a	27.8 \pm 4.53 a	24.3 \pm 2.98	8.7 \pm 0.84	12.1 \pm 1.32	12.3 \pm 1.11
	<i>Maackia amurensis</i>	39.4 \pm 2.37 a	41.9 \pm 1.97 a	40.7 \pm 1.52	14.0 \pm 0.90	20.8 \pm 1.53	20.8 \pm 1.34
	<i>Robinia pseudoacacia</i>	40.3 \pm 5.16 a	39.9 \pm 3.63 a	40.1 \pm 2.90	15.2 \pm 0.67	21.3 \pm 1.98	22.7 \pm 1.62
	<i>Cornus controversa</i>	25.3 \pm 4.18 a	32.2 \pm 3.79 a	28.7 \pm 2.87	8.7 \pm 0.63	9.0 \pm 1.70	11.8 \pm 1.19
	Mean				29.7 \pm 1.08 b	10.2 \pm 0.39 bc	14.1 \pm 0.67 c
Dilleniidae	<i>Populus maximowiczii</i>	24.8 \pm 0.91 a	26.7 \pm 3.47 a	25.8 \pm 1.75	7.8 \pm 0.39	10.1 \pm 0.94	12.9 \pm 1.26
	<i>Populus euroamericana</i>	34.1 \pm 2.60 a	40.6 \pm 3.55 a	37.3 \pm 2.32	7.8 \pm 0.37	10.0 \pm 0.79	14.4 \pm 1.25
	<i>Salix babylonica</i>	34.7 \pm 1.60 a	29.1 \pm 6.40 a	31.9 \pm 3.14	7.9 \pm 0.73	8.7 \pm 0.46	11.9 \pm 1.81
	Mean			31.2 \pm 1.61 bc	7.8 \pm 0.25 a	9.8 \pm 0.51 a	13.3 \pm 0.79 b
Hamamelidae	<i>Fagus crenata</i>	20.7 \pm 0.35 a	24.1 \pm 3.15 a	22.4 \pm 1.62	9.6 \pm 1.28	13.2 \pm 1.55	12.2 \pm 1.56
	<i>Quercus mongolica</i>	19.5 \pm 6.44 a	28.2 \pm 5.23 a	27.1 \pm 2.52	7.5 \pm 0.57	10.9 \pm 0.88	12.0 \pm 0.53
	<i>Betula maximowicziana</i>	32.8 \pm 1.88 a	40.6 \pm 4.27 a	37.0 \pm 2.62	10.7 \pm 0.68	9.2 \pm 0.91	16.2 \pm 0.94
	<i>Betula ermanii</i>	31.3 \pm 2.31 a	22.9 \pm 3.05 a	32.2 \pm 1.88	10.2 \pm 1.24	11.1 \pm 1.48	15.9 \pm 1.32
	<i>Alnus hirsuta</i>	28.5 \pm 1.50 a	35.7 \pm 6.83 a	32.1 \pm 3.52	13.3 \pm 1.72	14.9 \pm 2.55	19.0 \pm 1.71
	<i>Juglans ailantifolia</i>	30.5 \pm 1.22 a	34.2 \pm 1.91 a	32.2 \pm 1.17	9.1 \pm 0.49	13.8 \pm 1.04	15.6 \pm 1.06
	<i>Ulmus davidiana</i>	40.3 \pm 5.16 a	39.9 \pm 3.63 a	30.4 \pm 2.93	10.0 \pm 0.64	13.0 \pm 1.29	14.7 \pm 1.22
	Mean			31.6 \pm 1.05 bc	10.0 \pm 0.36 bc	12.0 \pm 0.53 b	15.3 \pm 0.49 c
Coniferopsidae	<i>Abies sachalinensis</i>	18.8 \pm 0.25 a	19.0 \pm 1.48 a	18.9 \pm 0.82	10.7 \pm 0.49	8.6 \pm 0.88	11.0 \pm 0.51
	<i>Picea glehnii</i>	12.7 \pm 1.752 a	16.2 \pm 0.40 a	14.4 \pm 1.26	10.4 \pm 0.70	7.8 \pm 0.33	10.1 \pm 0.21
	<i>Picea jezoensis</i>	21.6 \pm 1.60 a	20.4 \pm 0.40 a	21.0 \pm 0.76	12.1 \pm 0.99	9.5 \pm 0.83	11.7 \pm 0.50
	Mean			18.2 \pm 0.89 a	11.0 \pm 0.41 c	8.6 \pm 0.47 a	11.0 \pm 0.29 a

¹ Values are nitrogen concentrations of leaves in the 0 and 300 N treatments.

² Values are mean nitrogen concentrations of the 0 plus 300 N treatments.

The values shown are the means of six replicates. To determine phylogenetic differences in growth and nitrogen, cluster analysis was performed with the hierarchical cluster analysis program (SPSS 1994; SPSS Advanced Statistics, SPSS Inc., Chicago, IL) with RGR, leaf nitrogen concentration, N-production efficiency, N-distribution ratio to leaves and 1/N-use efficiency as the parameters.

Results

Nitrogen concentration

Nitrogen concentrations of leaves, stem and roots were high in *Maackia amurensis* Rupr. & Maxim. and *Robinia pseudoacacia* L. of the Rosidae, and low in leaves and roots of the Coniferopsidae (Table 2). From an evolutionary perspective, N concentration in the stem decreased and N concentration in leaves increased with the progress of evolution, indicating that recently evolved plants preferentially distribute N to functional organs (i.e., the leaf).

Relative growth rate

Relative growth rate (RGR) was higher in the Dilleniidae and

Hamamelidae (about $7 \text{ mg g}^{-1} \text{ day}^{-1}$) than the Asteridae or Rosidae (about $5 \text{ mg g}^{-1} \text{ day}^{-1}$), and lowest in the Coniferopsidae (about $2 \text{ mg g}^{-1} \text{ day}^{-1}$) (Table 3).

Nitrogen-production efficiency was low in the Coniferopsidae, and in *M. amurensis* and *R. pseudoacacia* of the Rosidae and highest in *Salix babylonica* L. (2.63 day^{-1}) (Table 3). Nitrogen-distribution ratio to leaves was higher in Dilleniidae and Hamamelidae than in other classes (Table 3). Nitrogen-use efficiency was not consistent among classes. High RGR of Dilleniidae and Hamamelidae was achieved through relatively high N-production efficiency and N-distribution ratio, whereas the low RGR of Coniferopsidae was mainly a result of low N-production efficiency (Table 3).

Photosynthetic rate, respiratory rate and specific leaf area

Net photosynthetic rate (A) was high in the Dilleniidae and Hamamelidae, especially in *Populus euroamericana* Rehd. and *Betula ermanii* Cham. (Table 4). Net photosynthetic rates in the Asteridae and Rosidae were about half of those in the Dilleniidae and Hamamelidae. Because there was little difference in respiratory rate (R) among the classes, the R/A ratio was higher in the Asteridae and Rosidae than in the Dilleniidae

Table 3. Relative growth rate (RGR), N-production efficiency, N-distribution ratio to leaves and N-use efficiency of the studied tree species. Class means within a row followed by different letters are significantly different at 5% (LSD).

Class	Species	RGR (mg g ⁻¹ day ⁻¹)	N-production efficiency (g g ⁻¹ day ⁻¹)	N-distribution ratio to leaves	N-use efficiency
Asteridae	<i>Fraxinus mandshurica</i>	5.30 b	1.22 a	0.420 a	97 a
Rosidae	<i>Acer mono</i>	3.07	0.68	0.415	93
	<i>Acer saccharum</i>	4.83	1.00	0.442	92
	<i>Prunus sargentii</i>	5.53	1.09	0.539	106
	<i>Prunus nipponica</i>	5.37	1.20	0.600	134
	<i>Sorbus commixta</i>	4.68	1.26	0.487	131
	<i>Maackia amurensis</i>	6.23	0.77	0.445	55
	<i>Robinia pseudoacacia</i>	5.07	0.59	0.327	38
	<i>Cornus controversa</i>	5.43	1.34	0.519	128
	Mean	5.03 ± 0.33 b	0.99 ± 0.10 a	0.472 ± 0.030 a	97 ± 13 a
Dilleniidae	<i>Populus maximowiczii</i>	6.67	1.27	0.555	106
	<i>Populus euroamericana</i>	6.37	0.86	0.608	82
	<i>Salix babylonica</i>	8.30	2.63	0.395	125
	Mean	7.11 ± 0.60 c	1.59 ± 0.53 b	0.519 ± 0.064 a	104 ± 12 a
Hamamelidae	<i>Fagus crenata</i>	4.13	1.92	0.190	88
	<i>Quercus mongolica</i>	7.53	1.41	0.496	93
	<i>Betula maximowicziana</i>	6.30	0.89	0.593	84
	<i>Betula ermanii</i>	8.43	1.20	0.681	97
	<i>Alnus hirsuta</i>	7.90	1.11	0.516	72
	<i>Juglans ailantifolia</i>	6.43	0.94	0.397	58
	<i>Ulmus davidiana</i>	4.83	0.90	0.550	102
	Mean	6.51 ± 0.60 c	1.20 ± 0.14 b	0.489 ± 0.060 a	85 ± 6 a
Coniferopsidae	<i>Abies sachalinensis</i>	1.93	0.39	0.520	106
	<i>Picea glehnii</i>	2.47	0.76	0.314	97
	<i>Picea jezoensis</i>	1.83	0.29	0.483	77
	Mean	2.08 ± 0.20 a	0.48 ± 0.14 a	0.439 ± 0.063 a	91 ± 9 a

Table 4. Photosynthetic rates (A), respiratory rates (R) and specific leaf areas (SLA) of the studied tree species. Class means within a row followed by different letters are significantly different at 5% (LSD).

Class	Species	Photosynthetic rate ($\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$)	Respiratory rate ($\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$)	R/A ratio ¹	SLA (m ² g ⁻¹)
Asteridae	<i>Fraxinus mandshurica</i>	0.244 ± 0.011 a	0.026 ± 0.005 a	0.109 ± 0.019 ab	124.9 ± 11.6 a
Rosidae	<i>Acer saccharum</i>	0.247 ± 0.020	0.041 ± 0.008	0.174 ± 0.033	132.1 ± 7.4
	<i>Prunus sargentii</i>	0.252 ± 0.038	0.029 ± 0.003	0.126 ± 0.015	128.2 ± 10.2
	<i>Maackia amurensis</i>	0.141 ± 0.025	0.032 ± 0.005	0.267 ± 0.052	119.5 ± 10.4
	<i>Cornus controversa</i>	0.250 ± 0.042	0.022 ± 0.010	0.107 ± 0.022	143.6 ± 11.5
	Mean	0.223 ± 0.075 a	0.029 ± 0.004 a	0.124 ± 0.037 b	130.8 ± 24.5 ab
Dilleniidae	<i>Populus maximowiczii</i>	0.296 ± 0.044	0.022 ± 0.002	0.084 ± 0.013	120.9 ± 3.1
	<i>Populus euroamericana</i>	0.486 ± 0.058	0.043 ± 0.008	0.097 ± 0.019	162.6 ± 16.5
	Mean	0.391 ± 0.049 b	0.033 ± 0.005 a	0.084 ± 0.009 a	141.7 ± 35.3 a
Hamamelidae	<i>Betula maximowicziana</i>	0.379 ± 0.028	0.028 ± 0.003	0.075 ± 0.009	174.7 ± 21.3
	<i>Betula ermanii</i>	0.448 ± 0.033	0.036 ± 0.001	0.083 ± 0.006	165.8 ± 13.5
	<i>Juglans ailantifolia</i>	0.351 ± 0.026	0.031 ± 0.005	0.091 ± 0.015	161.9 ± 6.7
	<i>Ulmus davidiana</i>	0.230 ± 0.019	0.019 ± 0.001	0.087 ± 0.010	105.1 ± 14.5
	Mean	0.352 ± 0.024 b	0.028 ± 0.002 a	0.082 ± 0.004 a	151.9 ± 8.5 b

or Hamamelidae. Among the species examined, R/A was highest in *M. amurensis* of the Rosidae. Specific leaf area (SLA) was higher in the Hamamelidae and Dilleniidae than in the Asteridae and Rosidae (Table 4).

Discussion

Because RGR comprises N-production efficiency, N-distribution ratio to leaves and N-use efficiency (Equation 1), physiological differences among classes were analyzed by hierarchi-

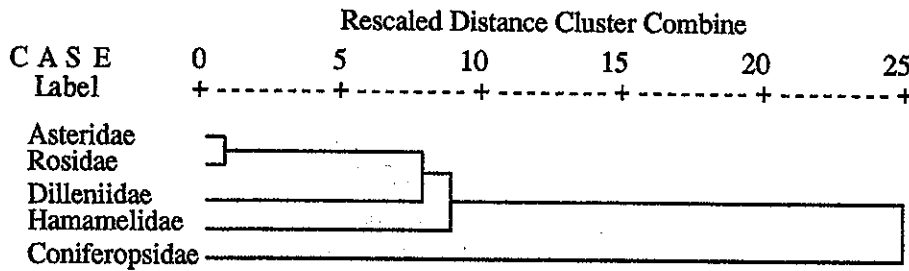


Figure 1. Dendrogram of the hierarchical cluster analysis of each class by leaf nitrogen concentration, relative growth rate, N-production efficiency, N-distribution ratio to leaf and 1/N-use efficiency.

cal cluster analysis with the parameters: RGR, N_{leaf} , N-production efficiency, N-distribution ratio to leaves and 1/N-use efficiency (SPSS 1994). As shown in the dendrogram in Figure 1, physiological characteristics were similar among species in the Asteridae and Rosidae, which are recently evolved Anthophyta (designated here as Group I), and similar among species in the Dilleniidae and Hamamelidae, which are early evolved Anthophyta (designated here as Group II). The Coniferopsidae (designated here as Group III) differed from the other classes in many physiological characteristics.

Relative growth rate was high in Group II, moderate in Group I, and low in Group III (Table 3). Although a positive relationship between RGR and N_{total} is frequently observed (Greenwood et al. 1991, Ingestad and Ågren 1992), the relationship changes relative to the growth stage of the species (Greenwood et al. 1991). We found no clear relationship between N_{total} and RGR in any group over the 3-year study period. However, there was a significantly positive linear relationship between N_{leaf} and RGR in Groups I and II (Figure 2), indicating that N_{leaf} rather than N_{total} regulates plant dry matter production at the whole-plant level.

Based on the RGR- N_{leaf} relationship, it was possible to distinguish three groupings among the 24 tree species studied. In the Pinaceae, both RGR and N_{leaf} were low. From an evolutionary perspective, the Coniferopsidae belongs to the oldest class in the current study, followed by the Hamamelidae and Dilleniidae. Classes Rosidae and Asteridae are relatively recently evolved. The regression coefficient for the RGR- N_{leaf} relationship was higher in Group II than in Group I.

Relative growth rate can also be analyzed in terms of net photosynthetic rate, SLA and leaf weight ratio. Among these parameters, SLA is known to have a positive relationship with RGR (Reich et al. 1997, Reich et al. 1998a, Wright and Westoby 2000). We observed a positive relationship between SLA and RGR when Groups I and II were considered together (Figure 3); however, when Groups I and II were analyzed separately no significant regression was observed in either group, indicating that SLA does not explain the differences in RGR among our species. We found a closer relationship between A and SLA than between SLA and RGR (Figure 3). This may indicate that RGR is regulated not only by CO_2 assimilation, but also by other factors including carbohydrate accumulation, carbohydrate distribution, and nitrogen. The relationship between SLA and A differed between Groups I and II: the SLA-A relationship in Group I was not significant at the 0.1% level ($r^2 = 0.242$), whereas the relationship was significantly

related at the 0.1% level ($r^2 = 0.415$) in Group II.

Photosynthesis is dependent on many enzymes, including Rubisco, and a strong positive relationship between N concentration and A, at least at the leaf level, has been documented (e.g., Gulmon and Chu 1981, Field and Mooney 1986, Hirose

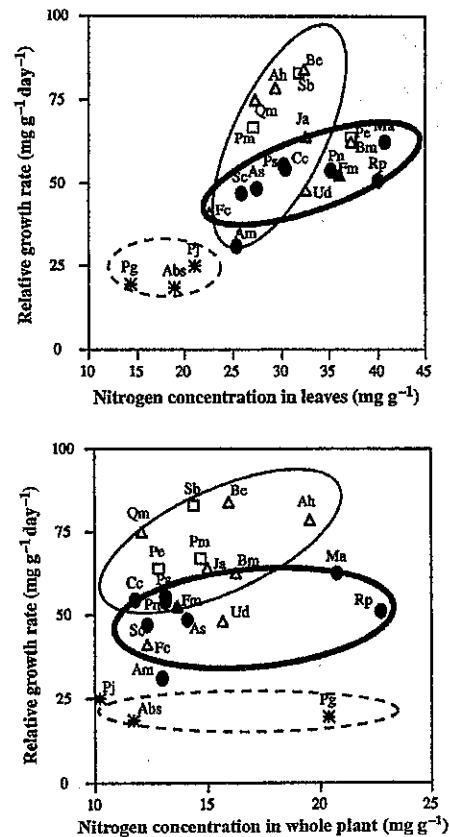


Figure 2. Relationships between relative growth rate (RGR; $\text{mg g}^{-1} \text{day}^{-1}$) and leaf nitrogen concentration (N_{leaf} ; mg g^{-1}) and whole-plant nitrogen concentration (N_{total} ; mg g^{-1}). Regressions of the relationships were: Group I: $\text{RGR} = 1.07 \times 10^{-4} \times \text{leaf Nc} + 1.81 \times 10^{-3}$, $r^2 = 0.452^*$; and $\text{RGR} = 7.27 \times 10^{-5} \times \text{total Nc} + 3.97 \times 10^{-3}$, $r^2 = 0.109^{\text{NS}}$; Group II: $\text{RGR} = 6.79 \times 10^{-5} \times \text{leaf Nc} + 4.59 \times 10^{-3}$, $r^2 = 0.048^{\text{NS}}$; $\text{RGR} = 2.20 \times 10^{-4} \times \text{total Nc} + 3.43 \times 10^{-3}$, $r^2 = 0.120^{\text{NS}}$; and Group III: $\text{RGR} = 6.45 \times 10^{-5} \times \text{leaf Nc} + 9.10 \times 10^{-4}$, $r^2 = 0.408^{\text{NS}}$; $\text{RGR} = -3.03 \times 10^{-5} \times \text{total Nc} + 2.51 \times 10^{-3}$, $r^2 = 0.241^{\text{NS}}$. An asterisk indicates significance at the 5% level; NS = not significant. Bold line includes Group I, thin line includes Group II and dotted lines includes Group III.

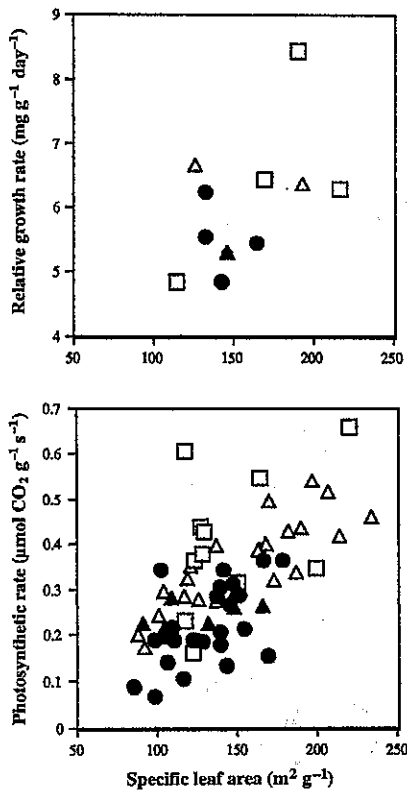


Figure 3. Relationships between relative growth rate (RGR; mg g⁻¹ day⁻¹) and specific leaf area (SLA; m² g⁻¹) and net photosynthetic rate (*A*; μmol CO₂ g⁻¹ s⁻¹). Symbols: ▲ = Asteridae, ● = Rosidae, △ = Dilleniidae and □ = Hamamelidae. Regressions of the relationships were: Group I: $RGR = -1.45 \times 10^{-2} \times SLA + 7.55$, $r^2 = 0.140^{NS}$; $A = 1.57 \times 10^{-3} \times SLA + 2.42 \times 10^{-2}$, $r^2 = 0.242^{**}$; and Group II: $RGR = 1.41 \times 10^{-2} \times SLA + 4.13$, $r^2 = 0.242^{NS}$; $A = 1.99 \times 10^{-3} \times SLA + 7.06 \times 10^{-2}$, $r^2 = 0.415^{***}$. Significance values: *** = significant at 0.1% level, ** = significant at 1% level and NS = not significant.

and Kitajima 1986, Evans 1989). The $A-N_{leaf}$ relationship was positive in Group II, but no significant relationship was observed in Group I (Figure 4). Thus, compared with the significantly positive RGR- N_{leaf} relationship among groups, there was no clear $A-N_{leaf}$ relationship. There was a positive relationship between A and R in Group II, but no clear relationship between A and R was observed in Group I (Figure 5). The R/A ratio was higher in Group I than in Group II, which is consistent with the data of Koike (1988a), who classified trees by their successional traits. Species in Group I belong to mid- or late successional species, and species in Group II belong to early successional species (Koike 1988a). Early successional species have higher photosynthetic rates, but shorter leaf longevities and thicker leaves than late successional species. Leaf longevity is an important parameter because of its relationships with tree growth and N nutrition (Larcher 1995). Compared with leaves of short longevity, long-lived leaves have considerably higher energy requirement in terms of construction costs for compounds such as protein, lipid, lignin and secondary compounds, which makes the leaves more sclero-

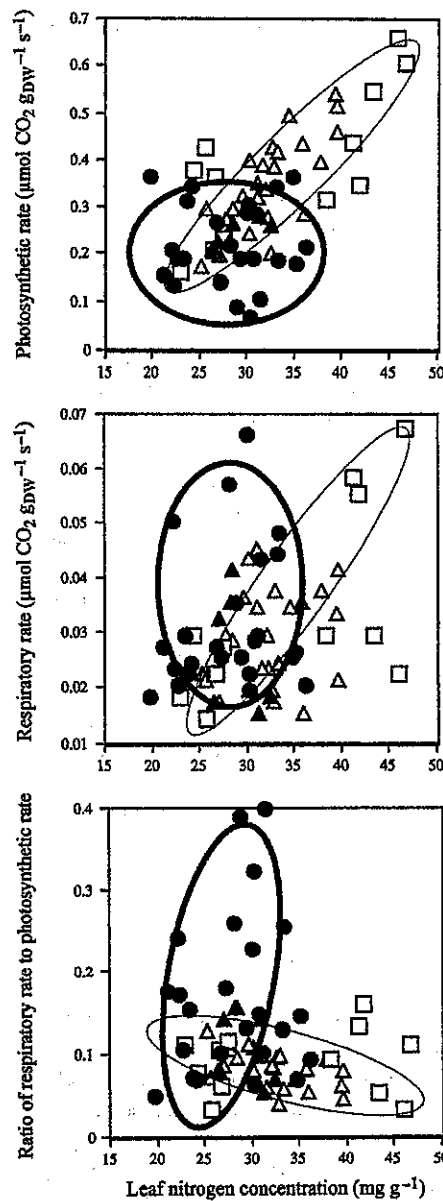


Figure 4. Relationships between leaf nitrogen concentration (mg g⁻¹) and net photosynthetic rate (A ; μmol CO₂ g_{DW}⁻¹ s⁻¹), respiratory rate (R ; μmol CO₂ g_{DW}⁻¹ s⁻¹) and R/A ratio. Regressions of the relationships were: Group I: $A = 4.81 \times 10^{-4} \times N_{leaf} + 2.14 \times 10^{-2}$, $r^2 = 0.001^{NS}$; $R = 3.08 \times 10^{-4} \times N_{leaf} + 2.20 \times 10^{-2}$, $r^2 = 0.012^{NS}$; R/A ratio = $1.64 \times 10^{-3} \times N_{leaf} + 0.110$, $r^2 = 0.006^{NS}$; and Group II: $A = 1.44 \times 10^{-2} \times N_{leaf} - 0.109$, $r^2 = 0.458^{***}$; $R = 1.03 \times 10^{-3} \times N_{leaf} - 3.74 \times 10^{-3}$, $r^2 = 0.278^{***}$; R/A ratio = $-5.04 \times 10^{-4} \times N_{leaf} + 0.103$, $r^2 = 0.110^{NS}$. Significance values: *** = significant at 0.1% level and NS = not significant. Bold line includes Group I and thin line includes Group II.

morphic; however, the prolonged leaf life span contributes to more carbon gain. Koike (1988b), in a comparison of several tree species, reported that the longevity of an individual leaf is linked to A . We found that, at the same N_{leaf} or N_{total} , RGR was higher in Group II than in Group I (Figure 4). This is consistent

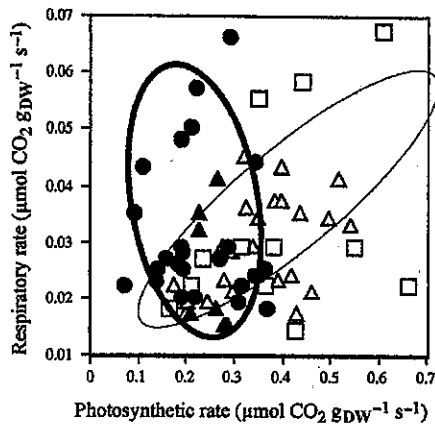


Figure 5. Relationship between net photosynthetic rate (A : $\mu\text{mol CO}_2 \text{ gDW}^{-1} \text{ s}^{-1}$) and respiratory rate (R : $\mu\text{mol CO}_2 \text{ gDW}^{-1} \text{ s}^{-1}$). Regressions of the relationships were: Group I: $R = 1.31 \times 10^{-3} \times A + 3.00 \times 10^{-2}$, $r^2 = 0.001^{\text{NS}}$; and Group II: $R = 4.19 \times 10^{-2} \times A + 0.145$, $r^2 = 0.171^*$. An asterisk indicates significant at 5% level and NS = not significant. Bold line includes Group I and thin line includes Group II.

with our observation that R/A was lower in Group II than in Group I, even at high N_{leaf} values (Figure 5).

The finding that N-production efficiency contributed mostly to RGR in all groups, and N-distribution ratio to leaf contributed to RGR in Groups I and II (Figure 6), indicates that N allocation to leaves partly determines the regulation of dry matter production. The importance of allocation and reallocation of N to leaves to maximize carbon gain is well known (Field and Mooney 1986). For example, in annual crops, productivity is regulated by N content (i.e., Rubisco content) and leaf duration (Osaki et al. 1993).

We conclude that the tree species investigated can be characterized into three groups based on parameter analysis of

RGR and various N traits. This classification was confirmed by the relationships between RGR and photosynthesis and respiration, and by the R/A ratio. Groups I and II both comprised deciduous broad-leaved trees, but they were separated into two groups based on traits that were consistent with their classification as mid- or late successional species and early successional species, respectively. Group III comprised coniferous trees that differ in many traits from the other groups.

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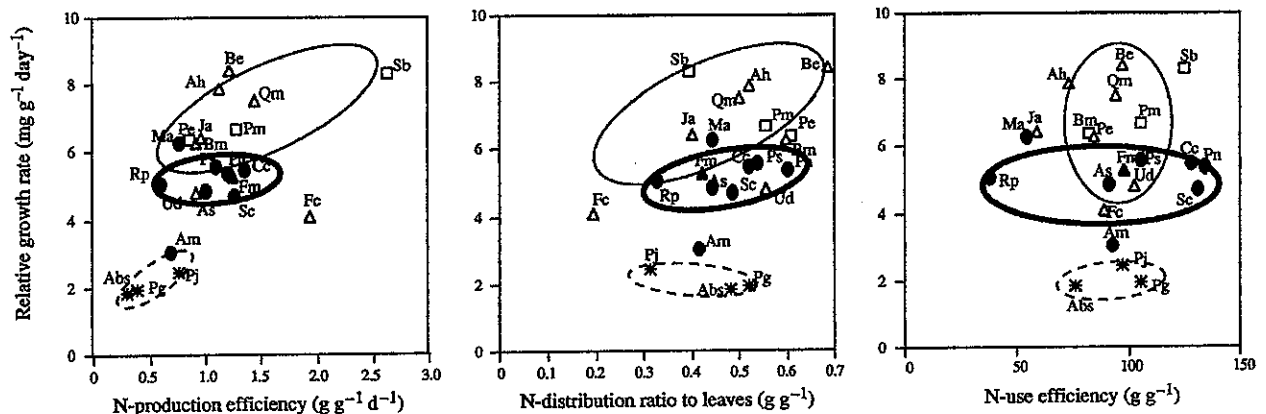


Figure 6. Relationship between relative growth rate (RGR: $\text{mg g}^{-1} \text{ day}^{-1}$) and N-production efficiency ($\text{g g}^{-1} \text{ day}^{-1}$), N-distribution ratio to leaf (g g^{-1}) and 1/N-use efficiency (g g^{-1}). Regressions of the relationships were: Group I: $\text{RGR} = 8.97 \times 10^{-4} \times \text{N-production efficiency} + 4.15 \times 10^{-3}$, $r^2 = 0.079^{\text{NS}}$; $\text{RGR} = 3.06 \times 10^{-3} \times \text{N-distribution ratio to leaf} + 3.63 \times 10^{-3}$, $r^2 = 0.080^{\text{NS}}$; $\text{RGR} = -2.91 \times 10^{-6} \times \text{N-use efficiency} + 5.34 \times 10^{-3}$, $r^2 = 0.012^{\text{NS}}$; Group II: $\text{RGR} = 4.86 \times 10^{-4} \times \text{N-production efficiency} + 6.05 \times 10^{-3}$, $r^2 = 0.037^{\text{NS}}$; $\text{RGR} = 4.62 \times 10^{-3} \times \text{N-distribution ratio to leaf} + 4.39 \times 10^{-3}$, $r^2 = 0.208^{\text{NS}}$; $\text{RGR} = 1.43 \times 10^{-5} \times \text{N-use efficiency} + 5.40 \times 10^{-3}$, $r^2 = 0.035^{\text{NS}}$; and Group III: $\text{RGR} = 1.36 \times 10^{-3} \times \text{N-production efficiency} + 1.42 \times 10^{-3}$, $r^2 = 0.996^*$; $\text{RGR} = -2.94 \times 10^{-3} \times \text{N-distribution ratio to leaf} + 3.37 \times 10^{-3}$, $r^2 = 0.904^{\text{NS}}$; $\text{RGR} = 8.66 \times 10^{-6} \times \text{N-use efficiency} + 1.27 \times 10^{-3}$, $r^2 = 0.146^{\text{NS}}$. An asterisk indicates significance at the 5% level and NS = not significant. Bold line includes Group I, thin line includes Group II and dotted lines includes Group III.

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