Estimating forest structure and shade tolerance of the species in a mixed deciduous broad-leaved forest in Abruzzo, Italy

Loretta Gratani & Irene Foti

Gratani, L. & Foti, I., Dipartimento di Biologia Vegetale, Università di Roma "La Sapienza", P. le A. Moro 5, I-00185 Rome, Italy

To explain the coexistence of plant species in a mixed deciduous broad-leaved forest in Abruzzo, Italy, a number of leaf traits were analyzed, and the shade tolerance was investigated. Bud break started at the end of April and the rapid leaf growth during the first stages was attested by the highest relative growth rates. The leaf area index (LAI) increased from 0.7 at the beginning of the leaf growth to 2.6 at full lamina expansion. Most of the species of the dominated layer were shade-tolerant and most of the species of the dominant and co-dominant layers were shade-intolerant. There was a fairly well defined specific leaf area (SLA) range between the shade-tolerant (271.1 cm^2 g^{-1}) and shade-intolerant species (159.2 cm^2 g^{-1}). The SLA, the chlorophyll content (Chl) and the leaf water content showed the same trend from the top to the bottom of the forest canopy. The chlorophyll *a/b* ratio ranged from 2.78 (dominant + co-dominant layers) to 2.95 (dominated layer). *Laburnum anagyroides* Medicus, one of the most shade-tolerant species (305.1 cm^2 g^{-1} SLA), showed the highest total chlorophyll content (2.69 mg g^{-1}) and *Quercus cerris* L.*,* one of the most shade-intolerant (148.2 cm^2 g^{-1} SLA), the lowest (0.70 mg g^{-1}).

Key words: chlorophyll content, LAI, plant biomass, RGR, RGR$_{LA}$, shade tolerance, SLA

INTRODUCTION

Barkman (1979, 1990) compared the utilitarian and fundamental floristic and structural classifications of forest and shrub communities, emphasizing the necessity of a structural classification, in addition to a floristic one. Kull *et al.* (1995) investigated models to describe foliage dry mass distribution among different layers of a community, and Tilman (1988) developed a theory to explain the coexistence of different plant species based on their ability to exploit environmental resources. Species within a community can be classified according to a number of structural and functional

traits (Montalvo *et al.* 1991, Reich *et al.* 1992, Orwig & Abrams 1995). When leaves are the chief element of interest, the vertical organisation of the foliage should be emphasized in addition to the distribution of individual stems and species within the forest (Parkhurst & Loucks 1972, Parker *et al.* 1989).

Different approaches treat the canopy in different ways and at various levels of complexity, so a detailed description of canopy structure would aid in comparing the approaches (Parker *et al.* 1989). Several reports (Wittner 1983, Pierce & Running 1988, Katsuno & Hozumi 1990, Welles 1990) identified the leaf area index (LAI) as the most important variable characterising vegetation energy and mass exchanges for global research. At a landscape scale, the LAI needs to be estimated across a range in canopy structure, land use patterns, and vegetation types (Sampson & Allen 1995).

Studies examining species in different light environments have reported altered leaf morphology (Carpenter & Smith 1981, Abrams & Kubiske 1990), and light is the environmental variable exerting the largest control on leaf morphology (Jarvis & Leverenz 1983). The specific leaf area (SLA) is known to vary vertically in a forest canopy (Tadaki 1970, Cermák 1989, Welles & Norman 1991, Niinemets 1995). Since the SLA is important in explaining differences in growth rate between species, it is imperative to obtain more insight into the interspecific variation (Van Arendonk & Poorter 1994). Knowledge of the quantitative relationships between light availability, the canopy structure and species composition may contribute to a more advanced indirect estimation of productivity (Niinemets 1995).

This study tested the hypothesis that the species which occupy similar canopy layers within a forest have morphological and physiological leaf traits that reflect species adaptation. In addressing this question, and explaining the coexistence of plant species in a mixed deciduous broad-leaved forest, this study develops a number of leaf traits that can be used to define the degree of shade tolerance among the species. Specialisation has allowed plant species to co-exist in the same forest; species with similar morphological and physiological traits reflect their evolutionary adaptation.

METHODS

Study site and climate

The study was carried out in a mixed deciduous broad-leaved forest dominated by *Quercus cerris* L. and *Q. pubescens* Willd., located at Macchia Grande, on the southern side of the Gran Sasso (Abruzzo, Italy, 42°25´N, 13°30´E, exposure SE, slope 15°, 1 100 m a.s.l.) (Barbagallo & Guglielmo 1975). The forest stand extends for ca. 350 ha.

Climatic data were provided by the Meteorological Station of Assergi (mean of the years 1960–1990). The total annual rainfall was 952 mm, most of it falling between October and December, and March and April. Maximum air temperature averaged 25.3°C (August), minimum air temperature averaged – 2.0°C (January) and temperatures below 0°C occurred from December to February.

Stand structure and plant biomass

Field measurements were carried out between 1994 and 1995. Measurements of the forest structure and plant biomass included plant height, plant diameter at breast height and at the base, stand density and total basal area.

Three sampling areas, 420 m^2, 100 m^2 and 100 m^2 respectively, were established in the forest. Non-destructive measurements were made within the two 100-m^2 sampling areas. Destructive measurements were carried out in the 420-m^2 sampling area. All plants in each area were measured and divided into diameter classes (≤ 1 cm; 1.1–3.0 cm; 3.1–5.0 cm … 27.1–29.0 cm). Three representative plants of each species in each class were harvested at random inside the 420-m^2 sampling area. Trees (subdivided into stem, branches and leaves) were weighed in the field, and fresh weights sub-sampled to enable conversion to a dry weight basis. Sub-samples were oven-dried at 105°C to a constant weight, and the conversion of field fresh weight to dry weight was carried out by the ratio of dry weight to fresh weight in the sub-samples, according to Bunce (1968) and Stewart *et al.* (1979).

Leaf area index (LAI)

The leaf area index of the forest was estimated during leaf growth from May to September by the LAI 2000 Plant Canopy Analyzer (LI-cor Inc., Lincoln, Nebraska, USA), according to Waring (1985), Gower and Norman (1991), Stenberg *et al.* (1994), Brenner *et al.* (1995), Morales *et al.* (1996) and Welles and Cohen (1996). Measurements were made below the canopy. The mean tilt angle of foliage (MTA) was determined with the same instrument, according to Welles and Norman (1991).

Leaf growth

Leaf samples were collected from the beginning of May (immediately after bud break) to the middle of September (full lamina expansion). On each sampling occasion, one hundred leaves were collected from the mean portion of the canopy of the three selected plants for each species. Measurements included the leaf surface area (measured by Image Analysis System Delta-T Devices, LTD, England), the leaf dry mass (oven-dried 90°C to constant weight), the specific leaf area of the whole lamina excluding the petiole (SLA, leaf area per unit leaf mass) according to Reich *et al.* (1992), the leaf water content, the relative growth rate (RGR) and the relative leaf area growth rate (RGR_{LA}) according to Fisher (1920) and Bazzaz and Harper (1977).

Leaf chlorophyll content

The chlorophyll content, at full lamina expansion (12 September), was analysed according to MacLachlan and Zalik (1963). Immediately after collection, the leaves were kept in a cool and dark place, and within 6 h the chlorophyll *a*, chlorophyll *b*, and total chlorophyll (*a* + *b*) contents were determined in triplicates. The leaves were grinded in acetone, and the homogenates were centrifuged in an A. L. C. 4237 R Refrigerate centrifuge. Absorbance of the supernatants was measured spectrophotometrically (Jasco model 7800).

RESULTS

Stand structure and plant biomass

The dominant layer of the forest, 15.3 ± 1.7 m tall, was constituted by *Quercus cerris* and *Q. pubescens*. The co-dominant layer, 13.1 ± 1.3 m tall, was characterized by *Fraxinus ornus* L., *Ostrya carpinifolia* Scop. and *Carpinus betulus* L. The dominated layer, 3.8 ± 0.9 m tall, was constituted by *Acer obtusatum* W. et K.*, Sorbus aria* (L.) Crantz,

Laburnum anagyroides Medicus, *Corylus avellana* L., *Crataegus monogyna* Jacq., *Cornus* spp., *Malus sylvestris* Miller, *Amelanchier ovalis* Medicus, *Rosa arvensis* Hudson, *Prunus spinosa* L., *Cytisus sessilifolius* L., *Ligustrum vulgare* L., *Euonymus verrucosus* Scop., and *Juniperus communis* L.

There were 29 060 plants ha^{-1} (Table 1). *Cornus* spp. and *Quercus cerris* dominated in terms of density, 29.4% and 22.1% respectively, and *Q. cerris* and *Q. pubescens* in terms of biomass (q ha^{-1}), 2 313.6 and 347.9 respectively (Table 2). The total basal area of the forest (sum of dominant, co-dominant and dominated layers) was 92.2 m^2 ha^{-1} (Table 1). The leaf biomass accounted for 2.1% of the total plant biomass (2 775.4 q ha^{-1}).

Leaf growth and leaf area index

Bud break started at the end of April–beginning of May in the co-dominant and dominated layers, and at the middle of May in the dominant layer. The rapid growth of leaves during the first stages after bud break was attested by the highest RGR (Fig. 1) and RGR_{LA} (Fig. 2). The dominated and co-dominant layers reached the full lamina expansion, attested by RGR ≈ 0 and RGR_{LA} ≈ 0.134 days after bud break, and the dominant layer 119 days after bud break.

The time of leaf growth was of importance in controlling the LAI. Since the LAI changed with leaf developmental stages, the maximum LAI was a good estimator of the leaf biomass accumulation. The LAI = 0.7 related to the first leaf growth stages and the LAI = 2.2 related to 90–96% of the full lamina expansion. The LAI = 2.6 corresponded to the full lamina expansion (Fig. 3) and it was representative of the 58.5 q ha^{-1} leaf bio-

Table 1. Plant density, height, total basal area, wood biomass, leaf biomass and total plant biomass of the dominant and co-dominant layers (D + CD) and of the dominated layer (Do).

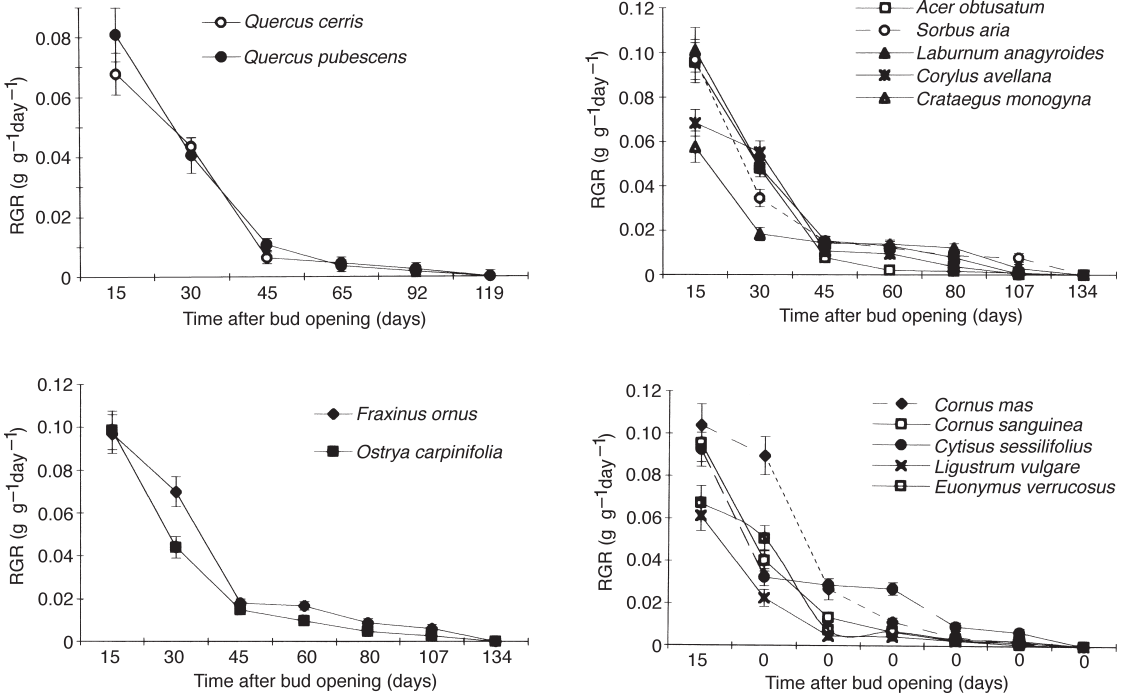|	D + CD layers (± SE)	Do layer (± SE)	Sum
Plant density (plant ha^{-1})	2 029.0 ± 197.2	27 031.0 ± 252.3	29 060.0
Height (m)	14.2 ± 1.5	3.8 ± 0.9	–
Total basal area (m^2 ha^{-1})	83.2 ± 12.1	9.0 ± 1.7	92.2
Wood biomass (q ha^{-1} above ground)	2 516.6 ± 280.4	200.3 ± 16.2	2 716.9
Leaf biomass (q ha^{-1})	38.4 ± 15.3	20.1 ± 8.5	58.5
Total plant biomass (q ha^{-1})	2 555.0 ± 295.7	220.4 ± 24.7	2 775.4

Fig. 1. Relative growth rate, g g^{-1} day^{-1} (RGR) during leaf growth of the most representative species of the forest. Vertical bars indicate standard error of the mean.

mass. The mean tilt angle of the forest foliage (35°), measured at full lamina expansion, indicated

Table 2. Plant biomass and percentage of plant density of the species.

Species	Biomass (± SE) q ha^{-1}	Plant density, %
Quercus cerris	2 313.59 ± 228.531	22.1
Q. pubescens	347.85 ± 57.235	3.3
Fraxinus ornus	10.65 ± 1.152	3.6
Ostrya carpinifolia	3.26 ± 0.936	0.3
Carpinus betulus	16.41 ± 1.726	1.4
Acer obtusatum	1.51 ± 0.091	0.2
Sorbus aria	4.07 ± 0.856	4.4
Malus sylvestris	0.45 ± 0.012	2.9
Laburnum anagyroides	0.72 ± 0.020	0.6
Corylus avellana	0.13 ± 0.063	0.2
Crataegus monogyna	0.53 ± 0.095	2.9
Cornus spp.	72.82 ± 8.520	29.4
Cytisus sessilifolius	1.42 ± 0.063	18.5
Ligustrum vulgare	0.15 ± 0.030	2.9
Euonymus verrucosus	0.31 ± 0.074	6.7
Prunus spinosa	0.06 ± 0.001	0.1
Juniperus communis	1.48 ± 0.232	0.3
Rosa arvensis	0.03 ± 0.001	0.1
Amelanchier ovalis	0.01 ± 0.001	0.1

that most of the leaves were horizontally oriented. The species of the dominant, co-dominant and dominated layers contributed to the LAI = 2.6 by their leaf morphological traits.

Leaf morphology and chlorophyll content

The data obtained showed a very defined SLA (the reciprocal of the specific leaf mass) range among the different layers of the forest, representing different modes of light utilization. Species that co-occur within the same layer showed a similar specific leaf area.

The species of the dominant and co-dominant layers were characterised by a SLA = 180.8 cm^2 g^{-1} (calculated as the mean value of all the species) (Table 3). *Ostrya carpinifolia*, with a higher SLA (255 cm^2 g^{-1}), was an exception among the species of the co-dominant layer. As a result of shading, the species of the dominated layer showed a higher SLA (232.7 cm^2 g^{-1}, calculated as the mean value of all the species); *Sorbus aria*, *Malus sylvestris* and *Crataegus monogyna* were exceptions (156, 154, and 140 cm^2 g^{-1}, respectively). The in-
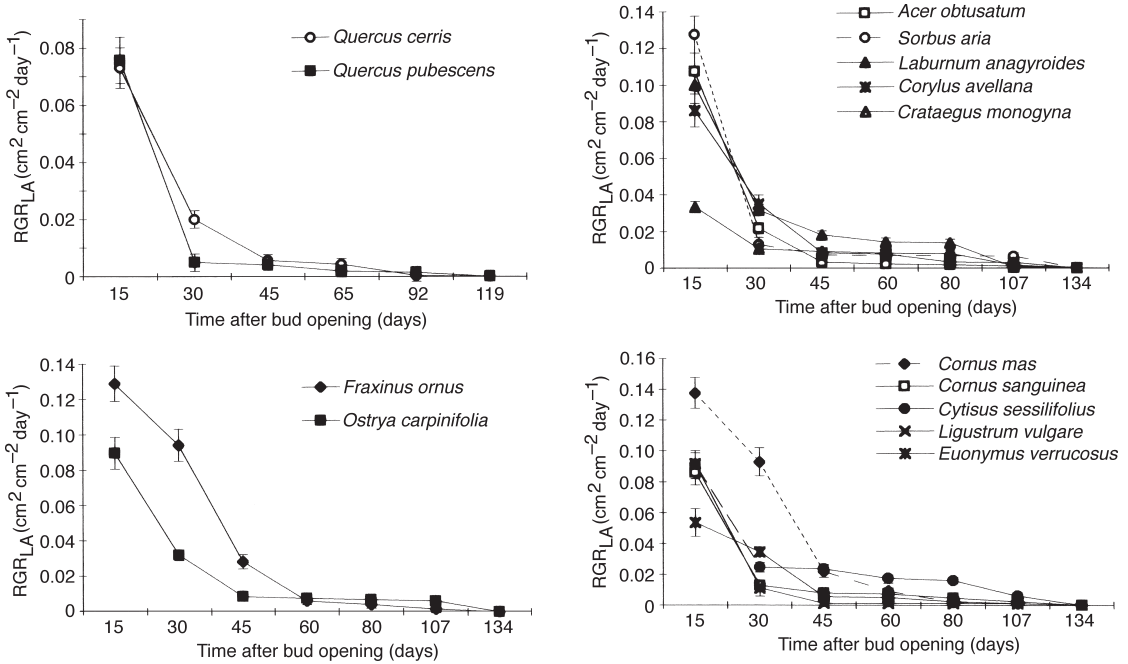
Fig. 2. Relative leaf area growth rate, cm² cm⁻² day⁻¹ (RGR_{LA}) during leaf growth of the most representative species of the forest. Vertical bars indicate standard error of the mean.

vestment of biomass per leaf area produced declined from the top to the bottom of the forest canopy; the lower SLA of the species in the dominant layer was advantageous in terms of thermoregulation and heat dissipation. Their leaves, in fact, were exposed to full sunlight during much of the day, while the total daily irradiance received by the dominated layers was correspondingly low.

Along the analysed vertical gradient, the reduction of light environment greatly influenced the mean leaf water content and leaf chlorophyll content. The leaf water content of the canopy ranged from 50% to 73%, and the highest average values were observed in the dominated layer (Table 3). There was evidence of an increase of total chlorophyll content from the dominant (0.87 mg g⁻¹, calculated as the mean value of all the species) to the dominated layer (1.53 mg g⁻¹, calculated as the mean value of all the species) (Table 3). The highest total chlorophyll content (2.69 mg g⁻¹) was observed in *Laburnum anagyroides*, which was one of the species showing the highest SLA (350.1 cm² g⁻¹), and the lower (0.70 mg g⁻¹) in *Quercus cerris*, which was one of the species showing the lowest SLA (148.2 cm²g⁻¹).

The chlorophyll *a/b* ratio was 2.80 in the dominant layer (calculated as the mean value of all the species), and 2.95 in the dominated layer (calculated as the mean value of all the species). *Sorbus aria*, *Malus sylvestris* and *Crataegus monogyna* showed a chlorophyll *a/b* ratio in excess of 3, characteristic of sun leaves.
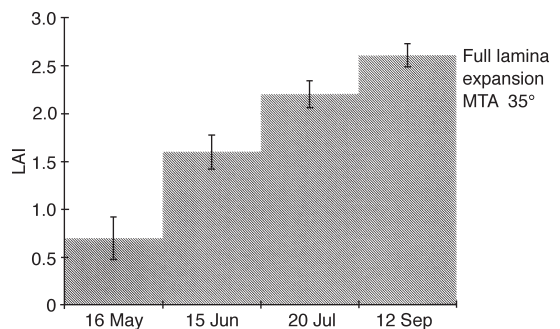

Fig. 3. Trend of leaf area index (LAI) during forest leaf growth. Vertical bars indicate standard error of the mean. Mean tilt angle of foliage in forest canopy (MTA) was measured in September, at full lamina expansion.

DISCUSSION

Several theories have been developed to explain coexistence of different plant species in multilayer plant communities (Ashton & Berlyn 1994, Van Arendouk & Poorter 1994, Farnsworth & Niklas 1995, Kull *et al.* 1995). Nevertheless, the definition of shade species and sun species is unsatisfactory because there are some species that have a combination of shade and sun characteristics (Anderson & Osmond 1987, Murchie & Horton 1997).

Since leaves adapt to long-term differences in light availability, canopy attributes may be derived from more easily attainable parameters which are linked to the inherent vertical light gradients across the canopy. The analysis of leaf morphological traits utilized in this study provides a basis to define the degree of shade-tolerance among the species. The results show an increase in leaf water content, SLA and chlorophyll content from the top to the bottom of the forest canopy. There is a fairly well defined SLA variation from the species of the dominant and co-dominant layers to the species of dominated layer, representing different modes of light utilisation. The larger and thinner leaves of the dominated layer (higher SLA) are more advantageous for light capture under low light, according to Rychnowska (1967),

Carpenter and Smith (1981) and Katsuno and Hozumi (1990).

Acer obtusatum, Laburnum anagyroides, Corylus avellana, *Cornus mas*, *C. sanguinea*, *Cytisus sessilifolius*, *Ligustrum vulgare* and *Euonymus verrucosus* are shade-tolerant species (263.7 cm² g⁻¹ mean SLA). *Crataegus monogyna*, *Malus sylvestris* and *Sorbus aria*, species generally inhabiting more open sites (Carpenter & Smith 1981), are less shade-tolerant (150 cm² g⁻¹ mean SLA). In contrast, the dominant and co-dominant layers are constituted mostly by shade-intolerant species; *Ostrya carpinifolia*, a shade-tolerant species according to Walters *et al.* (1993), is an exception.

The leaf traits of the different layers in the forest indicate their contribution to a LAI = 2.6. Because the shade-tolerant species, with thinner leaves, are dominant in the forest the LAI is low, in accordance to Shao *et al.* (1995) for deciduous mixed broad-leaved forest. The LAI = 2.6 was in the range observed by Schirone *et al.* (1985) and Piccoli and Borelli (1988) for mixed deciduous broad-leaved forests in Italy.

The chlorophyll content may be a good characteristic to express interspecific differences and shade-tolerance among the species. Both the total chlorophyll content and the chlorophyll *a/b* ratio are known to vary predictably with shading, ac-

Table 3. Specific leaf area (SLA), leaf water content (H₂O), total chlorophyll content (Chl) and chlorophyll *a*/chlorophyll *b* (Chl *a/b*) of the most representative species of the dominant (D), co-dominant (CD) and dominated (Do) layers.

Layer	Species	SLA (± SE) cm² g⁻¹	H₂O %	Chl (± SE) mg g⁻¹	Chl *a/b* (± SE)
D	*Quercus cerris*	148.16 ± 9.02	51.28	0.70 ± 0.05	2.89 ± 0.23
	Q. pubescens	144.81 ± 8.45	55.46	1.04 ± 0.08	2.71 ± 0.23
CD	*Fraxinus ornus*	175.38 ± 10.59	57.19	2.11 ± 0.13	2.58 ± 0.21
	Ostrya carpinifolia	255.00 ± 15.17	53.85	1.88 ± 0.12	2.92 ± 0.22
Do	*Acer obtusatum*	196.26 ± 11.92	54.54	0.76 ± 0.06	2.62 ± 0.20
	Sorbus aria	155.96 ± 9.62	52.73	1.63 ± 0.10	3.40 ± 0.23
	Malus sylvestris	153.80 ± 9.13	54.54	1.46 ± 0.09	3.17 ± 0.20
	Laburnum anagyroides	305.13 ± 22.94	68.08	2.69 ± 0.14	2.59 ± 0.22
	Corylus avellana	321.37 ± 26.07	60.00	1.22 ± 0.10	2.70 ± 0.24
	Crataegus monogyna	140.33 ± 7.81	50.00	1.57 ± 0.11	3.13 ± 0.23
	Cornus mas	201.20 ± 12.01	59.46	0.89 ± 0.07	3.00 ± 0.24
	Cornus sanguinea	273.07 ± 17.05	65.00	0.93 ± 0.07	3.04 ± 0.23
	Cytisus sessilifolius	280.00 ± 17.67	71.43	2.66 ± 0.14	2.75 ± 0.22
	Ligustrum vulgare	217.00 ± 13.46	71.43	1.59 ± 0.10	2.97 ± 0.20
	Euonymus verrucosus	315.67 ± 24.26	72.73	1.38 ± 0.09	3.06 ± 0.21

cording to Caesar (1989), Casal *et al.* (1990), Chow *et al.* (1991), Dale and Causton (1992) and Tinoco-Ojanguren and Pearcy (1995). The photosynthetic apparatus tends, in fact, to adjust to the specific environmental growth, so that the available light energy can be utilized most efficiently (Björkman & Holmgren 1963). There are at least four different ways in which changes in light interception can be achieved: changes in the leaf orientation, changes in the leaf reflectance, rearrangements of chloroplasts within the leaf, and changes in the chlorophyll content (Björkman & Demmig-Adams 1995). The 35° mean inclination angle of the forest canopy renders the leaves more efficient in the low light environment within the forest. The chlorophyll *a/b* ratio averages 2.9, according to Vyas and Vyas (1975) for deciduous species. *Laburnum anagyroides,* one of the most shade-tolerant species, shows the highest total chlorophyll content, and *Quercus cerris,* one of the most shade-intolerant species, shows the lowest chlorophyll content.

In conclusion, leaf traits and particularly the SLA and the chlorophyll content enable us to explain the coexistence of different plant species in the forest, their shade tolerance and therefore, their adaptability. Although total chlorophyll content expressed in a dry weight basis gives a realistic interpretation of light availability, the SLA is usually the preferred basis for expression (Linder 1974, Slade & Hutchings 1987, Dale & Causton 1992). Knowledge of the quantitative relationships between the forest structure, the leaf morphology and the light environment might contribute to forest classification. Similar comparative studies within a habitat can identify which plant traits are highly correlated. Such correlations determine the fundamental phylogenetic constraints of the organism and of its adaptation to a specific environment (Givnish 1990).

REFERENCES

Abrams, M. D. & Kubiske, M. E. 1990: Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade tolerance rank. — Forest Ecol. Managm. 31: 245–253.

Anderson, J. M. & Osmond, C. B. 1987: Shade–sun responses: compromises between acclimation and photoinhibition. — In: Kyle, D. J., Osmond, C. B. & Arntzen, C. J. (eds.), Photoinhibition: 1–36. Elsevier Sci. Publ., Amsterdam.

Ashton, P. M. S. & Berlyn, G. P. 1994: A comparison of leaf physiology and anatomy of Quercus (section Erythrobalanus -Fagaceae) species in different light environments. — Am. J. Bot. 81: 589–597.

Barbagallo, C. & Guglielmo, A. 1975: Flora e vegetazione della Macchia Grande (Gran Sasso d'Italia). — Boll. Sedute Acc. Gioenia Sci. Nat. Catania 4: 32–60.

Barkman, J. J. 1979: The investigation of vegetation texture and structure. — In: Werger, M. J. A. (ed.), The study of vegetation: 125–160. Junk, The Hague.

Barkman, J. J. 1990: A tentative typology of European scrub and forest communities based on vegetation texture and structure. — Vegetatio 86: 131–141.

Bazzaz , F. A. & Harper, J. L. 1977: Demographic analysis of the growth of Linum usitatissimum. — New Phytol. 78: 193–208.

Björkman, O. & Demmig-Adams, B. 1995: Regulation of photosynthetic light energy capture, conversion and dissipation in leaves of higher plants. — In: Schulze, E. D. & Caldwell, M. M. (eds.), Ecophysiology of photosynthesis: 17–47. Springer Verlag, Berlin.

Björkman, O. & Holmgren, P. 1963: Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. — Physiol. Plantarum 16: 889–914.

Brenner, A. J., Cueto Romero, M., Garcia Haro, J., Gilabert, M. A., Incoll, L. D., Martinez Fernandez, J., Porter, E., Pugnaire, F. I. & Younis, M. T. 1995: A comparison of direct and indirect methods for measuring leaf and surface areas of individual bushes. — Plant Cell Env. 18: 1332–1340.

Bunce, R. G. H. 1968: Biomass and production of trees in a mixed deciduous woodland. I. Girth and height as parameters for the estimation of tree dry weight. — J. Ecol. 56: 759–775.

Caesar, J. C. 1989: Effect of simulated shade radiation quality on the chlorophyll content of long and short early leaves of birch (Betula pendula Roth). — Photosynthetica 23: 123–129.

Carpenter, S. B. & Smith, N. D. 1981: A comparative study of leaf thickness among southern Appalachian hardwoods. — Can. J. Bot. 59: 1393–1396.

Casal, J. J., Whitelam, G. C. & Smith, H. 1990: Phytochrome effects on the relationship between chlorophyll and steady state levels of thylakoid plypeptides in light-grown tobacco. — Plant Physiol. 94: 370–374.

Cermák, J. 1989: Solar equivalent leaf area: an efficient biometrical parameter of individual leaves, trees and stands. — Tree Physiol. 5: 269–289.

Chow, W. S., Anderson, J. M. & Melis, A. 1991: The photosystem stoichiometry in thylakoids of some Australian shade-adapted plant species. — Austral. J. Plant Physiol. 17: 665–674.

Dale, M. P. & Causton, D. R. 1992: Use of the chlorophyll a/b ratio as a bioassay for the light environment of a plant. — Funct. Ecol. 6: 190–196.

Farnsworth, K. D. & Niklas, K. J. 1995: Theories of optimization, form and function in branching architecture in plants. — Funct. Ecol. 9: 355–363.

Fisher, R. A. 1920: Some remarks on the methods formulated in a recent article on "The quantitative analysis of plant growth?" — Ann. Appl. Biol. 7: 376.

Givnish, T. J. 1990: Economics of gas exchange.— In: Givnish, T. J. (ed.), On the economy of plant form and function: 11–24. Cambridge Univ. Press.

Gower, S. T. & Norman, J. M. 1991: Rapid estimation of leaf area index in conifer and broad-leaf plantations. — Ecology 72: 1896–1900.

Jarvis, P. G. & Leverenz, J. W. 1983: Productivity of temperate, deciduous and evergreen forests. — In: Lange, O. L., Nobel, P. S., Osmond, C. B. & Ziegler, M. (eds.), Physiological plant ecology, Encyclopedia of plant physiology, New Series: 233–280. Springer Verlag, Berlin.

Katsuno, M. & Hozumi, K. 1990: Estimation of leaf area at the level of branch, tree and stand in Cryptomeria japonica. — Ecol. Res. 5: 93–109.

Kull, O., Aan, A. & Soelsepp, T. 1995: Light interception, nitrogen and leaf mass distribution in a multilayer plant community. — Funct. Ecol. 9: 589–595.

Linder, S. 1974: A proposal for the use of standardised methods for chlorophyll determination in ecological and ecophysiological investigations. — Physiol. Plantarum 32: 154–156.

Maclachlan, S. & Zalik, S. 1963: Plastid structure, clorophyll concentration, and free aminoacids composition of clorophyll mutant of barley. — Can. J. Bot. 41: 1052–1062.

Montalvo, J., Casado, M. A., Levassar, C. & Pineda, F. D. 1991: Adaptation of ecological systems: compositional patterns of species and morphological and functional traits. — J. Veg. Sci. 2: 655–666.

Morales, D., Jimenez, M. S., Gonsales-Rodriguez, A. M., Cermák, J. 1996: Laurel forests in Tenerife, Canary Islands. 1. The site, stand structure and stand leaf area distribution. — Trees 11: 34–40.

Murchie, E. H. & Horton, P. 1997: Acclimation of photosynthesis to irradiance and spectral quality in British plant species: chlorophyll content, photosynthetic capacity and habitat preference. — Plant Cell Env. 20: 438–448.

Niinemets, U. 1995: Distribution of foliar carbon and nitrogen across the canopy of Fagus sylvatica: adaptation to a vertical light gradient. — Acta Oecol. 16: 525–541.

Orwig, D. A. & Abrams, M. D. 1995: Dendroecological and ecophysiological analysis of gap environments in mixed-oak understoreys of northern Virginia. — Funct. Ecol. 9: 799–806.

Parker, G. G., O'Neill, J. P. & Higman, J. P. 1989: Vertical profile and canopy organization in a mixed deciduous forest. — Vegetatio 85: 1–11.

Parkhurst, D. F. & Loucks, O. L. 1972: Optimal leaf size in relation to environment. — J. Ecol. 60: 505–537.

Piccoli, D. & Borelli, S. 1988: Introduzione agli studi fitometrici sulla cerreta di Roccarespampani (VT). — Inf. Bot. Ital. 20: 818–815.

Pierce, L. L. & Running, S. W. 1988: Rapid estimation of coniferouous forest leaf area index using a portable integrating radiometer. — Ecology 69: 1762–1767.

Reich, P. B., Walters, M. B. & Ellsworth, D. S. 1992: Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. — Ecol. Monogr. 62: 365–392.

Rychnovska, M. 1967: A contribution to the autecology of Phragmites communis Trin. I. Physiological heterogeneity of leaves — Folia Geobot. Phytotax. (Praha) 2: 179–188.

Sampson, D. A. & Allen, H. L. 1995: Direct and indirect estimates of leaf area index (LAI) for lodgepole and loblolly pine stands. — Trees 9: 119–122.

Schirone, B., Scarascia Mugnozza, G. & Valentini, R. 1985: Osservazioni preliminari sull'indice di area fogliare di Quercus cerris L. — Monti e Boschi 5: 47–51.

Shao, G., Shugart H. H. & Smith, T. M. 1995: A role-type model (rope) and its application in assessing climate change impacts on forest landscapes. — Vegetatio 121: 135–146.

Slade, A. J. & Hutchings, M. J. 1987: The effects of nutrient availability on foraging in the clonal herb Glechoma hederacea. — J. Ecol. 75: 639–650.

Stenberg, P., Linder, S., Smolander, H. & Flower-Ellis, J. 1994: Performance of the LAI-2000 plant canopy analyzer in estimating leaf area index of some Scots pine stands. — Tree Physiol. 14: 981–995.

Stewart, H. T. L., Flinn, D. W. & Aeberli, B. C. 1979: Above-ground biomass of a mixed eucalyptus forest in Eastern Victoria. — Austral. J. Bot. 27: 725–740.

Tadaki, Y. 1970: Studies on the production structure of forest (XVIII). Vertical change of specific leaf area in forest canopy. — J. Jap. For. Soc. 52: 263–268.

Tilman, D. 1988: Plant strategies and the dynamics and structure of plant communities. — Princeton Univ. Press, Princeton N.J.

Tinoco-Ojanguren, C. & Pearcy, R. W. 1995: A comparison of light quality and quantity effects on the growth and steady-state and dynamic photosynthetic characteristics of three tropical tree species. — Funct. Ecol. 9: 222–230.

Van Arendouk, J. J. C. M. & Poorter, H. 1994: The chemical composition and anatomical structure of leaves of grass species differing in relative growth rate. — Plant Cell Env. 17: 963–970.

Vyas, N. L. & Vyas, L. N. 1975: Distribution of chlorophyll and carotenoids in different canopy strata of a dry deciduous tropical forest at Udaipur, India. — Photosynthetica 9: 241–245.

Walters, M. B., Kruger, E. L. & Reich, P. B. 1993: Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. — Oeco-

logia 94: 7–16.

Waring, R. H. 1985: Imbalanced forest ecosystems: assessments and consequences. — Forest Ecol. Managm. 12: 93–112.

Welles, J. M. 1990: Some indirect methods of estimating canopy structure. — In: Goel, N. S. & Norman, J. M. (eds.), Instrumentation for studying vegetation canopies for remote sensing in optical and thermal infrared bands: 31–43. Remote Sensing Reviews, Harwood Acad. Publ., London.

Welles, J. M. & Cohen, S. 1996: Canopy structure measurement by gap fraction analysis using commercial instrumentation. — J. Exp. Bot. 47: 1335–1342.

Welles, J. M. & Norman, J. M. 1991: Instrument for indirect measurement of canopy architecture. — Agron. J. 83: 818–825.

Wittner, S. 1983: Land related global habitability science issues. — NASA National Aeronautics and Space Administration, Washington D.C., USA. Technical Memorandum Number 85841.