Towards a functional trait based research program within the Center for Tropical Forest Science

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The Center for Tropical Forest Science (CTFS) commissioned a working group to explore how a trait based research program might capitalize on the existing CTFS program. The working group met on 25 and 26 June 2006 and included Dan Bunker, Jim Dalling, Stuart Davies, Sandra Díaz, Bettina Engelbrecht, Kyle Harms, Kaoru Kitajima, Nathan Kraft, Christian Marks, Peter Reich, Renato Valencia, Ian Wright, Joe Wright and Amy Zanne. This report summarizes their recommendations.

Plant functional traits – a brief introduction

Functional traits capture fundamental tradeoffs that determine species' ecological roles. The tradeoff between the number of seeds produced and the size of each individual seed provides a clear cut example. Large seeds provision robust seedlings able to succeed where competition is intense and resources are scarce, but can only be produced in relatively small numbers. In contrast, tiny seeds fail where competition is intense, but can be produced in copious numbers that increase the chance of dispersing to ephemeral sites with few competitors and high resource availability. Thus, seed size is an easily measured functional trait that is likely to provide insight into the relative dispersal and competitive abilities of different plant species. Other key functional traits are believed to provide similar insights with respect to light capture (specific leaf area or leaf area per unit leaf dry mass), photosynthesis (leaf nutrient concentrations), defense against pests (wood density, leaf toughness) and other aspects of competitive ability (plant size). Collectively, these and other key functional traits help to determine the ecological roles of different plant species.

There is growing recognition that many ecological questions can be addressed effectively beginning with a thorough understanding of how and why key "functional'" traits are related, and how these traits affect ecological outcomes such as where a species grows best and where it is most competitive. Functional traits have been used recently to address a wide range of ecological questions including (1) to parameterize dynamic global vegetation models, (2) to parameterize carbon, nutrient and water budget models, (3) to predict impacts of environmental change including climate change, (4) to predict vegetation change along physical gradients, (5) to predict plant effects on ecosystem function and resilience, (6) to test fundamental trade-offs in plant design and ecophysiology, (7) to parameterize land management models, (8) to test evolutionary and phylogenetic relationships among species, and (9) as a data source for zoologists and others to evaluate many additional hypotheses (Westoby et al 2002, Cornelissen et al. 2003, Reich et al 2003, McGill et al. 2006, Westoby and Wright 2006). Several international efforts are now underway to compile existing functional trait data for both plants and animals; however, the existing trait data is severely limited for tropical species. We also lack any large-scale quantification of how well functional traits actually do determine ecological outcomes and the ecological roles of species.

The 18 large tropical forest plots maintained by the Center for Tropical Forest Science (CTFS) provide four unique resources to evaluate and develop a trait-based research program that will allow us to tackle questions such as these for tropical forests.

The four unique resources are vital rates measured for up to 6,200 species, spatially explicit plant performance measured in fully mapped tree neighborhoods, large spatial scales of 1 km by 0.5 km (50 ha), and replication across tropical Africa, America and Asia. The continuously monitored vital rates include individual recruitment, growth and mortality at all 18 CTFS sites and population-level seed production at five of those sites. These life history data offer the opportunity to evaluate the ecological significance of the functional traits adopted by the global plant trait research program by evaluating relationships between vital rates and functional traits for hundreds to thousands of species. The second unique resource – spatially explicit plant performance in fully mapped neighborhoods – offers the opportunity to explore how plant traits might contribute to stand structure in tropical forests. The third unique resource – large spatial scale – offers the opportunity to evaluate the ability of trait-based models to scale up from individuals to stand-level properties. The final unique resource – pantropical replication – permits the broadest possible biogeographic and phylogenetic perspective. The recommendations described later in this document return to these opportunities.

Plant functional trait data also enable many other types of research. As just one example, zoologists studying pollinators, herbivores, frugivores and granivores require plant trait data including information on phenology, leaf, flower, fruit, diaspore and seed traits. The future availability of plant functional trait data will attract both botanists and zoologists to the CTFS plots. This report will next describe the present-day availability of plant trait data for CTFS species. The limited availability of functional trait data is then used to motivate the three recommendations made by the working group.

The availability of plant trait data for species in the CTFS plots today

Traits included in every recent listing of the most important functional traits of plants include adult plant height, specific leaf area (SLA; leaf area per unit dry mass), leaf size, seed size and wood density (Weiher et al; Westoby et al 2002; Cornelissen et al 2003; Diaz et al 2004; Westoby & Wright 2006). Even these key traits have been determined for very few tropical species. Historically, wood density and seed mass have been measured for many more species than have other traits, the former due to its importance to the timber industry, and the latter due to long-term efforts by workers at the Kew Botanical Gardens. Still, just 33% and 13% of the species at 12 CTFS plots have had wood density and seed mass, respectively, determined for a conspecific population (Tables 1 and 2). Even the best studied CTFS sites have wood density and seed mass recorded for just 56% and 51% of their species, respectively (Tables 1 and 2). The percentages of species with conspecific determinations for other functional plant traits are much lower than for wood density and seed mass.

One way to address this paucity of data has been to substitute mean values for all congeneric or confamilial species when trait data are missing for a particular tropical species. This approach is unlikely to work well because trait variation is often large even among closely related species. The well-known negative relationship between tree growth rates and wood density provides a clear example of the limitations involved in substituting congeneric or confamilial mean values for missing species-level trait data (Fig. 1). Pearson correlation coefficients for this relationship are consistently negative and relatively strong when sapling growth rates are compared to the mean of all wood density determinations for conspecific populations (Fig. 2A). The correlations are less strong when the mean for congeneric populations is substituted (Fig. 2B) and cluster around zero when the mean for confamilial populations is substituted (Fig. 2C). Wood density is also known to vary among conspecific populations with environmental conditions (e.g., lower wood densities where rainfall is higher). The measurement of plant traits at CTFS sites will eliminate the variation introduced by using values for conspecific and more distantly related populations from other sites and improve relationships observed within the CTFS data sets. In the meantime, the limited availability of plant trait data for the 6,200 tree and shrub species in the CTFS plots limits progress on a trait-based research program.

Recommendations of the plant traits working group

The working group made three recommendations to facilitate a trait-based research program that capitalizes on the CTFS data. The first is to draw upon published florulas and herbaria to create databases for selected plant traits for CTFS species. The second recommendation is to jump start the collection of additional data for key functional traits for the many CTFS plots that lack such data. This will require new field work. The third recommendation is to undertake preliminary analyses for BCI where the most trait data are now available. The implementation of these three recommendations will create databases that will attract other investigators to CTFS sites and facilitate successful proposals to fund further trait-based research at CTFS sites. The three recommendations will now be described in greater detail.

Recommendation 1: Trait data from florulae and herbarium specimens

Plant taxonomy is based on floral traits because flowers are morphologically consistent across conspecific populations. Botanists also have a long-standing interest in fruit and seed traits. As a consequence, most herbarium specimens include flowers or fruits and florulae describing the plant species present in a geographic region (e.g., Croat 1978) often provide detailed descriptions of flowers, fruits and seeds. These resources could be used to accumulate species by trait databases quickly for most CTFS sites.

Flower traits are now largely overlooked in trait based research programs (e.g., Cornelissen et al. 2003) but are important for many reasons. Dioecism (male and female individuals) versus monoecism (hermaphroditic individuals) is crucial demographically, and dioecy is much more common in the tropics than at higher latitudes. Dioecy and other flower morphologies can prevent inbreeding. Flower colors and size determine pollination syndromes. Flowering phenology (timing) determines the seasonal availability of nectar and pollen resources for flower visitors. The free availability of flower trait by species data bases would attract zoologists working with bees, hummingbirds and other flower visitors to CTFS sites. And, as with any trait by species data base, a wide range of hypotheses could be evaluated immediately. Topical questions range across subjects as diverse as physiology (Does the quality of forest light influence floral color and pollination syndromes?) to community assembly (Are coexisting species more or less similar than expected by chance?).

Fruit traits are also overlooked in trait based research programs with the exception of diaspore mass and shape and seed mass (e.g., Cornelissen et al. 2003). Fruit colors and size determine seed dispersal syndromes, and fruiting phenology determines the seasonal availability of fruit and seeds for frugivores and granivores. Fruit and seed traits are particularly difficult to collect because many tropical species fruit successfully at multi-year intervals, fruit crops are often infested with insects and pathogens, and frugivores and granivores compete relentlessly with biologists for sound fruit and seeds. Fruit color, size and season are often described in florulae and on herbarium sheets. Diaspore shape can be measured directly from herbarium sheets. There is an excellent relationship between seed dry mass and diaspore volume estimated as length by width by depth measured from herbarium specimens for the BCI flora ($r^2 = 0.94$, NCEAS plant life history working group unpublished data). As with flowers, the free availability of fruit/diaspore/seed trait by species data bases would facilitate tests of a wide range of hypotheses and attract zoologists working with frugivores and granivores to CTFS sites.

The working group did not feel that it would be cost effective to screen the published literature for other plant functional traits for CTFS species. A plant life history working group convened at NCEAS has already discovered that even the most widely measured plant functional traits are generally unavailable for tropical forest plants. In sum, the first recommendation is to assemble flower, fruit and seed trait data from published florulae and from herbarium specimens.

Recommendation 2: The collection of new plant trait data across CTFS sites

The working group identified five key traits to be targeted for new data collection. The five key traits are adult plant height, wood density, specific leaf area, leaf nutrient concentrations, and seed mass. Collectively, these five key traits help to determine relative competitive and dispersal abilities, light capture and photosynthetic efficiencies and herbivore and pathogen defenses as briefly described in the Introduction (also see Westoby et al. 2002, Reich et al. 2003, Wright et al. 2004). The working group also identified nine additional traits that are each important in their own right and that are easily measured as the key trait is measured. For example, crown dimensions can be recorded as plant height is recorded, a variety of leaf traits can be measured on the same leaf samples, and several traits can be measured for the same diaspores. Table 3 presents the 14 plant functional traits to be measured for selected species at as many CTFS sites as possible. Each trait has a well established association with competitive ability, defenses against herbivores, responses to gradients in climate, and/or responses to gradients in disturbance regime (Table 3). We note that root traits are conspicuously absent from Table 3. It would be premature to include root traits because inter-individual variation in root traits of field-grown plants is still unknown, which makes it impossible to identify root traits that can be used to characterize species in a consistent, reliable manner. Due to the variation in plant traits among closely related species (Fig. 2) and even among conspecific populations, it will be important to measure the 14 key traits for plants growing naturally at the CTFS sites.

The procedure used to select species will be crucial. Randomly selected species are required to scale up to ecosystem properties. The most abundant species are required to evaluate neighborhood structure. Phylogenetically diverse species are required to evaluate many evolutionary questions. The working group recommends that trait data be collected for a core of randomly selected species. These randomly selected core species should also be supplemented by targeting the most abundant species in each CTFS plot and phylogenetic pairs of closely related species growing under contrasting conditions across the CTFS plots. Carefully chosen phylogenetic pairs can be used to evaluate the key hypothesis that functional traits shift in a consistent manner with growing conditions. Examples include fertile versus infertile soil, rain forest versus dry forest, and New versus Old World forests. Metadata should carefully note the reason each species was selected for measurement so that future analyses can isolate a truly randomly selected set of species. The numbers of species to be targeted must be tailored to the species diversity and the financial and human resources available at each CTFS site.

The methods used to measure plant functional traits are well established, and the adoption of standard methods will facilitate comparisons of CTFS trait data with other global trait data sets. The working group recommends that the CTFS adopt the methods described by Cornelissen et al. (2003) for 12 of the 14 traits in Table 3. Standardized methods to measure crown depth and crown diameter are still being identified by S. J. Wright. Basic soil fertility measurements are also needed for each CTFS plot to inform comparisons with other trait data sets. These soil fertility measures should include the depth of the mineral soil and, for the upper 15 cm of mineral soil and for any organic layer found above the mineral soil, total N, P and organic C concentrations, pH, silt/sand/clay fractions, cation exchange capacity, and plant-available P. The working group recommends that the methods of the RAINFOR alliance (http://www.geog.leeds.ac.uk/projects/rainfor/) be adopted for soil analyses to facilitate comparisons with other tropical forests.

It will be crucially important to standardize plant trait measurements across CTFS sites. This might be accomplished by sending the same team of technicians to all sites. Alternatively, technicians from as many sites as possible might be brought together for training, with technicians sent only to those sites that lack appropriate personnel. Training might take place at a CTFS site with limited human resources (i.e., not BCI). Wright, Valencia and Kraft could lead a training program at Yasuni in March 2007 that would also jump start the trait data set for Yasuni. In sum, the second recommendation is to collect new data for 14 plant functional traits from as many CTFS sites as possible.

Recommendation 3: Preliminary analyses of trait and demographic data for BCI

Successful proposals are based on the demonstrated value of the proposed research. The existence of relatively extensive plant trait data for the trees and shrubs of the BCI 50-ha plot offers an opportunity to demonstrate the potential power of the full CTFS data set for trait-based studies. The working group proposes that an analysis of the BCI data proceed in four steps.

The first step would be to evaluate relationships between vital rates and plant functional traits. This first step will extend our understanding of plant functional traits because the vital rates known for all CTFS species are so rarely available elsewhere. Well known relationships will be confirmed (Fig. 1), but there will also be surprises. For example, figure 3 presents a previously unsuspected relationship between sapling mortality and seed dry mass from available CTFS data. Seed dry mass does not directly influence the mortality of saplings of 15-50 mm in diameter at breast height. Rather, seed dry mass must be correlated with other traits that do influence mortality. It should be possible to evaluate relationships among seed mass, correlated traits, and sapling mortality for BCI to explore the causal relationships that underlie figure 3. The trait-based research program has firmly established relationships among functional traits (McGill et al. 2006, Westoby and Wright 2006). The CTFS offers the opportunity to explore the crucial and so far little documented relationships among functional traits and ecological outcomes manifested through vital rates.

The second step would be to estimate vital rates for standardized levels of resource availability and then to use these standardized vital rates to refine relationships with functional traits. Figures 1 and 3 use mean vital rates calculated for all individuals in a population. These mean vital rates are influenced by intrinsic physiological differences among species and also by resource availability where saplings grow. For example, light-demanding species grow faster than shade tolerant species both because of inherent physiological differences and also because shade tolerant species are distributed widely throughout the shaded understory where low light levels limit growth rates while light demanding species tend to be located in high light microsites in forest gaps. Maps of resource availability are available over the BCI 50-ha plot for light (Welden et al. 1991), nutrients and water (J Dalling, K Harms, R Stallard, JB Yavitt, unpublished data). These mapped resource availabilities make it possible to map sapling performance relative to resource availability for BCI species (Welden et al. 1991, Wright et al. 2003). Vital rates can then be calculated for saplings growing at sites characterized by a small range of low and contrasting small range of high resource levels. This will limit the unexplained variation in vital rates and help to identify the contribution of habitat-dependent resource availability and intrinsic physiological differences to interspecific variation in vital rates.

The third step of the proposed BCI research protocol would be to use vital rates standardized for resource levels to explore how functional traits influence ecological outcomes. As an example, it is frequently hypothesized that specific leaf area (SLA = single sided leaf area divided by leaf dry mass) is positively correlated with carbon gain and hence plant growth in high light environments. This hypothesis leads to the prediction that sapling growth and SLA should be positively related in high light environments but not necessarily in low light environments. The evaluation of this and similar hypotheses will explore mechanisms that have been hypothesized to explain relationships between functional traits and vital rates.

The final step of the research protocol proposed for BCI would use vital rates standardized for resource availability to examine how local tree neighborhoods are assembled. Local tree neighborhoods might be composed of individuals whose resource-dependent vital rates converge on local resource levels if those resource levels persist over long time scales (i.e., nutrient availability related to bedrock or moisture availability related to topography and runoff). Alternatively, local tree neighborhoods might be composed of individuals whose resource-dependent vital rates are very different if resource levels vary at temporal scales shorter than the lifetimes of some trees (i.e., light availability related to tree fall gaps) or if competitive interactions are stronger and lead to competitive exclusion by species with similar resource-dependent vital rates. Phylogeny could be incorporated into similar analyses that evaluated the phylogenetic dispersion of vital rates standardized for resource availability and the divergence or convergence of local neighborhoods on these traits. The demonstration of each of the four steps of this proposed research protocol for BCI would generate intense interest in determining whether the relationships discovered held across the biogeographic regions, soil fertility differences, and seasonal and annual rainfall regimes present among the 18 CTFS sites.

Conclusions

The classification of terrestrial plant species by continuously varying functional traits promises solutions to important ecological questions at community, ecosystem, biome and global scales. The CTFS databases offer unique opportunities to evaluate the underlying assumptions of these trait based research programs and also to extend and develop such research. The working group recommends that the CTFS move quickly to accumulate functional trait data for flowers, fruits and seeds from published florulae and herbaria (recommendation 1), collect new trait data for leaves and stems (recommendation 2), and conduct preliminary analyses of the vital rate and functional trait data already available for BCI (recommendation 3). These three activities will attract a wide range of investigators to the CTFS sites by providing basic information on the natural history of hundreds to thousands of tree species that is missing for other tropical forests and set the stage for future proposals to develop a trait based research program for tropical forests.

Table 1. The closest taxonomic level available to supply an estimate of wood density for tree and shrub species from 12 CTFS plots. The best wood density estimate is the mean value for all wood density measurements for confamilials when no congeneric data are available, for congeners when no conspecific data are available, and for conspecifics when the appropriate data are available. Data were compiled from the literature by Jerome Chave and Helene Muller-Landau.

	Taxonomic level used to supply value			
CTFS site	family	genus	species	Number of species
BCI	9.8	42.3	48.0	317
Congo – Ituri	40.2	42.4	17.4	455
HKK	7.0	49.8	43.2	301
Korup	37.6	49.2	13.2	492
Lambir	4.0	58.5	37.5	1190
La Planada	21.3	71.5	7.2	221
Luquillo	10.2	38.8	51.0	147
Mudumalai	12.2	31.1	56.8	74
Palanan	9.4	61.9	28.6	339
Pasoh	6.0	40.5	53.5	819
Sinharaja	10.2	75.7	14.1	206
Yasuni	12.2	61.3	26.5	1142
Total	13.7	53.5	32.8	
Number of species	780	3051	1872	

Table 2. The closest taxonomic level available to supply an estimate of seed mass for tree and shrub species from 12 CTFS plots. The best seed mass estimate is the mean value for all seed mass measurements for confamilials when no congeneric data are available, for congeners when no conspecific data are available, and for conspecifics when the appropriate data are available. Seed mass data were compiled by Jerome Chave and primarily from data bases maintained at the Kew Botanical Garden.

	Taxonomic level used to supply value			
CTFS site	family	genus	species	Number of species
BCI	6.6	42.7	50.6	316
Congo - Ituri	29.5	62.6	7.9	441
HKK	14.3	65.3	20.3	300
Korup	34.6	61.7	3.7	491
Lambir	19.6	72.7	7.7	1181
La Planada	27.8	69.1	3.1	223
Luquillo	8.2	54.8	37.0	146
Mudumalai	2.8	50.7	46.5	71
Palanan	18.9	73.7	7.4	338
Pasoh	21.5	66.6	11.9	817
Sinharaja	15.1	75.1	9.8	205
Yasuni	17.9	70.5	11.6	1147
Total	20.2	66.9	12.9	
Number of species	1147	3795	734	

Table 3. Fourteen plant functional traits to be targeted in a survey across 18 CTFS plots. '+' marks denote well established associations with environmental gradients in climate, environmental gradients in disturbance regime, competitive ability, and defense against herbivores and pathogens. Recommended sample sizes are numbers of individuals and numbers of items (i.e., leaves, diaspores or seeds) per individual (Cornelissen et al. 2003).

Trait (units)	Literature association of trait with				Sample Size	
	Response to		Com-petitive ability	Defense	Indi-viduals	Items
	Climate	Distur-bance				
Whole-plant traits						
Growth form (categorical)	+	+	+	+	-	-
Plant height (m)	+	+	+	+	10-25	-
Crown depth (m)		+	+		10-25	-
Crown diameter (m)		+	+		10-25	-
Leaf traits						
Size (mm^2)	+		+	+	5-10	2
Specific leaf area ($m^2\ kg^{-1}$)	+		+	+	5-10	2
N concentration ($mg\ g^{-1}$)	+	+	+	+	5-10	2
P concentration ($mg\ g^{-1}$)	+	+	+	+	5-10	2
Dry matter content ($mg\ g^{-1}$)				+	5-10	2
Fiber content ($mg\ g^{-1}$)				+	5-10	2
Stem traits						
Wood density ($mg\ mm^{-3}$)	+	+		+	5-10	-
Regenerative traits						
Diaspore shape (unitless)		+			3-10	5
Diaspore mass (mg)		+			3-10	5
Seed mass (mg)		+	+	+	3-10	5

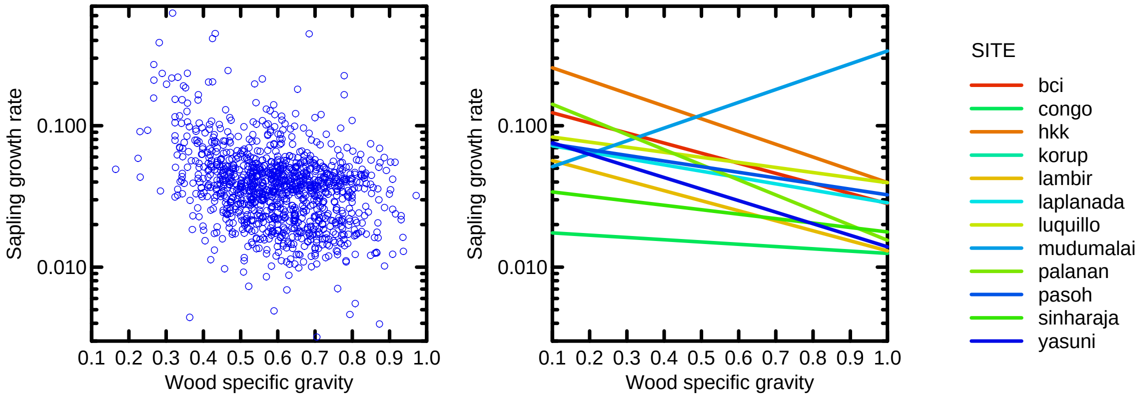

Figure 1. The well-known negative relationship between tree growth rates and wood density or specific gravity for 1,127 sapling (15-50 mm in diameter at breast height) populations from 12 CTFS plots. The percentage of variation in growth rates explained by wood density (the r^2-value) is just 10% when all sites are pooled (left panel) but rises to 50% when site is included in the analysis as a grouping factor (right panel). The positive slope for Mudumalai represents just four species and their exclusion does not alter the high r^2-value when site is included. Wood densities are the mean of determinations for conspecific populations compiled from the literature by Jerome Chave and Helene Muller-Landau.

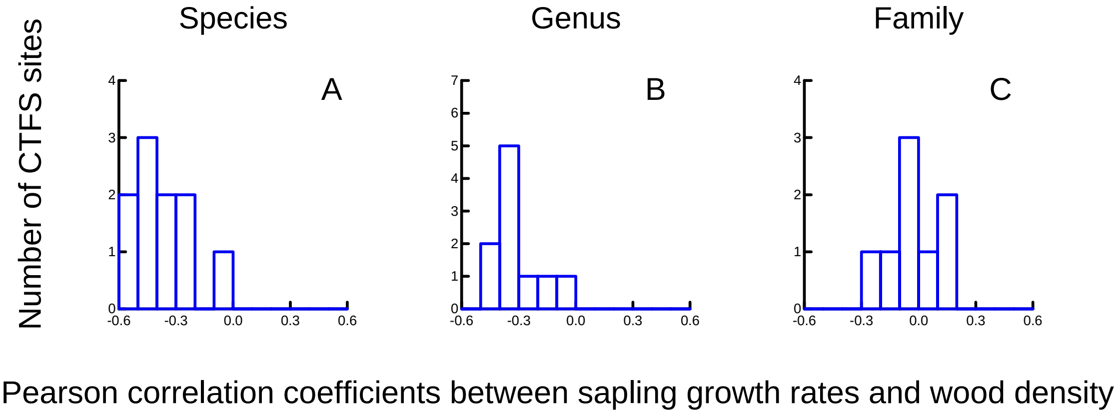

Figure 2. The negative relationship between sapling growth rates and wood density (see Fig. 1) decays rapidly with the taxonomic level used to provide wood density estimates. Each histogram presents the number of CTFS sites characterized by Pearson correlation coefficients between sapling growth rates and the best available estimate of wood density for each species. The best available estimate of wood density is the mean value for all conspecific populations (panel A), for all congeneric populations when conspecific populations are lacking (panel B), and for all confamilial populations when congeneric populations are lacking (panel C).

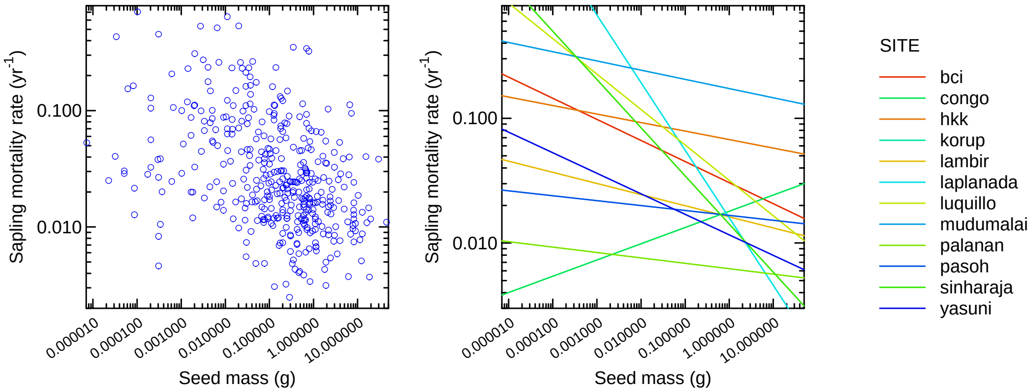

Figure 3. A surprising negative relationship between sapling mortality and seed dry mass for 404 sapling (15-50 mm in diameter at breast height) populations from 12 CTFS plots. The percentage of variation in survival explained by seed mass (the r^2-value) is just 17% when all sites are pooled (left panel) but rises to 54% when site is included as a grouping factor (right panel) in an analysis of covariance. The positive slope for the Congo-Ituri represents 12 species and their exclusion does not alter the ANCOVA r^2-value. Seed dry masses are the mean of determinations for conspecific populations compiled from the literature and mostly from the Kew Botanical Garden seed mass database by Jerome Chave.

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