

Functional Diversity of Tree Species in Warm-Temperate Rain Forest Communities of Yakushima Island

Sachi Tanabe¹, Takuya Kubo¹, Shin-ichiro Aiba², Takashi Kohyama¹

¹*Faculty of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan*
tanabe@ees.hokudai.ac.jp

²*Faculty of Science, Kagoshima University, Kagoshima 890-0065, Japan*

Introduction

Natural plant communities are composed of many plant species sharing common traits as autotroph, or competing with each other for common limiting resources. Their coexistence has been examined in terms of differential requirement of multiple resources, spatio-temporal heterogeneity, disturbance-mediated non-equilibrium states and so on. In any situation, it is crucial to describe how species are similar to, or different from each other. From the view of community organization *via* interspecific trade-offs (Silvertown 2004), community response to natural and human disturbance is demonstrated by differential response of species thereby overall ecosystem functioning is maintained efficiently compared to single-species-dominated ecosystems.

We characterize plant species composing warm-temperate rain forests in lowland Yakushima Island from the view of ecomorphological and demographic traits. Yakushima Island located in south from Kyushu Island, Japan, is characterized by well-reserved primary warm-temperate rain forests at around 300-800 m altitude. We show how species differentiation in regeneration process contributes to the resilience of forest ecosystems to various types of perturbation. The within site, and within vegetation type comparison of traits will provide us basic information for among site/type comparison. We paid attention to leaf and seed characteristics in relation to regeneration traits in particular, where detailed examination of leaf longevity with Bayesian analysis is to be presented separately (Kubo, Ushihara and Kohyama, in preparation). In this report we focus on the relationship between seed size, seedling architecture and the choice of regeneration sites among co-occurring warm-temperate rain forest tree species.

Research Sites and Methods

Research sites were set on warm-temperate rain forests in southwestern part of Yakushima Island, mainly watersheds along River Segire, River Ohko and River Koyohji. The detail of the sites can be found in literature (Kohyama 1986, Kohyama and Grubb 1994, Aiba and Kohyama 1996). We use dataset first appeared in these papers.

Roadside census was carried out in the exposed, mountainside berm edge of the Ohko Forestry Road in Ohko Basin. We set two transects, ca. 35 m long and 55 m long with 1 m wide. All saplings taller than 50 cm and less than 2 cm diameter at breast height were monitored, just like the sapling census in nearby Segire River Basin (Kohyama 1986).

Allometry examination was first made at various sites on the southwestern side of Yakushima Island in early July 2006. The unique topography of the warm-temperate forest consists of uniform Miocene granite covering the entire mountain body. Fourteen commonest shade-tolerant tree species were previously studied in a mature closed canopy with no influences of tree-fall gaps (Kohyama and Grubb 1994). 6 tree species

frequently seen along roadside banks, 3 of which also observed in shaded forest floors (*Eurya japonica*, *Rhododendron tashiroi*, and *Neolitsea aciculata*), were additionally selected for detailed study. Healthy, well-established seedlings with no breakage, resprouting, or root death, were then carefully excavated with a shovel for minimum root breakage in late October to early November 2006. Seedlings were defined as being less than 30 cm tall; shoot height ranging from 2-27 cm, excluding current-year seedlings. Total sample size summed up to 150 seedlings; 22 to 30 samples for each canopy and subcanopy species. Each seedling was carefully washed and dimensions measured. After dividing the plant into leaves, stems, and roots, each part was photocopied before being dried in an oven at 80 degrees Celsius for two full days. Although the root system was flattened for photocopying, the images were taken so that roots did not overlap with each other so that we could distinguish the actual root distribution. Seventeen species were sampled from habitats at two light conditions (forest floor and exposed road side).

Biomass allocation among root (below-ground) *versus* shoot (above-ground) and that within shoot dimensions (stem *versus* foliage) were analysed using a hierarchical Bayesian model for handling co-occurring all species at once. In this statistical model, factors affecting biomass allocation was categorized into two types—fixed and random effects. We set total seedling weight as the fixed effect that change the mean of the probabilistic distributions, leaving random effects to explain the change in variances dependent on unobservable factors such as unknown or individual seedling characteristics. Four parameters interpreting the fixed effects, deriving from prior distributions based on field data, were used in order to explain and infer the consequences of weight dependency and species difference in biomass allocation of shoot *versus* root and stem *versus* foliage dimensions. The Monte Carlo Markov Chain (MCMC) method was carried out using R2WinBUGS package on R 2.4.1 for acquiring the estimated posterior distributions of parameters. We assume that the probability biomass allocation to shoot p (thus root allocation is $1-p$) would follow the linear logistic model,

$$p = 1/[1+\exp(-z)], \quad (1)$$

where $z = \beta_1 + \beta_2[\log \text{ total biomass of seedling}]$. Equally, stem (q) *versus* foliage ($1-q$) biomass allocation were similarly presented,

$$q = 1/[1+\exp(-z')], \quad (2)$$

where $z' = \beta_3 + \beta_4[\log \text{ shoot biomass of seedling}]$. Each parameter contains a hierarchical structure consisting of a species-specific characteristic and a common characteristic among all 17 species.

Results and Discussion

Figure 1 shows the tendency across 14 shade-tolerant species, examined using dataset by earlier studies. Recruitment capacity is negatively correlated with maximum height (Fig. 1A), that is in accordance with the expected trade-off by the forest architecture hypothesis (Kohyama 1993). Density ratio of canopy gaps to closed stands is higher for shorter species (Fig. 1B), which supports the model implication that lower-layer species show the density spike at a younger stage of community development (T. Kohyama and T. Takada, in preparation).

Figure 2, summarizing the roadside species composition of saplings, suggests that the abundance there

(Fig 2B) is negatively correlated with seed size, but not for the sapling composition in forest gaps (Fig 2A). The two species, *Rhododendron tashiroi* (Rt) and *Eurya japonica* (Ej), are most abundant shade-bearing species in shallow-soil mountainside roadside. The occurrence of such shade-intolerant species as *Aleurites cordata* (Ac) and *Mallotus japonicus* (Mj) was restricted to valley-side road side with deep soil accumulation. When we plot maximum tree height against seed size among 14 shade-bearing species, there was a tendency that tall tree species have large seed size as compared to short tree species (Fig. 3). Such seed mass *versus* maximum adult size correlation is along general trends found in a wide diversity of land plants (Rees and Venable 2007). The dominance of short-stature species in gap-phase regeneration (Fig. 1B) may partly be explained by producing many regenerates (Fig. 1A) with small per-seed size.

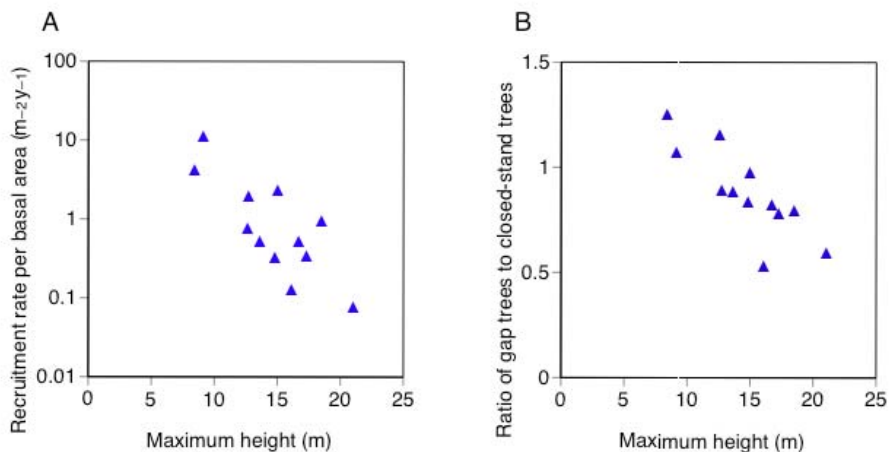


Fig. 1. Interspecific comparison of demographic performance among a dozen abundant shade-tolerant tree species in a primary warm-temperate rain forest in the Segire basin, Yakushima Island, southern Japan. (A) Recruitment rate per species basal area, and (B) ratio of tree densities at canopy gaps to those at closed-canopy stands, plotted against observed maximum height. Density and recruitment rate are defined above 2-cm trunk diameter at breast height. Based on census data of permanent plots monitored since 1981 (Kohyama 1986; Aiba and Kohyama 1996).

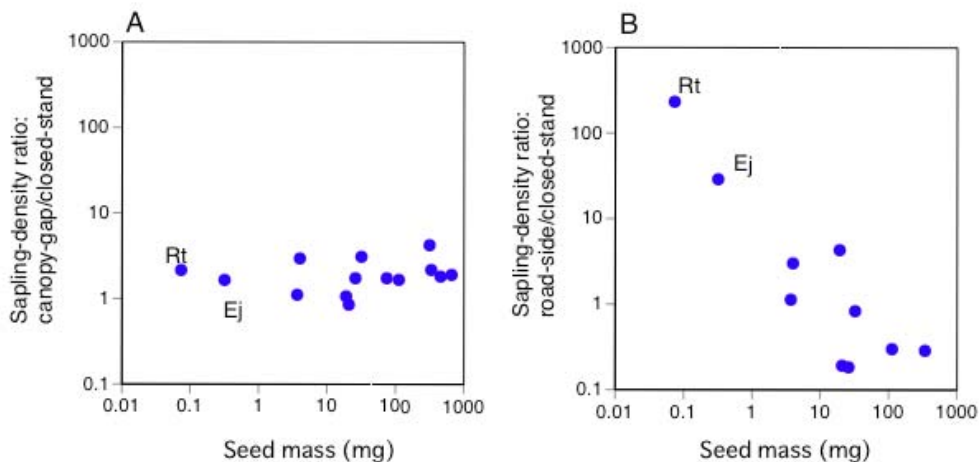


Fig. 2. Ratio in density of saplings (> 50 cm tall and < 2 cm dbh) between tree-fall gaps and closed stands (A), and that between roadside rocky banks and closed stands (B) for 14 abundant shade-tolerant species of warm-temperate rain forest in Yakushima, plotted against dry weight of seeds. Studied area is 2000 and 650 m² for closed stands and gaps (in Segire River basin), respectively, and is 90 m² for roadside banks (in Ohko River basin).

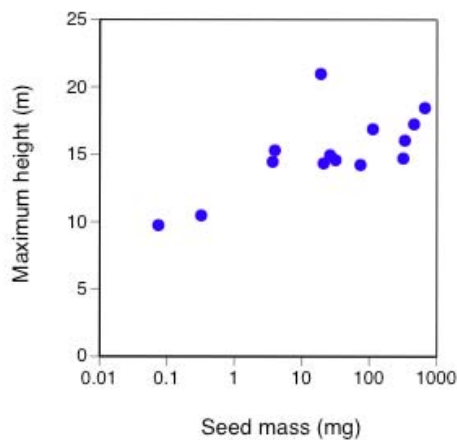


Fig. 3. Relationship between seed size and maximum attainable tree size of common 14 abundant shade-tolerant species in Segire River basin of Yakushima Island.

Two combinations of biomass allocation patterns among species were examined: (1) allocation patterns between root and shoot parts and (2) those within shoot, i.e. stem and foliage. In root versus shoot allocation, results showed that an average-sized individual, ignoring interspecific differences, would allocate resources to shoot biomass (Fig. 4). Species difference was found for eight species including large-seeded *Camellia sasanqua* (Cs) and small-seeded *Eurya japonica* (Ej), where significant species difference was recognized for those that do not include the mean of hyperspecies posterior distribution within the 95% confidence interval. When examining only the differences among species, *Eurya japonica* (Ej), *Cleyera japonica* (Cl), and *Litsea acuminata* (La) showed a positive response to shoot allocation within all 17 species. *Stewartia monadelphica* (Sm), *Aleurites cordata* (Ac), *Camellia sasanqua* (Cs), *Neolitsea aciculata* (Na) and *Acer morifolium* (Am), on the other hand, showed root allocation to be more significant. Overall, there was no significant dependency on total dry mass allocation with change in seedling size.

When comparing stem to foliage allocation, as Fig. 5 shows, allocation in shoot dimensions showed to slightly invest in foliage biomass. *Eurya japonica* (Ej) and *Symplocos tanakae* (St) were “foliage-investing” species, while two deciduous, shade-intolerant species *Stewartia monadelphica* (Sm) and *Aleurites cordata* (Ac) were classified as “stem-investing” species. Results showed that stem-investing species allocated biomass in roots, while foliage-investing species *Eurya japonica* was a shoot-allocating species when root-shoot biomass allocation was compared. No species difference was found for foliage dry mass dependency in stem versus foliage biomass allocation.

A distinctive interspecific difference in biomass allocation and its dependency on total dry mass or shoot dry mass in root versus shoot and stem versus foliage allocation patterns, respectively, was not established from these results. However, architectural differences in species were visible among species from observations. *Rhododendron tashiroi*, for example, developing shallower horizontal roots compared to other shade-tolerant species, nevertheless it did not show a significant trait in biomass allocation patterns. It can thus

be considered that factors other than biomass allocation would be involved with regulation in seedling architectural performance related to species diversity; even among root-allocating species, difference may occur between seedling height *versus* width dimensions. Results regarding biomass-allocating patterns would simply characterize one aspect of species' architecture; it would be insufficient in extensive comparison of species' architecture. Further analysis therefore, including architectural dimensions comparing above-ground and below-ground, such as depth *versus* height and crown *versus* root width, within above-ground and below-ground architectures will be necessary. It is also interesting to note that small-seeded species such as *Eurya japonica* and *Rhododendron tashiroi* and large-seeded species *Aleurites cordata* were both commonly seen along rocky roadside banks. While hypothesized that seedling architecture is correlated with seed size and its choices in sites for establishment, the classical proposal of the relationship between seed size and shade-tolerance may not directly apply for species studied here.

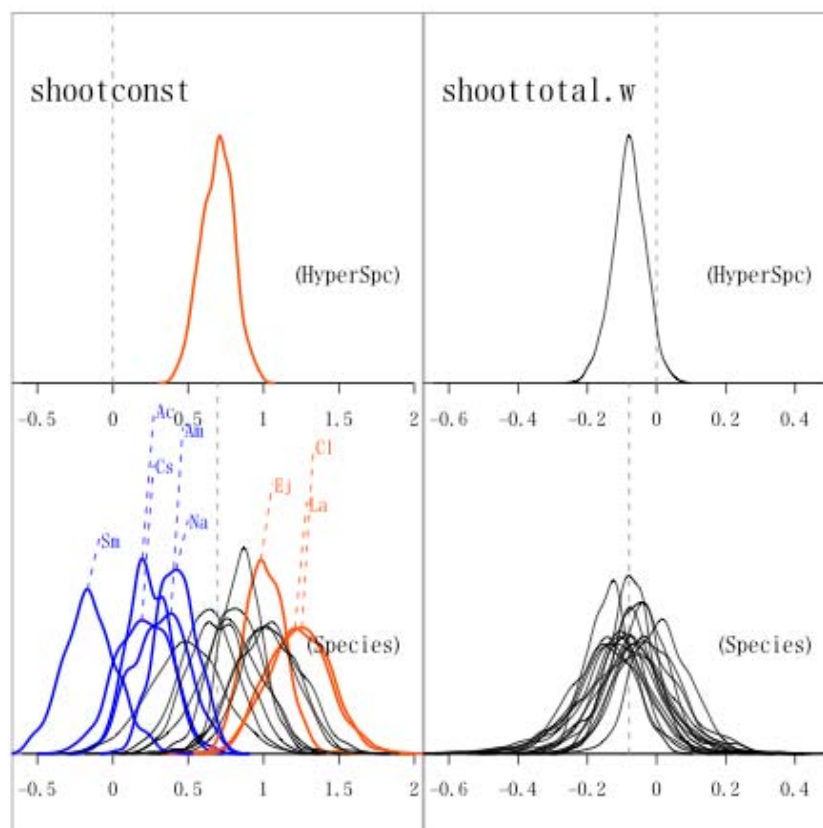


Fig. 4. Biomass allocation among root and shoot. The posterior distribution results of the hierarchical Bayesian model, each parameter expressed with 2 distribution panels. Vertical axes indicate frequency of distributions for posterior probabilities. Top panels, parameter distributions considering a common characteristic among all species (hyperspecies). Parameters which do not include a mean value of 0 within the confidence interval are shown in following colors; red as to those distributing in positive probabilities, blue for those in negative, black for those including the mean value within the confidence interval. Bottom panels, parameter distributions considering species difference, each line representing a species. Colors are sorted accordingly to the mean value derived from the posterior hyperspecies distribution. Panels on the **left** show results for constant term (β_1) for shoot *versus* root allocation patterns. Panels on the **right** show total mass dependency (β_2), in eqn (1).

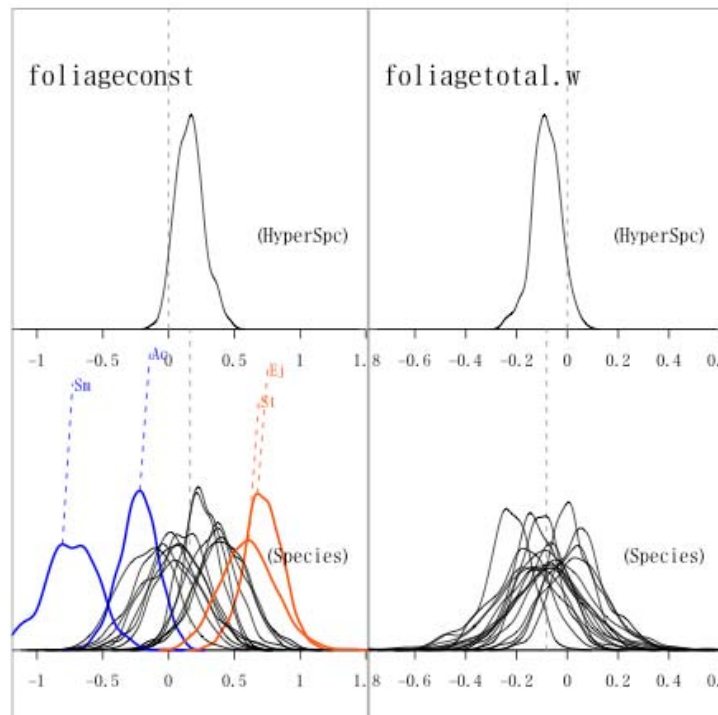


Fig. 5. Allocation patterns in stem and foliage. The posterior distribution results of the hierarchical Bayesian model, each parameter expressed with 2 distribution panels. Vertical axes indicate frequency of distributions for posterior probabilities. Top panels, parameter distributions considering a common characteristic among all species (hyperspecies). Parameters which do not include a mean value of 0 within the confidence interval are shown in following colors; red as to those distributing in positive probabilities, blue for those in negative, black for those including the mean value within the confidence interval. Bottom panels, parameter distributions considering species difference, each line representing a species. Colors are sorted accordingly to the mean value derived from the posterior hyperspecies distribution. Panels on the left show results for constant term (β_3) for foliage allocation patterns. Panels on the right show shoot mass dependency (β_4), in eqn (2).

Acknowledgments

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References

- Aiba S, Kohyama T (1996) Tree species stratification in relation to allometry and demography in a warm-temperate rain forest. *J Ecol* 84:207-218
- Kohyama T (1986) Tree size structure of stands and each species in primary warm-temperate rain forests of southern Japan. *Bot Mag Tokyo* 99:267-279
- Kohyama T (1987) Significance of architecture and allometry in saplings. *Funct Ecol* 1:399-404
- Kohyama T (1993) Size-structured tree populations in gap-dynamic forest - the forest architecture hypothesis for the stable coexistence of species. *J Ecol* 81:131-143
- Kohyama T, Grubb PJ (1994) Below- and above-ground allometries of shade-tolerant seedlings in a Japanese warm-temperate rain forest. *Funct Ecol* 8:229-236.
- Rees M, Venable DL (2007) Why do big plants make big seeds? *J Ecol* 95:925-936
- Silvertown J (2004) Plant coexistence and the niche. *Trends Ecol Evol* 19:605-611