

1 **Tight coupling between leaf area index and foliage N content in arctic plant**
2 **communities**

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1 **Abstract**

2 The large spatial heterogeneity of arctic landscapes complicates efforts to quantify key
3 processes of these ecosystems, for example productivity, at the landscape level. Robust
4 relationships that help to simplify and explain observed patterns, are thus powerful tools for
5 understanding and predicting vegetation distribution and dynamics. Here we present the same
6 linear relationship between leaf area index and total foliar nitrogen, the two factors
7 determining the photosynthetic capacity of vegetation, across a wide range of tundra
8 vegetation types in both Northern-Sweden and Alaska between leaf area indices of 0 and 1 m²
9 m⁻², which is essentially the entire range of leaf area index values for the Arctic as a whole.
10 Surprisingly, this simple relationship arises as an emergent property at the plant community
11 level, whereas at the species level a large variability in leaf traits exists. As the relationship
12 between LAI and foliar N exists among such varied ecosystems, the arctic environment must
13 impose tight constraints on vegetation canopy development. This relationship simplifies the
14 quantification of vegetation productivity of arctic vegetation types as the two most important
15 drivers of productivity can now be estimated reliably from remotely sensed NDVI images.

16

17 **Keywords:** arctic ecosystems, productivity, vascular plants

1 **Introduction**

2

3 Arctic terrestrial ecosystems are important components of the global C cycle (Callaghan and
4 Maxwell 1995; Oechel et al. 1993), and, of all terrestrial vegetation types, are expected to
5 undergo the greatest degree of future climate change (Maxwell 1992; Chapin et al. 1995).
6 However, the Arctic is a mosaic of diverse ecosystems; its plant communities differ in
7 species, growth form, biomass, and productivity (Bliss et al. 1981; Shaver et al. 1996), and its
8 soils vary in organic matter content, nutrient stocks, depth to permafrost, and depth to water
9 table (Giblin et al. 1991; Walker and Everett 1991; Walker et al. 1994). Despite this
10 variability, previous research in the Alaskan Arctic indicated a relatively strong correlation
11 between plant community level leaf area index (LAI, m^2 leaf area m^{-2} ground area) and foliar
12 nitrogen (N, g N m^{-2} ground area) (Williams and Rastetter 1999), the key vegetation
13 parameters controlling carbon uptake via photosynthesis in Arctic environments during the
14 growing season. We set out to investigate the existence and generality of this correlation by
15 collecting new data in the arctic of Northern Sweden, and by analyzing the previously
16 collected data in more detail, at both the community and the species level. The tundras in the
17 two regions differ in species and plant type composition, biomass, productivity, climate, and
18 geology (Walker et al. 1995; Walker et al. 1989; Shaver and Jonasson 1999; Graglia et al.
19 2001; Michelsen et al. 1996; Van Wijk et al. 2004). In comparing these two regions, we tested
20 whether the LAI- foliar N correlation is a local phenomenon, or whether it is a more general
21 emergent property in arctic plant communities.

22

1 **Materials and methods**

2

3 Near Toolik Lake (68°38'N, 149°34'W, elevation 720 m), Alaska, between 19-26 July 1997,
4 and near Abisko (68°21'N, 18°49'E, above the tree line, elevation between 540 and
5 1000 m), Sweden, between 15-30 July 2002, different dominant arctic vegetation types were
6 sampled in 20 by 20 cm quadrats. Climatic information about the two regions is given in
7 Table 1.

8 The Alaskan sites were selected in such a way that the whole range of vegetation types
9 occurring in the northern foothills of the Brooks Range were represented in the dataset. The
10 vegetation types were wet sedge tundra, tussock tundra, heath tundra, and shrub tundra. The
11 Alaskan data were published earlier in a summarized form (Williams and Rastetter 1999).
12 Also in Northern Sweden, the most important vegetation types were defined and sampled in
13 an area of 5 km². The most important vegetation types here were heath tundra, shrub tundra,
14 wet sedge tundra and peat tundra. For both regions the individual quadrats were located in
15 separate spatial clusters of the different vegetation types within the area to avoid possible
16 problems with pseudoreplication. The distance between the sample points was highly
17 variable, but never smaller than 4 m. Peat tundra in Sweden was less abundant than the other
18 vegetation types around Abisko above the tree line, therefore only 5 independent samples
19 (meaning not within the same spatial cluster of a vegetation type) could be taken. Care was
20 taken that for each vegetation type the samples were distributed in such a way that the whole
21 range of vegetation densities present was sampled.

22 We sampled 94 20 by 20 cm quadrats in the Toolik Lake region and 92 quadrats in the
23 Abisko region. Of each of the harvested 20 by 20 cm quadrats, we removed and separated
24 green foliage by species (except graminoids, which were sampled as a combined group). In

1 total we sampled 24 plant species in the Abisko region and 26 plant species in the Toolik
2 Lake region. We did not collect woody material. We determined one-sided projected leaf area
3 of vascular plants using a Li-Cor LI-3000 leaf area meter in Alaska, and with a camera (JVC
4 TK-S310) and accompanying software (Delta-T digital Analysis System, version 1.1) in
5 Sweden. All samples were oven-dried at 60°C for 3 days, weighed, and %N determined in a
6 Perkin-Elmer CHN analyzer. For %N determination we selected the minimum set of species
7 that accounted for 85% of the total leaf area at each quadrat (mean number of species sampled
8 per quadrat = 4.9). For those species at a site that were not sampled for %N (because for these
9 species there was not enough leaf biomass to be able to determine %N) we made estimates
10 using the N concentration determined for that species at a nearby location. We calculated total
11 foliar N per ground area in each quadrat for each site, using data on foliar N concentration (%
12 by mass) and leaf mass per ground area (g m^{-2}).

13

1 Results

2

3 The vegetation types we investigated in this study are different in the contributions that the
4 several plant types made to the total leaf area of the vascular plant communities (Table 2).

5 The wetland vegetation type is dominated by graminoid plant species (especially *Carex* and
6 *Eriophorum* species). The shrub vegetation type is dominated by deciduous shrubs (especially
7 *Betula nana* and *Salix* species), whereas the heath vegetation type is dominated by both
8 evergreen (especially *Vaccinium vitis-idea*, *Empetrum nigrum* and in Alaska *Ledum palustre*)
9 and deciduous shrubs (especially *Betula nana*). The Alaskan tussock tundra is a mixture of the
10 aforementioned graminoid, evergreen and deciduous species. In the Swedish peat systems
11 *Rubus chaemaemorus* is also very important.

12 Despite this large difference in plant type composition between the vegetation types
13 investigated, we found for both regions a very strong relationship between site LAI and total
14 vascular-plant foliar N per ground area (Fig. 1A). For the two regions the measurements of
15 site LAI and total vascular-plant foliar N per ground area show the same relationship for LAI
16 values up to $1 \text{ m}^2 \text{ m}^{-2}$ (Fig 1A; linear regression lines for LAI up to $1 \text{ m}^2 \text{ m}^{-2}$ are for Sweden y
17 $= 1.87x$ and for Alaska $y = 1.95x$; difference in slope is not statistically significant). In the
18 foliar N versus leaf biomass scatter plot, clear data-clustering was visible among individual
19 regions and different vegetation types (Fig 1B), whereas this clustering was absent for the
20 foliar N versus LAI scatter plots.

21 The strong coupling between foliar N and LAI is absent at species level, as is shown
22 by the large range of values for the key variable foliar N per unit leaf area (NLA; Table 3).
23 There were also strong differences in other important leaf traits at species level like specific
24 leaf area (SLA) and foliar N per unit leaf mass (NLM). For each individual species a

- 1 consistent value of NLA can be derived with a relatively low uncertainty, but between species
- 2 there are clear consistent differences (Fig 2A and B).

1 **Discussion**

2

3 The tight correlation of the data up to LAI $1 \text{ m}^2 \text{ m}^{-2}$ in both regions shows that the arctic
4 vegetation types seem to control the relative amounts of canopy N and leaf area within similar
5 constraints, and suggests a single controlling process for the pan-Arctic region. This
6 relationship up to LAI-values of $1 \text{ m}^2 \text{ m}^{-2}$ covers essentially the entire range of LAI-values
7 that occurs in the Arctic as a whole. This means that we can predict foliar N from LAI
8 estimates using a relationship that has a coefficient of determination that is unusually high for
9 ecological data. This tight correlation at community level occurs along a whole range of
10 vegetation types with different species composition, both within and between the two regions,
11 and despite the differences in climate (see Table 1 and Van Wijk et al. (2004)) between the
12 two regions. As the slopes of the regression lines are not significantly different, the same
13 relationship can be used for both regions to predict leaf nitrogen from the variable LAI.

14 The LAI-N relationship would not be surprising if it occurred in a plant canopy with a
15 single species (e.g. Field and Mooney 1986; Field 1983), but this study shows that the
16 relationship exists over a variety of arctic community types with different groups of species.
17 An important conclusion of this work is that because the relationship between LAI and foliar
18 N is so tight across a range of LAI values and among such varied functional plant types, the
19 arctic environment must impose tight constraints on vegetation canopy development. The
20 latitude of the two regions is similar, maybe suggesting that radiation is the determining factor
21 controlling the relationship between LAI and foliar N, although there could be differences in
22 cloudiness between the two regions. It would be interesting to make the same measurements
23 in similar arctic vegetation but at different latitudes (e.g. at Svalbard, or at an alpine system at
24 lower latitude, for example in southern Norway). As LAI and foliar N are the key biotic

1 controls on ecosystem carbon accumulation via photosynthesis, the coupling results in a tight
2 control of ecosystem photosynthetic capacity, independent of species composition.

3 Surprisingly, the signature of this control only shows up at the community level;
4 important individual species in both arctic regions showed clear differences in their leaf traits.
5 The tight LAI – foliar N relationship at the community level is an emergent property, arising
6 out of the complex interactions of individual plants, which one would not expect to occur
7 given the large variability at the species level. The whole range of arctic plant communities
8 investigated here, despite having different species composition and different dominant
9 species, are composed of plant species in such a way that the overall community LAI – foliar
10 N value remains close to 1.90 g N m^{-2} leaf area (Fig 1A). Somehow, plant communities are
11 never composed solely of plant species with low or high NLA values.

12 The small data set on individual species present in both Sweden and Alaska (Table 2),
13 suggests that, compared to the measurements of Sweden, higher N per leaf mass values in
14 Alaska are offset by higher specific leaf area values, thereby resulting in more similar N per
15 leaf area values (see Table 3; data of *B. nana*, *V. vitis-idea* and *V. uliginosum*). This implies
16 that it is the higher rate of change in leaf area with change in leaf mass that brings the Alaskan
17 data into line (Fig. 1A), and the reverse for the Swedish data.

18 The conclusion that plant communities are never composed solely of plant species
19 with low or high NLA values is also important when Figures 1 and 2 are compared. If we
20 compose plant communities of a certain LAI artificially by taking randomized draws of the
21 plant characteristics of species present in the Arctic, this also results in an average slope of
22 LAI – foliar N relationship at community level of 1.90 g N m^{-2} leaf area. However, the spread
23 around this line using such a randomizer is larger than the spread shown in reality, as also
24 communities are formed with species that have similar low or high NLA values. Such a

1 randomizer for example results in values of the community foliar N values at an LAI of 0.5
2 $\text{m}^2 \text{m}^{-2}$ between the extremes of 0.45 and 1.65 g m^{-2} ground area, a range that is more than
3 two times the range found in the field.

4 If we consider the three components of Table 3, we can define the following
5 relationship:

$$6 \quad \text{TFN} = \text{NLM} * \text{LMA} * \text{LAI}$$

7 Where TFN is Total Foliar Nitrogen (g m^{-2}). The relatively tight relation between TFN and
8 LAI as shown in Fig 1A means that at ecosystem level NLM and LMA are negatively
9 correlated. This was already known for individual plant species (e.g. Wright et al 2004), but
10 here is shown that this correlation also exists at ecosystem level across a range of LAI values
11 in the Arctic.

12 The difference in coupling between foliar N and LAI, and foliar N and leaf biomass
13 (Fig 1) shows that the tight coupling between LAI and foliar N is not just simply an auto-
14 correlation. At the community level, there is a much stronger coupling of the plant functional
15 characteristics LAI, important for radiation interception, and foliar N, an important indicator
16 of photosynthetic capacity, than with a structural variable like leaf mass. The much tighter
17 relationship between LAI and foliar N is remarkable from a measurement point of view, as
18 the leaf mass together with leaf nitrogen content of individual species determines total foliar
19 N, whereas foliar N and LAI are more independent measurements.

20 The occurrence of the LAI - Foliar N relationship over a wide range of different
21 vegetation types in two different regions shows that these communities seem to balance the
22 relative costs and benefits of C and N in much the same way. Previous studies in the Arctic
23 have indicated niche differentiation in plant nitrogen uptake: plant species have been shown to
24 differ in the chemical form in which they capture nitrogen, as well as in the timing and in the

1 spatial distribution of this capture (McKane et al. 2002). It has also been shown that in
2 herbaceous plant communities in temperate regions, different morphological strategies for
3 light capture can result in similar efficiencies in terms of light ‘foraging’ (Hirose and Werger
4 1995; Anten and Hirose 1999). However, our data suggest that at the plant community level in
5 arctic systems, there is only one optimal relationship between leaf area and amount of N in the
6 canopy. The tight relationship indicates that nutrient availability limits the total amount of
7 foliage that can be produced and sustained, while the strong competition for the capture of
8 light assures that this upper limit for leaf area is attained. If this relationship is truly
9 conservative, there are important implications for the response of current arctic plant
10 communities to global change. Any response will be restricted so that the novel canopy
11 structure conforms to the relationship we have observed, and thereby to the tight control on
12 productivity. The close relationship between LAI and N is also of interest because it aids our
13 interpretation of remotely sensed vegetation data and simplifies the information required to
14 generate landscape-level predictions of canopy production (Williams et al. 2001). In the latter
15 case, LAI data can be used to infer canopy foliar N up to LAI values of around $1 \text{ m}^2 \text{ m}^{-2}$. The
16 existence of a linear relationship between LAI and foliar N simplifies the task of generating a
17 regional C budget, because it removes the need for species level data and for chemical
18 analyses of foliage. Furthermore, Williams et al. (2001) showed that the slope of the LAI-N
19 relationship has a relatively large effect on the GPP predicted at landscape level: a shift of 1
20 SE (standard error) of the slope of the LAI-N regression line resulted in a change of 8-9% in
21 predicted landscape level GPP. The implication of the study presented in this paper is that we
22 can use the same relationships as in Williams et al. (2001) to make predictions along
23 continents.

1 For LAI values greater than $1 \text{ m}^2 \text{ m}^{-2}$ the relationships for the two regions slightly
2 deviate, mainly because of the curvature of the LAI and foliar N relationship found in Alaska
3 (Fig 1A). The deviation between the regions at higher LAI-values indicates that the tight
4 control of foliar N and LAI is only present in situations in which nutrients are the most
5 important limiting factor in the ecosystems; at higher foliar N and higher LAI values other
6 factors also come into play, and the relationships in the two regions deviate. There are various
7 explanations possible for this deviation, and they will have to be tested in future research.
8 First, the deviations may be caused by permafrost in the Alaskan tundra. In terms of
9 optimization of carbon this could mean that at certain values of N in the ecosystem,
10 investment of plant C into roots is not effective anymore in the Alaskan tundra, and relative
11 investment in leaves can be increased, whereas this belowground limitation is absent in
12 northern-Sweden. A second factor could be the difference in climate (see Table 1); possibly
13 this difference does not lead to large deviations in LAI versus foliar N tradeoffs at low leaf
14 area values, but at larger values it could be that differences in photosynthesis and respiration
15 caused by the differences in for example air temperature lead to other values of C and N
16 allocation (Körner 1989). A third explanation could be the difference in carbon investment by
17 the plant in secondary components in more productive vegetation. Craglia et al. (2001)
18 showed that the phenolics concentration in *Betula nana* leaves was significantly higher in
19 Swedish tundra, possibly caused by heavier grazing, as compared to the Alaskan tundra. A
20 fourth possible explanation could be differences in soil nitrogen cycling and hydrology
21 between the two regions. The Toolik Lake region is characterized by permafrost and thick
22 layers of organic matter in the soil, whereas in the Abisko region there is permafrost only in
23 some small bog areas near Lake Torneträsk and the soil is generally characterized by good
24 drainage (Jonasson et al. 1999).

1 Until now, as far as we know, no other consistent comparisons of leaf nitrogen and
2 leaf area over different ecosystems exist. This is mainly due to the difficulty of measuring in a
3 reliable manner total living leaf area and total leaf nitrogen of an ecosystem; we have not
4 found individual datapoints for other ecosystems in which both variables were quantified at
5 ecosystem level; always only parts of the ecosystem were measured. The divergence of the
6 Abisko and Toolik datasets at higher LAI-values suggests that the tight relationship between
7 leaf nitrogen and leaf area breaks down at nutrient richer systems, but further research must
8 be performed to confirm this.

9

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1 **Table 1: Climate information for the Toolik Lake and Abisko regions**

2

Region	Annual precipitation (mm) (percentage that falls as snow)	Average annual temperature (°C)	Average January temperature (°C)	Average July temperature (°C)
Abisko, Sweden	225 – 475 (47%)	-1	-12	11
Toolik Lake, Alaska, USA	200 – 400 (45%)	-10	-24	14

3

1 **Table 2: Contribution in percentages to total plant community leaf area by the dominant**
 2 **plant types in the vegetation types investigated in this study**

3

Vegetation type	Plant type	Percentage of total leaf area of the vascular plant community	
		Alaska	Sweden
Wetland	Graminoids	85 – 90	85 – 95
	Pteridophytes	0 – 10	0 – 5
Shrubs	Deciduous	70 – 100	60 – 90
	Evergreen	0 – 30	10 – 35
Heath	Evergreen	35 – 60	45 – 100
	Deciduous	30 – 60	0 – 50
Tussock tundra	Graminoids	10 – 60	-
	Evergreen	30 – 60	-
	Deciduous	5 – 40	-
Peat tundra	Deciduous	-	25 – 70
	Graminoids	-	20 – 40

1 **Table 3: Leaf traits of important plant species in Alaska and Sweden: Specific leaf area**
 2 **(SLA), foliar nitrogen per unit leaf area (NLA) and foliar nitrogen per unit leaf mass**
 3 **(NLM); given are mean and between parentheses the standard error**
 4

Species (nr of replicates)	Plant type	SLA [$10^{-4} \text{ m}^2 \text{ g}^{-1}$]	NLA [g m^{-2}]	NLM [10^{-3} g g^{-1}]
Alaska				
<i>Betula nana</i> (26)	deciduous	144 (5)	1.50 (0.09)	20 (1)
<i>Vaccinium vitis-idea</i> (44)	evergreen	65 (2)	1.46 (0.11)	9.2 (0.4)
<i>Vaccinium uliginosum</i> (16)	deciduous	145 (5)	1.34 (0.09)	19 (1)
<i>Ledum palustre</i> (38)	evergreen	65 (1)	2.10 (0.11)	14.2 (0.2)
<i>Arctostaphylus alpinus</i> (14)	deciduous	135 (1)	1.27 (0.11)	17.3 (0.1)
<i>Equisetum spec.</i> (10)	pteridophyte	55 (5)	3.32 (0.22)	17.1 (0.2)
Sweden				
<i>Betula nana</i> (50)	deciduous	100 (2)	1.72 (0.03)	17.0 (0.3)
<i>Vaccinium vitis-idea</i> (36)	evergreen	53 (3)	1.42 (0.04)	7.4 (0.2)
<i>Vaccinium uliginosum</i> (56)	deciduous	104 (2)	1.43 (0.03)	14.7 (0.3)
<i>Empetrum nigrum</i> (62)	evergreen	41 (1)	2.21 (0.04)	8.8 (0.2)
<i>Andromeda polifolia</i> (45)	evergreen	57 (3)	2.14 (0.07)	12.0 (0.2)
<i>Carex bigelowii</i>	graminoid	76 (6)	2.5 (0.2)	16 (1)
<i>Equisetum spec.</i> (18)	pteridophyte	56 (4)	3.17 (0.24)	16.6 (0.5)

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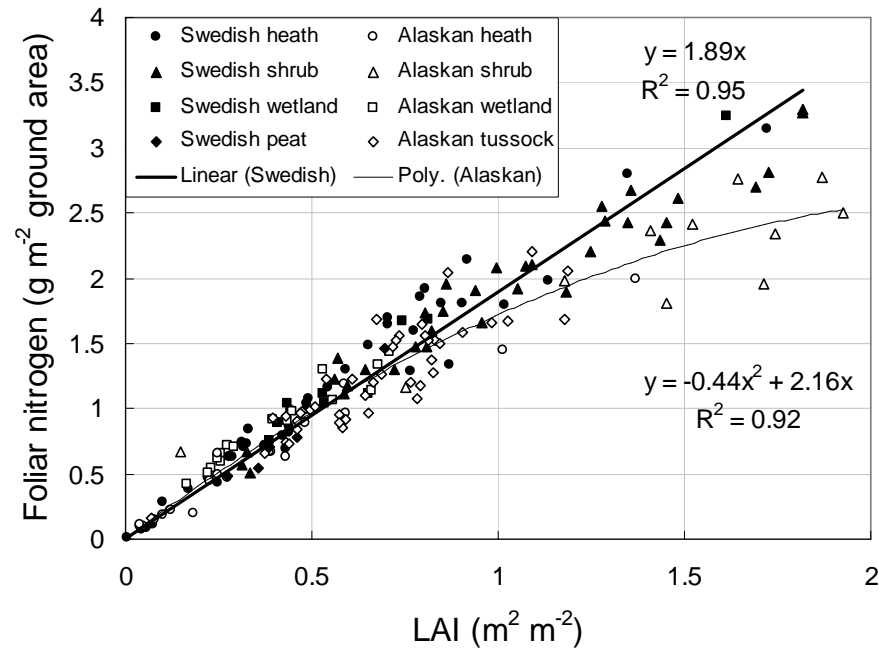
1 **Figure captions**

2

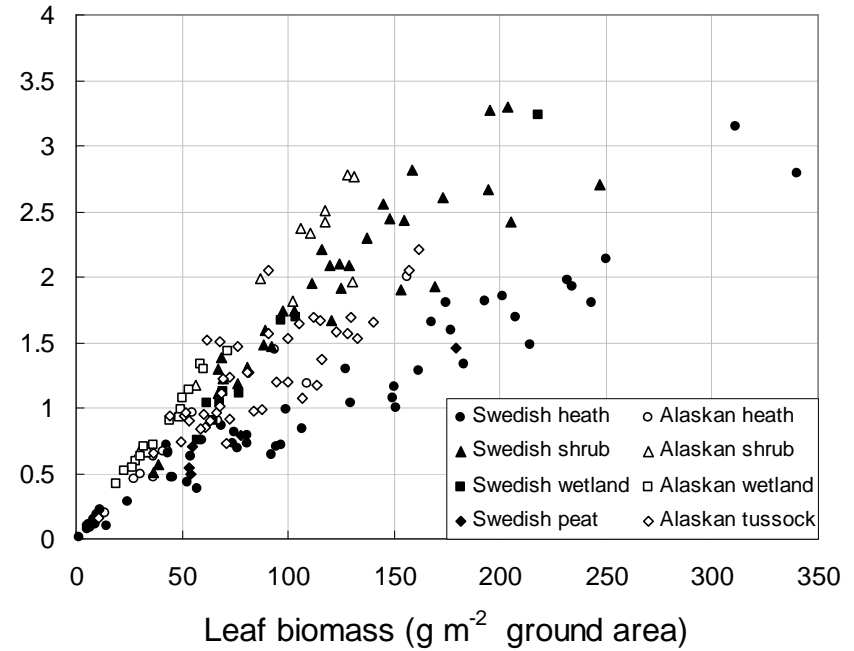
3 Figure 1: Relationships between total vascular plant foliar N and leaf area index (A) and
4 total vascular plant foliar N and leaf mass (B) for both Alaska and northern
5 Sweden; each data-point represents the results of a 20 by 20 cm quadrat

6 Figure 2: Scatter plots of foliar N and leaf area of key species of and the Abisko region (A)
7 and Northern-Alaska (B)

1 A

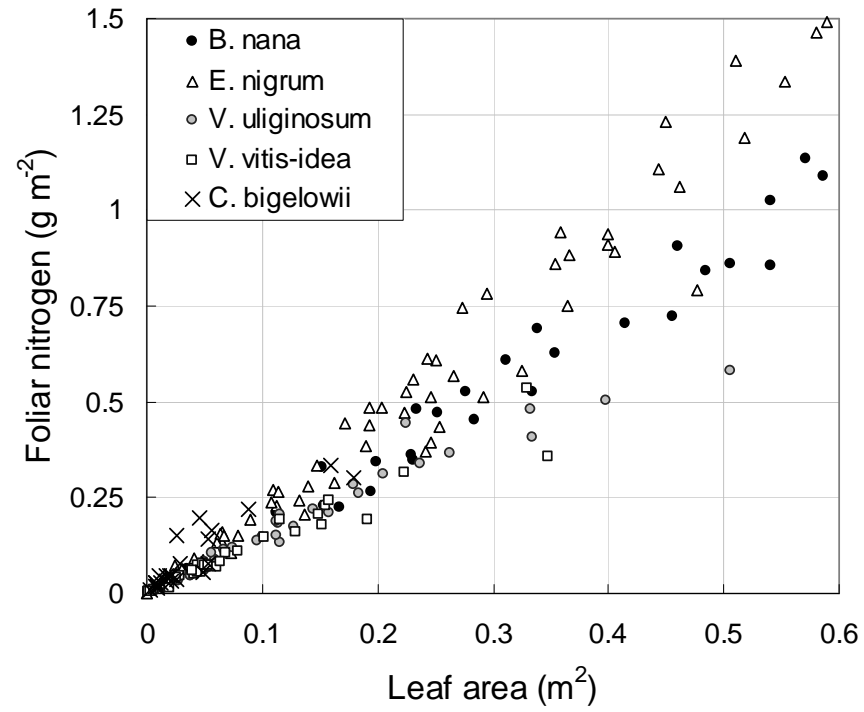


B

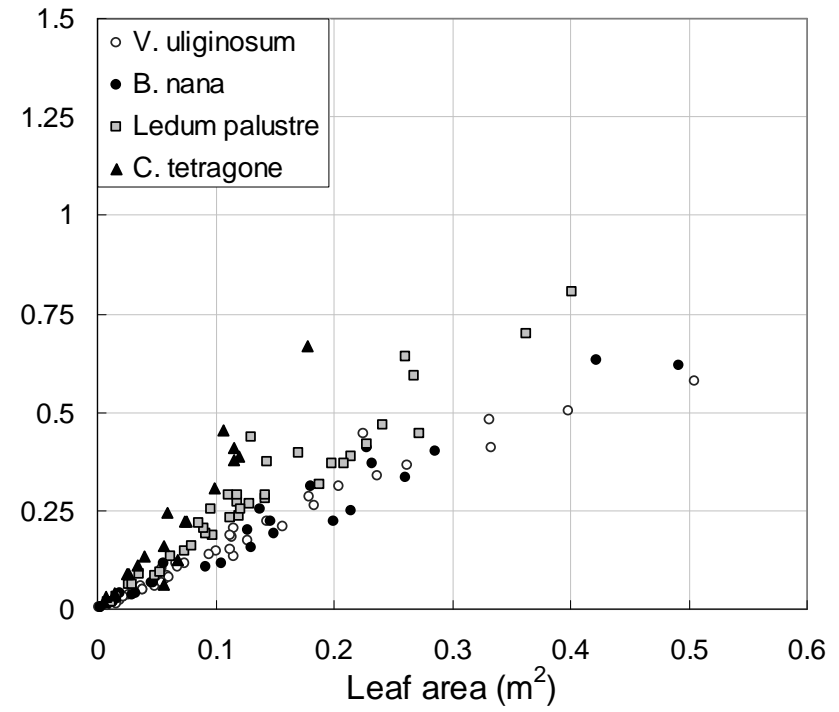


2
3 Figure 1

1 A



B



2
3
4

Figure 2