Size-related scaling of crown structure and principles of space equivalence influence structure and dynamics of natural forests

Sudip Pandey[1], Marco Carrer[1], Giai Petit[1]

[1]*Dipartimento Territorio e Sistemi Agro Forestali, University of Padova, Legnaro (PD), Italy*

E-mail: sudip.pandey@phd.unipd.it

BACKGROUND

- Natural and uneven-aged forest ecosystems are commonly characterized by a typical reversed J-shaped frequency distribution of tree sizes.

- The allometric scaling of crown architecture with tree sizes has been proposed to determine the structure and dynamics of these forest ecosystems (West et al. 2009; Simini et al. 2010), assuming that all the energy resources are equally distributed among the different tree size classes (Energy Equivalence Rule, EER).

- According to these allometric models, the number of individuals of a given size class (N) scales with tree height (H) as $N \propto H^{-(a+b)}$, where a and b are the exponents of the scaling of crown length and area with H ($L_{CRO} \propto H^a$ and $A_{CRO} \propto H^b$; i.e. crown volume, $V_{CRO} \propto H^{a+b}$).

- The application of the energy equivalence concept to forest ecology is not entirely clear, as the process of photosynthesis can be limited by several factors, and primarily by soil water availability and light interception.

- Therefore, EER could be applied in two different ways, i.e. whether the different tree size classes have equal access to soil water resources (i.e. equal soil volume) or equally shares the 2D-space (i.e. equal soil area) to minimize shading between neighbours.

- In this study, we investigated the energy equivalence concept in forest communities, grounding our analyses on the assumption that leaf metabolism (Q_L) and individual crown density ($DCRO = NL/V_{CRO}$) are independent of tree size.

HYPOTHESIS

To test whether the scaling of crown volume (V_{CRO}) or crown area (A_{CRO}) with tree height (H) is the main driver of the structure of natural forest according to a principle of equal availability of soil resources or space for light interception, respectively.

STUDY AREA

Fig.1 The location of the 8 forest permanent plots (black circle)

- Eight forest permanent plots (1 to 4 hectares) across Eurasia (Fig. 1)

- Two from Nepal, namely Pangboche (PAN, 4100 m., a.s.l) and Debuche (3800 m., a.s.l)

- Two from Romania, namely Slatioara (SLA, 1450 m., a.s.l) and Giumalau (GIU, 1150 m., a.s.l)

- Four from Italy, namely Millifret (MIL, 1250 m., a.s.l), Baldassarre (BAL, 1400 m., a.s.l), Latemar (LAT, 1900 m., a.s.l), Croda da Lago (CRO, 2002 m., a.s.l)

MATERIAL AND METHODS

- Dead logs and snags and all standing trees taller than 1.3 m were tagged and georeferenced

- Diameter at breast height (DBH), total tree height (H), height of lowest living branches (H_{CRO}) and crown radii (r_{CRO}) were measured

- The mean crown radius (R_{CRO}) was calculated as the arithmetic mean of four measured r_{CRO}

- We calculated the crown length ($L_{CRO} = H - H_{CRO}$), crown area ($A_{CRO} = \pi \cdot R^2_{CRO}$), crown volume ($V_{CRO} = A_{CRO} \cdot L_{CRO}$) and the allometric scaling of these parameters with H ($Y = \alpha \cdot H^\beta$).

- Assuming V_{CRO} or A_{CRO} to be constant in each H-class in the two respective models, we calculated the total number of trees in each H-class according to the assessed scaling relationships of V_{CRO} and A_{CRO} with H, respectively.

RESULTS AND DISCUSSION

- The scaling exponent of L_{CRO} vs H in all the plot except MIL (b=0.68) was higher than 1, demonstrating the relationship is not isometric (i.e. taller trees have proportionally longer crown than smaller trees) (Fig. 2, Table 1)

- The scaling of A_{CRO} vs H was higher in high altitude plots (PAN, b=2.23) suggesting crown enlarge at faster rates than tree height growth in higher altitude (Fig. 2, Table 1)

Fig.2 Scaling of crown parameters with H (structure of individual trees)

Table 1. Results of regression parameters of 8 different permanent forest plots, where, a is intercept and b is scaling exponent with 95% confidence interval (CIs) of regression parameters; R^2 is coefficient of determination. The different superscripts in confidence interval indicates they are significantly different

Site name	V_{CRO} - H a	b	R^2	A_{CRO} - H a	b	R^2	L_{CRO} - H a	b	R^2
DEB	0.27 (0.24 to 0.31)ᵃ	2.60 (2.52 to 2.69)ᵃ	0.77	0.44 (0.39 to 0.49)ᵃ	1.58 (1.50 to 1.66)ᵃ	0.58	0.48 (0.46 to 0.51)ᵃ	1.19 (1.15 to 1.22)ᵃ	0.77
PAN	0.06 (0.04 to 0.09)ᵇ	3.46 (3.25 to 3.68)ᵇ	0.69	0.16 (0.12 to 0.21)ᵇ	2.23 (2.06 to 2.41)ᵇ	0.58	0.31 (0.26 to 0.36)ᵇ	1.38 (1.29 to 1.49)ᵇ	0.62
SLA	0.18 (0.16 to 0.20)ᶜ	2.47 (2.42 to 2.53)ᶜ	0.79	0.70 (0.64 to 0.76)ᶜ	1.20 (1.16 to 1.24)ᶜ	0.57	0.19 (0.18 to 0.20)ᶜ	1.40 (1.38 to 1.43)ᵇ	0.82
GIU	0.20 (0.19 to 0.22)ᶜ	2.17 (2.14 to 2.21)ᵈ	0.87	0.33 (0.30 to 0.36)ᵈ	1.16 (1.12 to 1.19)ᵈ	0.66	0.57 (0.55 to 0.59)ᵈ	1.05 (1.03 to 1.06)ᶜ	0.90
MIL	0.20 (0.12 to 0.33)ᵈ	1.93 (1.77 to 2.08)ᵉ	0.18	0.20 (0.13 to 0.29)ᵈᵉ	1.24 (1.12 to 1.37)ᵈ	0.12	1.01 (0.75 to 1.35)ᵉ	0.68 (0.58 to 0.77)ᵈ	0.07
BAL	0.29 (0.24 to 0.35)ᵈ	2.26 (2.18 to 2.33)ᵈ	0.68	0.84 (0.71 to 0.98)ᶠᶜ	1.12 (1.05 to 1.18)ᶜ	0.43	0.27 (0.24 to 0.29)ᵇ	1.23 (1.20 to 1.27)ᵃ	0.76
LAT	0.07 (0.06 to 0.08)ᵇ	2.55 (2.49 to 2.61)ᵃ	0.77	0.79 (0.74 to 0.83)ᶠ	0.70 (0.68 to 0.72)ᶠ	0.65	0.30 (0.27 to 0.33)ᵇ	1.21 (1.17 to 1.24)ᵃ	0.73
CRO	0.21 (0.20 to 0.25)ᶜ	2.49 (2.47 to 2.52)ᵃ	0.92	0.31 (0.30 to 0.32)d	1.45 (1.42 to 1.47)ᵇ	0.82	0.68 (0.67 to 0.69)ᶜ	1.05 (1.04 to 1.06)ᶜ	0.93

Table 2. Results of regression parameters of 8 different permanent forest plots, where, a is intercept and b is scaling exponent with 95% confidence interval (CIs) of regression parameters; R^2 is coefficient of determination. The different superscripts in confidence interval indicates they are significantly different

Site name	Real data a	b	R^2	V_{CRO} - H model a	b	A_{CRO} - H model a	b
DEB	2931 (581 to 14793)ᵃ	-2.18 (-2.91 to -1.46)ᵃ	0.73	9095	-2.60	1780	-1.58
PAN	529 (53 to 5249)ᵇ	-1.73 (-2.90 to -0.55)ᵇ	0.51	24451	-3.46	2042	-2.23
SLA	687 (327 to 1444)ᶜ	-1.63 (-1.88 to -1.39)ᶜ	0.81	7518	-2.47	213	-1.20
GIU	97 (28 to 337)ᵈ	-0.90 (-1.31 to -0.49)ᵈ	0.32	13690	-2.17	456	-1.16
MIL	0.009 (0.0004 to 0.11)ᵉ	2.41 (1.55 to 3.26)ᵉ	0.56	13706	-1.93	1395	-1.24
BAL	18 (13 to 25)ᶠ	-0.13 (-0.24 to -0.019)ᶠ	0.16	9213	-2.26	308	-1.12
LAT	30 (8 to 115)ᵍ	-0.37 (-0.86 to 0.10)ᵍ	0.07	33287	-2.55	107	-0.70
CRO	726 (322 to 1639)ᵇ	-1.61 (-1.93 to -1.28)ᶜ	0.82	8557	-2.49	580	-1.45

Fig.3 Frequency distribution of alive trees

Fig.4 Frequency distribution of dead trees

- Reversed J-shaped pattern of the distribution of alive trees per H-class at each plot was clearly found at DEB, SLA and CRO (Fig. 3).

- Reversed J-shaped pattern of the distribution of dead trees per H-class at DEB, BAL and CRO (Fig. 4).

- The condition of equal energy use by the different H-classes (EER) was never satisfied in all plots (left panels of Fig. 5); ΣA_{CRO} (use of light resources) and ΣV_{CRO} (the consumption of soil and water resources) were compared with real field data.

- The A_{CRO} model better predict the increase in the use of soil resources with increasing H (left panels of Fig. 5).

- H–frequency distribution of A_{CRO} model better described the actual reversed J-shaped pattern of the structure of our more natural forests (**DEB, SLA, and CRO**) (right panels in Fig. 5, Fig. 4, Table 2).

- The H-frequency distribution predicted by energy equivalence based on V_{CRO} was significantly different from the real forest structure in all the sites (right panels in Fig. 5, Fig. 4, Table 2).

Fig.5 Left panels: variation of the total V_{CRO} of each H-class (i.e., use of soil resources per H-class) with H. **Right panels**: number of alive trees per H-class (as Fig. 4), and prediction by V_{CRO} and A_{CRO} model.

CONCLUSIONS

- The frequency distribution in H-classes was typically reverse J-shaped in unmanaged forest, where the best model predictions were those based on the scaling of $A_{CRO} \propto H^b$.

- Our study provides evidence that the scaling of crown geometry is site-specific and regulates the inter–and intra specific competition for space according to a fundamental principle of equal probability to fit the necessary space for survival irrespective of tree size.

REFERENCES

Simini, F., Anfodillo, T., Carrer, M., Banavar, J.R., Maritan, A., 2010. Self-Similarity and scaling in forest communities. Proc. Natl. Acad. Sci. 107, 7658 –7662.

West, G.B., Enquist, B.J., Brown, J.H., 2009. A general quantitative theory of forest structure and dynamics. Proc. Natl. Acad. Sci. U.S.A. 106, 7040-7045.