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SHORT COMMUNICATION

Does disturbance prevent total basal area and biomass in indigenous forests from being at equilibrium with the local environment?

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Understanding the determinants of the amount of biomass in various forests is presently a global imperative because forests may (e.g. Phillips *et al.* 2002) or may not be carbon sinks (Clark 2002). Presently, the assumption for modelling and empirical studies is that forest biomass and net primary production (NPP) are in equilibrium. For example, Beerling & Woodward (2001) modelled world-wide plant biomass on the basis of how net primary productivity (NPP) and annual transpiration rates affect tree size. They predicted that the largest stands of organic carbon are in the wet tropics. Similarly, in a recent textbook, Chapin *et al.* (2002) indicate that amongst forests, tropical forests have the greatest biomass and greatest NPP. In contrast, Midgley (2001) drew attention to the negative correlation between basal area and disturbance rates in some tropical forests. Also, Enquist & Niklas (2001) demonstrated that biomass is not correlated with latitude. Indeed, many indigenous forests with exceptionally large total basal areas and thus total standing stem biomass occur in the cool-temperate areas. For example, the Pacific Northwest redwood and Tasmanian mountain-ash forests have a total basal area of 300+ $m^2 ha^{-1}$, which exceeds the mean of many tropical forests (i.e. 35 $m^2 ha^{-1}$) (see Midgley 2001 and references therein).

We continue with the theme that forest basal area is not at equilibrium with local environment. To demonstrate this we show that basal area in a plot is strongly correlated with the size of the biggest trees and that density effects cannot compensate for size effects. In other words, the determinant of plot basal area, and thus biomass, is the size that co-occurring trees grow to. We argue that disturbance regimes determine maximum size that trees achieve.

To explore the relationship between total forest stem basal area and the basal stem areas of individual trees, we used the Gentry database (Phillips & Miller 2003). This large database has been used for various studies, such as analyses of size-class distributions and biomass (Enquist & Niklas 2001, Niklas *et al.* 2003). For each of 226 communities, this world-wide database provides the number and breast height diameter (dbh) for all woody stems measuring > 2.5 cm within 10 transects each measuring 2×50 m in area (total sampled area per site = 0.1 ha). We readily acknowledge that the Gentry database has important limitations. Gentry measured the diameter of buttress trees above their buttresses and this may have implications for determinants of basal area (e.g. the 'buttress problem' see Clark 2002 and Phillips *et al.* 2002). More seriously, the total plot size sampled for each site is small (0.1 ha), and there is no replication for individual sites. The Gentry database thus provides sample, rather than stand, properties. Whilst further replication and larger sample areas are needed for the determination of more accurate and representative mean stand basal areas (e.g. taking into account local heterogeneity), we nevertheless feel 0.1-ha plots are sufficient to give a perspective on local (i.e. amongst near neighbours) community features such as basal stem areas and plant densities. Finally, whilst stand-level biomass is dominated by stand-level basal area (Baker *et al.* 2003), wood density is also an important factor (Baker *et al.* 2003). There are no wood density data in the Gentry data set, although in Baker *et al.* (2003), it fortunately appears to vary positively with total basal area.

We determined stem basal area for each plant recorded in each individual Gentry site. Ordinary least squares

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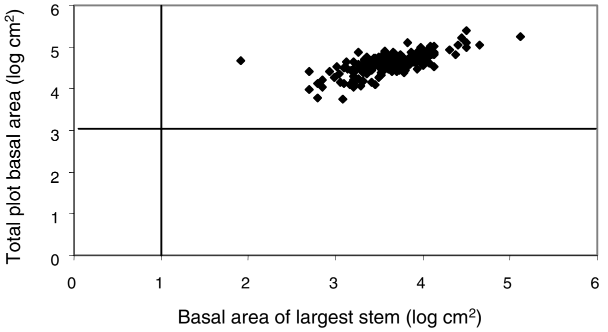

Figure 1. The relationship between basal area of the largest tree and total basal area in the Gentry data set ($n = 226$, total basal area $= 2.82$ (max. basal area)$^{0.49}$, $P < 0.01$).

$\log_{10}$–$\log_{10}$ regression was then used to determine the effects of the basal stem areas of larger trees on total sample site basal area.

Total basal area per 0.1-ha plot varied from 5.65 m^2 ha^{-1} at Pande (6° S, Tanzania) to 247.43 m^2 ha^{-1}at Puheyue (40° S, Chile). Plant density ranged from a minimum of 43 at Kitlope2 (52° N, Canada) to a maximum of 1010 at Brisefer (20° S, Mauritius). The total basal area correlated strongly with the size of the largest tree in each site (Figure 1, Table 1), although the largest tree only contributed an average of 10% of total forest stem basal area. The maximum contribution by an individual tree per site was 30% of total stem basal area (Makokou2 0°, Gabon). The four largest trees, on average contributed only 12.5% of the total forest basal stem area in each plot. The individual basal area of the four largest trees reported for each sample site was also individually, and in total, strongly correlated with total basal area (Table 1). For example, this means that the size of the second biggest tree across all plots explains 66% of the variation in total basal area per plot (Table 1). Contra the prediction that exceptionally large forest basal areas should occur in wet-tropical sites (see above), the largest trees and the plots with the most massive basal area occurred in the extra-tropical Puheyue sample site (in cool-temperate Chile). Stem numbers (plant density) and total forest stem basal areas were not statistically significantly correlated (Table 1). Therefore, in terms of total basal area, the presence of large trees cannot be compensated for by the presence of numerous smaller trees.

Table 1. Coefficients of correlation for $\log_{10}$–$\log_{10}$ regression of total basal area against plant density N and the basal stem areas of the largest four trees in each of 226 Gentry transects.

	Basal area of				
Number of stems	Largest	2nd	3rd	4th	Sum 1–4
0.07^{ns}	0.75*	0.81*	0.84*	0.85*	0.84*

ns = not significant, * = $P < 0.01$.

The Gentry database is dominated by tropical rather than temperate sites and does not include data from potentially exceptional communities like the Northwest redwood or Tasmanian mountain-ash forests. It thus remains to be seen whether other environmental factors, such as low night-time temperatures and respiration rates, correlate with the presence of high basal areas in some cool-temperate areas. It is nevertheless clear that some extra-tropical indigenous forests rival wet-tropical communities in terms of total stem basal areas and thus presumably total standing plant biomass (i.e. when allowance is made for variation in species allometry and wood density).

Local disturbance rates are likely to be an important determinant of maximum plant size and thus total community basal stem area and biomass (Niklas *et al.* 2003). Arguably, individual trees require time to achieve a large size and the presence of a series of large individuals in a community sample suggests the absence of immediate biotic or abiotic disturbance. In this regard, the basal area of the largest tree per sample site is strongly correlated with that of the second largest tree per plot (log-log $r = 0.83$), the third largest ($r = 0.79$) and with the fourth largest ($r = 0.76$). Similarly, the basal area of the second largest tree is strongly correlated with that of the third largest ($r = 0.95$), and that of the third largest tree with the fourth largest ($r = 0.95$). Thus, the presence of a large tree reflects the presence of other large trees and this is correlated with high basal area. Together with relatively low disturbance rates, high basal area may also be due to the presence of long-lived large tree species, especially conifers.

Beerling & Woodward (2001) incorporate disturbance (a fire module) in their dynamic global vegetation model (DGVM) to explain why the biomass of savannas is so much lower than predicted on the basis of their NPP models. Similarly, Chapin *et al.* (2002) indicate that tropical savannas despite having second highest NPP (behind tropical forests), only have fifth highest biomass. We argue that disturbance may also need to be invoked to explain variation in basal area and biomass amongst indigenous forests.

At a more fundamental level, large tree size may be associated with high basal area and biomass because large trees use fewer resources than predicted on the basis of their size alone. Large and arguably old individuals contain proportionally less living matter (in the form of secondary non-living, albeit mechanically functional tissues; see Franco & Kelly 1998) and they may have more rotten stems or defective or smaller crowns than their smaller and presumably younger counterparts. Finally, there are statistical and sampling issues that need to be resolved before we more comprehensively understand the determinants of total forest stem basal area. For example, we note that the basal area of the largest tree,

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or trees, and the total basal area of a particular forest sample are interrelated and thus present problems in terms of statistical auto-correlation. One statistical way to deal with this potential problem is to determine the relationship between the basal area of the largest tree or trees and the basal area of the "rest" (= total − largest) of the community sample. When used, this protocol still obtains a high correlation between these two parameters of interest using the Gentry data base ($r = 0.62$). An additional methodological problem exists. The canopies of large trees rooted in the narrow plots (2 m wide) such as those sampled by Gentry may exceed plot boundaries significantly, thus artificially inflating local basal area. Unfortunately, Gentry typically provided data on a single-transect basis, and so we have no measure of the variance in total basal area within each site. However, the fact that total basal area is strongly correlated with size of not only the largest tree but also the second, third and fourth largest tree suggests that this potential sampling artifact (i.e. inclusion of an occasional large tree on the margin) is not serious.

In summary, we have shown that the size of the largest trees is strongly correlated with total forest basal area. We believe that the most plausible reason for this correlation is the ecological or evolutionary effects of disturbance, which allows for the evolution of large size, the accumulation of secondary plant tissues (necromass), and thus an increase in plant size and longevity. If true, then we predict that latitudinal or other world-wide patterns observed for standing forest biomass may reflect ecological factors influencing disturbance regimes, far more than plant community subsistence levels or respiration and photosynthetic rates. Also, if global change impacts disturbance regimes in forests, this can be expected to impact biomass levels.

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