Stand structure links up canopy processes and forest management

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Abstract. Above- and belowground biomass and net primary production \( P_n \) of a maturing Norway spruce \((Picea abies (L.) Karst.)\) forest (80 years old) established on brown soil in central Estonia were 227, 50 and 19.3 Mg ha correspondingly. Stand structure is determined mostly by mean height and stand density, used widely in forestry, but both are difficult to measure with high precision in respect of canopy processes in individual trees. However, trunk form quotient \( q_2 \) and proportion of living crown in relation to tree height are useful parameters allowing describe stand structure tree by tree. Based on 7 model trees, leaf unit mass assimilation activity and total biomass respiration per unit mass were determined graphically as mean values for the whole tree growth during 80 years of age. There are still several possible approaches not used carefully enough to integrate experimental work at instrumented towers with actual forestry measurement. Dependence of physiological characteristics on individual tree parameters is the missing link between canopy processes and forest management.

Key words: net primary production, stand structure, carbon allocation, assimilation, respiration, Norway spruce.

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Introduction

Canopy processes and forest management are related but in no way closely linked phenomena. It is due to the fact that forest stand is fashioned by three classes of processes, viz. energy flow, nutrient cycling and structural information (spatial arrangement) in their long-term temporal pattern. Canopy processes, however, are being studied in short-term scales on individual shoots or/and trees, and therefore the results do not reveal biomass allocation strategies. Canopy processes have an overwhelming importance in respect of energy input via photosynthesis, but energy usage in carbon allocation depends mostly on stand structure including such properties as shoot/root ratio and living crown proportion.

A forest stand may be considered from at least three viewpoints reflecting interests of forestry, ecology and eco-physiology (Figure 1). Forestry concentrates on trunk timber productivity in volume units using stand mean tree height \( H \) and stand basal area \( G \) determined as sum of intersection areas of all trees (calculated through tree diameters measured at breast height, \( d_{1.3} \)). Ideally, a tree volume might equal to volume of a cylinder with length equal to tree height, \( H \), and bottom area equal to \( \pi(d_{1.3}/2)^2 \), but due to the conic form of tree trunks their volume is less than
that of the cylinder. The ratio between the real volume and volume of the cylinder, the form coefficient $f$, is valuable in determining the total trunk volume of the stand:

$$V = fHG$$  \hspace{1cm} (1)$$

as well as a characteristic of trunk quality. In dense stands (Figure 1, tree silhouette marked with a) the coefficient has higher value indicating that the role of branches is small, but in sparsely populated stands the branches grow larger and survive longer, so that the extent of living crown (C) as well role of branches in total timber amount, is high (Figure 1, c). It means that trunk timber proportion in total above-ground biomass is smaller and trunk as saw material has, due to a lot of branch segments, comparatively low quality. The relative trunk share in total volume of woody organs is just a measure of surplus of assimilates (Warning, 1980), i.e. all other tree organs or compartments are physiologically more active.

Forestry has developed a special thinning theory considering possibilities to manage stands having optimal density which allows to maximize trunk timber, total timber or high quality timber yields (e.g. Assmann, 1968; Schober, 1979/80), but in recent years such considerations became more and more ecologically minded (Nilsson et al., 1995).

Ecology pays attention to biomass in all compartments of forest stand including roots, and to biomass increment and its dead parts (mortmass) formation in litter fall. In long-term scale, energy input is determined by chlorophyll amount per stand unit area, often measured as leaf area index.
Eco-physiology (Figure 1) deals with gas exchange techniques aiming at instrumental estimation of photosynthetic activity or gross production \( P_g \), respiration losses \( R \), and gas exchange balance or net photosynthesis \( P_n \) of individual trees:

\[
P_n = P_g - R
\]

(2)

determining the coefficients \( a \) and \( r \) experimentally. In long-term perspective, however, the hourly, daily, weekly or even monthly mean values of photosynthesis, transpiration, respiration, leaf inclination angle etc., measured mostly at comparatively very small trees, are worth handling on the level of dissertations and may serve as useful illustrations in handbooks, but are of limited value in forest management.

Considering forest stand productivity the leaf (needle) biomass \( B_L \) should be preferred in order to calculate gross photosynthesis using leaf mass unit assimilation rate \( a \), expressed in the same units as respiration \( r \) per total plant biomass \( B_T \) unit, so that net photosynthesis \( P_n \) equals:

\[
P_n = a B_L - r B_T
\]

(3)

So it may be stated that eco-physiology deals with energy flow, ecology with carbon allocation and nutrients’ cycling, and forestry with structural information within forest stand. The key question lies in leaf biomass proportion per an individual tree resulting trunk form (forestry), leaf biomass proportion per total biomass determining stand growth and turnover rates (ecology), and leaf unit mass productivity as function of ecological factors (eco-physiology).

Material and Methods

Study site
The study was carried out during several years on a large drumlin area in central Estonia, 40 km north from Tartu, at Vooremaa Ecology Station. A detailed geographical, climatologic and phytographic description of the study area has been given by Frey (1977, 1981). A hemiboreal Norway spruce stand on brown pseudopodzolic soil, having mean age of 80 years, was studied initially as IBP area, later on ecologically, eco-physiologically and eco-graphically, including study of pollutants’ load.

The tree layer was dominated by *Picea abies* (L.) H.Karst. with negligible role of *Betula pendula* Roth, *Populus tremula* L., *Pinus sylvestris* (L.) and some smaller deciduous broad-leaved trees, mainly *Acer platanoides* L., *Quercus robur* L. and *Tilia cordata* Mill.

All the trees were mapped with crown projection and height, diameter, age and radial increment measured. The stand had stock density of 362 trees per ha, mean tree height 26 m, mean diameter at breast height 31 cm, basal area 29.8 m².

On the permanent plot of 1.4 ha, 513 trees were mapped and measured and they were divided according to their height into 5 ecological horizons:

I - 35.3–34.3, II - 34.2–32.6, III - 32.5–29.9, IV - 29.8–25.7 and V - less than 25.6 m.

The threshold values divide total leaf biomass into five equal (each 20 per cent) vertical layers. The mapped and measured trees were distributed within these horizons as follows: 0.4, 3.5, 13.5, 45.6, and 37.0 per cent correspondingly.
Destructive sampling

In total, 7 model trees were selected for destructive study by the help of map and computer: 2, 3 and 2 from the last tree horizons but forming one bio-group. According to median dimensions, 7 model trees forming one bio-group on the surface area of about 330 m$^2$ were investigated separately in 1 metre trunk sections for biomass vertical allocation and biomass increment by compartments (needle, shoot, branch, trunk).

About 55 m$^2$ of the bio-group area was situated under the crowns and was excavated for root investigation. The roots were excavated carefully by hand in full amounts of all 7 trees separately as stump and four compartments according to their diameter, using threshold values of 10, 3 and 1 cm, tracing to the diameter of less than 5 mm.

Fine roots were sampled separately on 10 neighbouring plots of 1 square metre to 1-m depth by 10-cm horizons. After washing out fine roots from soil samples, the roots of spruce were separated from those of other plants. Spruce roots were sorted into dead and living categories based on visible and mechanical criteria (see Vogt & Persson, 1991) and the living ones into four diameter classes using threshold values of 3, 1 and 0.2 mm. All samples were weighted in full amount for fresh weight. Owen-dry (105 °C) masses were determined in subsamples and dry weights of aboveground parts and root compartments, based on corresponding dry/fresh weight ratios were calculated. Disk samples were taken at 1-m intervals, and annual ring widths of trunk, branch and coarse root disk samples were measured along four radii to 0.01 mm accuracy, with the aid of a dissecting microscope.

Estimation of stand biomass

Aboveground biomass was defined as the sum of dry weight of needles, stems, branches and stems in the permanent plot. Dry weights of the compartments were determined from allometric relationships developed by the least squares regression method between several size parameters and dry weights of the seven model trees. Fine root biomass was calculated on the basis of the mean dry weight of living fine roots in 100 soil samples corresponding to total 10 m$^3$ of soil volume. Respiration rates of woody organs at Vooremaa Experimental Area were determined experimentally both on intact trees and on tree samples (Frey & Kull, 1985).
Estimation of net production

Net primary production \((P_n)\) was estimated by summing annual biomass increments by compartments (stem, branch, shoot, current year needle) and corrected for annual litter fall (Kira & Shidei, 1967). Calculation of biomass increment of woody organs, including roots, was based on positive correlation between mean annual volume increment and measured dry weights of the seven model trees.

Results and discussion

It should be emphasized that canopy leaf mass profile of dense forest stands consists of light-adapted elements supporting nearly equal leaf mass unit illumination throughout the profile. The total leaf biomass from crown base to its top is distributed according to information probability function \((p_i \ln p_i)\), but the sun (leaf one-side area per leaf dry weight kg = 8.5), intermediate (11.0) and shade (14.0) needles show different patterns (Figure 2), allowing leaf specific area to rise in correlation of the illumination weakening. In addition to this, the chlorophyll content was 2 to 3 times higher in shade than in sun leaves. At Vooremaa forest these eco-morphological results of Frey & Frey (1985) were supported by experiments carried out by Kull & Koppel (1987). The maximum leaf biomass for a tree species is a geographical feature like annual mean temperature, precipitation amount, length of growing season, etc.

However, leaf biomass assimilation activity varies with short term patterns of temperature and other ecological factors (Pisek & Winkler, 1958, 1959). As the canopy processes have been investigated during short periods and mostly on young trees, the results do not offer special interest to forest management, connected with long period phenomena.

Forestry is fully satisfied knowing the real values of \(a\) and \(r\). Surprisingly enough, it is generally misunderstood that a simple procedure allows to determine the coef-

![Figure 2. Percentage share of needle groups in canopy profile of 80-year-old Norway spruce stand, Vooremaa.](image-url)
ficients’ numeric value using the above formula (2) in form:

\[
P_{n} / B_{TOT} = a \frac{B_{L}}{B_{TOT}} - r \frac{B_{T}}{B_{TOT}}
\]  

Having determined the biomass data \( P_{n}, B_{L} \) and \( B_{TOT} \) for seven 80-year-old model trees (Table 2), the graphic plotting (Figure 3) results in \( a = 1.29, r = 0.034 \) as mean values. These results coincide with the conclusions made by Kira (1977), who used a similar method based on aboveground woody organs instead of total biomass (Tadaki, 1968; Tadaki et al., 1970) in studying subalpine \( \textit{Abies veitchii} \) in Japan. However, variation in stand density influences branch-and-leaf share in total biomass (Figure 4), and consequently, \( B_{L} / B_{TOT} \) ratio in wide limits. A philosophical conclusion from this is that whatever apparatuses in crown space are unable to give the mean for the whole forest management period. It is to emphasise that the values of coefficients \( a \) and \( r \) are dependent on shoot/root and other compartments ratios (Figure 5), what show non-linear changes with age. Unfortunately we have no adequate data illustrating such relationships precisely.

Table 2. Biomass characteristics of model trees, \( \textit{P. abies} \), Vooremaa.

| Tree Nos | \( B_{\text{leaf}} \) kg | \( B_{\text{shoot}} \) kg | \( B_{\text{branch}} \) kg | \( B_{\text{trunk}} \) kg | \( B_{\text{AboveG}} \) kg | \( B_{\text{BelowG}} \) kg | \( B_{\text{TOT}} \) kg | \( P_{n} \) kg | \( B_{L} / B_{TOT} \% \) | \( P_{n} / B_{TOT} \% \) |
|----------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|-------------|----------------|----------------|
| 8        | 134.0          | 91            | 163            | 1609           | 1997           | 462            | 2459           | 157         | 5.4            | 6.4            |
| 9        | 57.9           | 30            | 50             | 611            | 749            | 157            | 906            | 72          | 6.4            | 8.0            |
| 10       | 10.7           | 5             | 6              | 183            | 205            | 45             | 249            | 16          | 4.3            | 6.6            |
| 11       | 30.8           | 14            | 21             | 310            | 376            | 94             | 618            | 44          | 5.0            | 7.2            |
| 12       | 81.2           | 47            | 116            | 1338           | 1582           | 242            | 1676           | 106         | 4.8            | 6.3            |
| 13       | 45.4           | 21            | 28             | 507            | 601            | 118            | 720            | 51          | 6.3            | 7.1            |
| 14       | 196.9          | 101           | 202            | 1596           | 2096           | 550            | 2646           | 198         | 7.4            | 7.5            |
| Mg ha\(^{-1}\) | 16.7          | 9.3           | 17.6           | 184.3          | 227.7          | 50.0           | 277.7          | 19.3        | 6.0\%         | 7.0\%         |

Figure 3. Variability of tree productivity ratios in Norway spruce stand, Vooremaa.

\( \text{Joonis 3. Hariliku kuuse üksikpuude produktiivsuse suhtarvude muutlikkus puistus, Vooremaa.} \)
In terms of forest management, the most important characteristic is the proportion of living crown, heavily depending on stand density (stand basal area, $G = \pi \sum (d_{1.3}/2)^2$) which has been the main object of thinning theories. A compromise between maximum trunk volume ($V = HGq^2$) and maximum leaf biomass is the link between canopy processes and forest management. Unfortunately, there exist few data documenting quantitative relationship (Figure 4) between living crown proportion ($CP = C/H$, see Figure 1), stand density ($p$) and trunk form coefficient ($q_2 = D_{1/2}/D_{1.3}$).

Unfortunately, there exist few data documenting quantitative relationship between living crown proportion ($CP = C/H$), stand density ($p$) and trunk form coefficient ($q_2 = D_{1/2}/D_{1.3}$) value. An exception may be found in older German literature concerning forestry measurements in Bavaria (Figure 5). From this we concluded approximate relationship between stand density and proportion of living crown (Figure 6) as follows:

$$CP = 0.4 + 0.5 (1 - p)$$  

(5)

As far as CP has to be strongly correlated with $B_L/B_{TOT}$, this relationship links up $B_L$ and $P_n$ according to Figure 2, i.e. crown structure to stand productivity.

**Conclusion**

There are still several possible approaches not used enough to integrate actual forestry measurements with experimental work at instrumented towers. Functional dependence of physiological gas exchange characteristics on individual tree parameters is the missing link between canopy processes and forest management.
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Figure 5. Partitioning of total biomass between different tree parts in dependence of stand age. Compiled using data from Cannell, 1982, Palumets, 1991 and other published biomass data on 13 boreal, 11 hemiboreal and 5 alpine stands on *P. abies* in Europe.

Figure 6. Tree trunk characteristics *f* and *q*₂ in relation to stand density and proportion of living crown. Compiled using data from Schiffel (1899).

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**Võraprotsesse ja metsamajandust seob puu ja puistu ülesehitus**

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*Kokkuvõte*

Kesk-Eestis pruunmullal kasvanud küpeva 80-aastase kuusiku maapealne ja maalune biomass ning nende ühine aastane juurdekasv olid vastavalt 227, 50 ja 19.3 Mg ha$^{-1}$. Metsanduses puistu ülesehituse kirjeldamisel talaviselt kasutatavad keskmine kõrgus ja puistu tihedus ei sobi üksikpuude ja nende võraprotsesside kirjeldamiseks. Üksikpuude võrdlemisel on kasulikeks tunnusteks tüve vormiav a elusvõra ulatus. Kasutades 7 mudelpuu osade (okas, oks, tüvi, juur) biomasside ja juurdekasvude detailse massimõõtmise andmeid, leiti graafiliselt viimase kasvuaasta okkamassi ühiku assimilatsiooni aktiivsus ja biomassi põhihingamise tegur.

Metsanduslikud hooldusraied võtted vöimaldavad kujundada elusvõra ulatust ja sellega seotud vormi koefitsienti, ja seeläbi on metsamajandus ja võraprotsessid seostatud. Mitmesugused vaatlustornides tehtavad instrumentaalsed puu füsioloogiat kirjeldavad täppismõõtmeid ühes puul ei võimalda tulemusi siduda puu ja puistu ülesehitusega, ilma et võetakse ette väga töömahukas biomassi kirjeldamine. Seetõttu jääb ökofüsioloogiline metsateadus praktilisest metsamajandusest eemalseisvaks, sest teaduse tulemus on vaatluse all kogu puu, palki saab aga ainult tõvest.

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