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Rank distributions and biomass partitioning of plants

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Highlights: We study how well biomass partitioning patterns of plant compartments (organs) follow mathematical rank distributions using empirical data from the tree and dwarf shrub species in temperate-boreal zone as a test material. The simplest form of a rank distribution (Zipf's law) shows a good statistical fit to the data and its semi-empirical dependencies can successfully be applied also in a complex ecosystem models.

Keywords: Zipf's law, optimal plant organs partitioning, dwarf shrubs, trees, ranks and classification

INTRODUCTION

Certain statistical regularities as attributes of complex systems in the form of power laws are observed everywhere (Clause et al. 2009): these include many social and economic effects, and some applications in different branches of biology (Furusawa and Kaneko, 2003). One of the earliest applications of power laws are modelling the numbers of species in biological taxa (Willis and Jule, 1922).

These regularities have common mathematical structure and can be formulated as some properties of statistical rank distributions known as Zipf's, Pareto's, Heaps' and some other laws. Soukhovolsky (1996) applied Zipf-Pareto distribution for description of plant biomass partitioning. He used this distribution for evaluating the root biomass of trees.

Consider Zipf-Pareto law as the simplest example of a power rank distribution (Mandelbrot, 1969). It can be written for a ranked data in a form

$$x(i) = A/i^b,$$

where i denotes rank, A and b are parameters, maximal rank is set to 1, next ranks in size are increasing consequently. A and b can be easily evaluated after simple log-log transformation by least-squares method.

Main conditions for applying the rank distributions are as follows. Assume that available resource for total unit is distributed among its parts proportionally to its rank, i.e. to the ordered sequence of distributed resource, then distribution of resource parts has the form of Zipf's law. Accordingly, many mechanisms have been presented to explain the emergence of the Zipf's law (Newman 2005).

We analyzed partitioning of biomass to the main plant compartments of vascular plants (trees and dwarf shrub species in ground vegetation) using empirical data from the taiga zone in Russian North-West and Finland.

MATERIALS AND METHODS

We analyzed two data sets, one representing a deciduous tree (*Betula pendula*) and another deciduous dwarf shrub (*Vaccinium myrtillus)* biomass data, as a test material. The tree-wise data consists of measured biomass compartments (kg dry weight) of nine different-sized trees from a 38-years-old birch stand (*Oxalis* forest type) in Karelia (Kazimirov et al., 1978). For each tree we calculated the proportions (%) of the following biomass compartments: stem, (coarse) roots, branches, and leaves (Table 1).

The biomass data of *Vaccinium myrtillus* (kg dry weight/ha) is from 12 intensively monitored forest plots in Finland. Both in South and North Finland there were three Norway spruce and three Scots pine plots. The spruce plots represented mesic and moist site types whereas the pine plots represented poor and dry site types. The data of 28 small sample units (30x30 cm) have been joined for accurate description of the total biomass of *V. myrtillus* at each plot. We calculated the proportions (%) of the biomass compartments (rhizomes, living shoots and branches, fine roots, leaves and flowers) to normalize the heterogeneous data. The averages of the three plots in the same site type (separately in north and south) are given in Table 2.

Table 1. Proportion (%) of biomass compartments (out of the total biomass) for *Vaccinium myrtillus*. Averages and standard deviations (sd) for southern and northern pine and spruce plots (n=3 plots) given

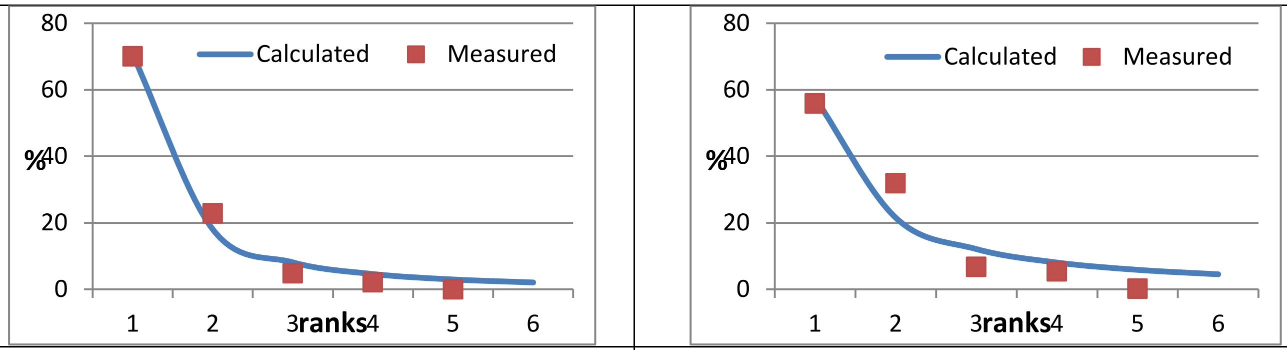
		Rhizomes (diameter > 2 mm)	Living shoots and branches	Fine roots (diameter < 2 mm)	Leaves	Flowers and flower buds
South pine stand	Average	70.09	22.80	4.80	2.08	0.045
	sd.	6.31	4.81	0.9	0.69	0.016
South spruce stand	Average	55.87	31.89	6.77	5.37	0.1
	sd.	8.73	12.03	4.38	2.46	0.12
North pine stand	Average	67.22	22.92	7.79	2.03	0.47
	sd.	3.10	5.13	3.37	1.24	0.42
North spruce stand	Average	75.86	17.02	4.41	2.62	0.87
	sd.	4.80	4.12	0.65	1.32	0.88

Table 2. Proportions (%) of biomass compartments (out of the total biomass) for nine *Betula pendula* trees. Av. – averages, sd. – standard deviation.

	1	2	3	4	5	6	7	8	9	Av.	sd.
Stem	65.62	67.0	68.03	67.87	69.97	69.31	70.93	71.73	72.86	69.26	1.867
Roots	22.92	18.78	18.03	18.12	17.71	17.76	17.15	16.25	16.34	18.12	1.867
Branches	8.33	8.63	7.82	8.21	7.81	7.63	7.27	8.03	7.22	7.88	0.445
Leaves	3.12	5.58	6.12	5.80	4.51	5.29	4.65	3.99	3.58	4.74	0.979

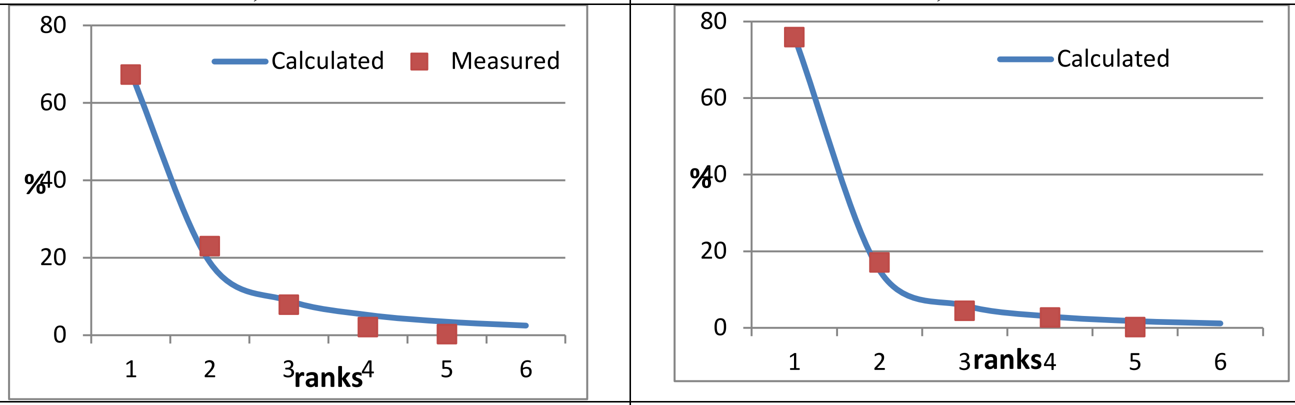
RESULTS AND DISCUSSION

Biomass compartments (%) of *V. myrtillus* and *B. pendula* in relation to ranks with fitted power equations are presented in Figs. 1 and 2, respectively.



South pine stand. Power equation y=ax^b, coefficient data: a = 70.64; b = -1.97. R= 0.9929.

South spruce stand. Power equation y=ax^b, coefficient data: a = 57.66; b = -1.42. R= 0.9588.



North pine stand. Power equation y=ax^b, coefficient data: a = 67.78; b = -1.85. R= 0.9935.

North spruce stand. Power equation y=ax^b, coefficient data: a = 76.04; b = -2.34. R= 0.9986.

Fig. 1. Dependency between ranks and corresponding averages of biomass compartments (%) of *Vaccinium myrtillus* in different sites (Table 1). Quadrats are empirical data

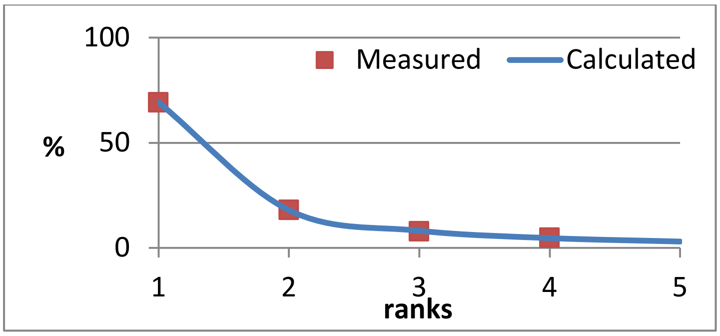


Fig. 2. Dependency between ranks and corresponding averages of biomass compartments (%) at a 38-year-old birch stand (Table 2). Line is power equation y=ax^b, coefficient data: a = 69.27; b = -1.95. R= 0.999980. Quadrats are empirical data.

Both *V. myrtillus* and *B. pendula* biomass data showed persistently good fit to power equations, which is equivalent to Zipf law. In all cases the shape of the power dependency stayed the same. We found that for the same species ranks correspond to the same biomass compartments in different climatic and edaphic conditions. However, coefficients of the power distributions can be different for the same species and reflect different response of the species to changed conditions. Thus, in Fig. 1 we clearly see that for *V. myrtillus* in spruce stands the portion of rhizomes (1st rank) is larger in northern conditions than in south.

An interesting question is whether ranks change along plant development stage and changing site conditions. In general, they can change as a result of long-term local unstable conditions (MacArthur, 1955). It seems that the populations of *V. myrtillus* in spruce stands with dense canopy (Fig.1, southern spruce stands) are more unstable. This question claims further studies for establishing of limits of applicability of the approach.

Our biomass distributions were close to the results of Enquist and Niklas (2002) on the log-log relationship between above- and belowground biomasses of tree stands. They averaged world wide dataset from stand characteristics and found pairwise linear allometric relationships among standing leaf, stem, and root biomass basing on general allometric model. Power-law rank distributions allow for obtaining more general relationships between plant organs linking all main biomass compartments together. Additionally, power-law dependencies can also be applied for descripting of organs' increment. Further, it would be interesting to compare the sequence of ranks between different functional plant groups for better understanding their role in carbon cycling in ground vegetation.

The study of power-law distributions is an area in which there is considerable current research interest. From a mathematical point of view, these dependencies are similar to first integral in complicated systems of differential equations. Usually knowledge of such links between variables helps to find solutions in these systems. Such dependencies will help to obtain rules needed for development of the forest simulation models. While the examples presented here certainly offer some insight, there is much work to be done both experimentally and theoretically before we can say we really understand the main processes driving these systems.

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