Carbon Allocation and Growth-Survival Trade-Offs in Temperate Tree Species

著者	IMAJI Aya, SEIWA Kenji
journal or publication title	Journal of Integrated Field Science
volume	7
page range	9-13
year	2010-03
URL	http://hdl.handle.net/10097/48829

JIFS, 7 : 9 − 13 (2010) Symposium Paper

Carbon Allocation and Growth–Survival Trade-Offs in Temperate Tree Species

Aya IMAJI[1*] and Kenji SEIWA[2]

[1]Nara Forest Research Institute, Takatori, Nara, 635-0133, Japan
[2]Field Science Center, Graduate School of Agricultural Science, Tohoku University, Naruko-Onsen, Osaki, Miyagi, 989-6711, Japan
*e-mail:imaji@nararinshi.pref.nara.jp

Keywords: competition, defense, shade tolerance, species diversity, storage

Received 12 January 2010; accepted 1 February 2010

Abstract

The growth–survival trade-off is an important mechanism in maintaining species diversity in forest communities. The model hypothesizes that a negative correlation between growth rates in gaps and survival rates in the forest understory across tree species allows their coexistence in spatially heterogeneous light environments. Seedling survival in the shaded understory depends on the ability to defend against herbivores and pathogens, and/or ability to recover from biotic damage. However, relatively few studies have demonstrated carbon investment in defense and storage as a mechanism of the trade-off, and no studies have simultaneously examined carbon allocation to both defense and storage. We examined carbon allocation patterns to defense, storage, and growth in seedlings of two temperate species of differing shade tolerance. Carbon allocation to growth was higher for the shade-intolerant species compared to the shade-tolerant species, whereas carbon allocation to defense was greater for the shade-tolerant than shade-intolerant species. This contrasting carbon allocation pattern would result in a growth–survival trade-off. In addition, we found that the shade-tolerant species preferentially invested more carbon in defense than in storage, suggesting that optimal carbon allocation is inherent to individual tree species.

Trade-off model

Trade-off between growth and survival based on tree species specialization along resource gradients can contribute to species diversity in forest communities. This model proposes a trade-off between low-light survival and high-light rapid growth among co-occurring tree species in a forest (Fig.1). Rapid growth in gaps and low survival rates in the forest understory characterize light-demanding species, whereas high survival in the forest understory and slow growth rates in gaps characterize shade-tolerant species. In a heterogeneous environment, the trade-off has a role in equalizing overall recruitment success among tree species, thus generating species coexistence. In both tropical and temperate forests, evidence is increasing for the growth–survival trade-off (Kitajima 1994; Baraloto et al. 2005; Gilbert et al. 2006; Seiwa 2007).

Ability to persist in a shaded forest understory

The term “shade tolerance” is usually used to refer to the ability of plants to survive in low-light environments. It is thought that shade tolerance largely depends on physiological, morphological, and phenological mechanisms for light capture and utilization at low light intensity to maximize present and future

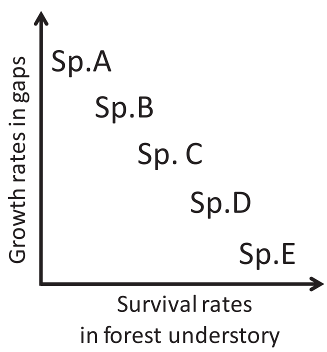

Fig. 1. Trade-off between growth rates in gaps and survival rates in the forest understory among tree species.

growth in the forest understory. These mechanisms include the capacity to maintain a positive carbon balance under low light flux, efficient use of sunflecks, optimal architecture favoring light interception, and phenological avoidance of shade stress (see references in Seiwa 1998). However, recent demographic studies clearly revealed that the most important cause of seedling mortality in the forest understory is attack by herbivores and pathogens (Seiwa 1998; Nakashizuka 2001), whereas seedling death directly caused by a negative carbon balance under low-light conditions is rare. It is likely that a lower ability to capture light under shaded conditions could lead to reduced investment of resources for defense against herbivores and pathogens, resulting in more severe attacks by natural enemies. Thus, increased ability to defend against natural enemies or ability to recover from biotic damage would enhance seedling survival in the forest understory. Previous studies found that shade-tolerant species usually invest more carbon in defense to protect against biomass loss from herbivores and pathogens (Coley 1987; Alverz-Clare and Kitajima 2007) and that shade-tolerant species invest more carbon in storage for recovery following tissue loss (Kobe et al. 1997; Myers and Kitajima 2007; Poorter and Kitajima 2007). Therefore, it seems that shade tolerance (i.e., ability to persist in the shaded understory) is largely determined by the ability to allocate as much carbon as possible to defense and storage in order to resist biotic stresses.

Ability to survive in gaps

In gaps, severe competition for light with neighboring plants usually occurs. Thus, to establish in gaps, carbon allocation to vertical growth is critical, particularly for light-demanding pioneer species (Myster 1993). Because of the limit to total carbon fixation, this can be achieved by preferentially investing carbon into new tissue at the expense of allocation to survival-enhancing traits such as defense and storage. These conflicting selective pressures predict that shade-tolerant species will lack competitive ability under high-light conditions, whereas light-demanding species are unable to persist for a long time in shaded conditions. Therefore, the trade-off between growth and survival is most likely caused by a trade-off between carbon allocation to growth and allocation to defense and storage (e.g., Kitajima 1994; Seiwa 2007; Kitajima and Poorter 2008; Fig.2).

Defense vs. Storage

A growing body of evidence supports the trade-off model in both tropical and temperate forests. However, most studies have focused on a single relationship, either between defense and growth (Coley 1987; Kurokawa et al. 2004) or between storage and growth (Myers and Kitajima 2007; Poorter and Kitajima 2007). Few studies have simultaneously examined relationships among defense, storage, and growth. Carbon allocation to defense and storage is important for the survival of seedlings, and both defense and storage incur carbon costs. Thus, the potential carbon investment to survival-enhancing traits remains to be determined. If preferential carbon investment is made in either defense or storage in plant species, these species may have different survival strategies, i.e., investment in deterrence or investment in damage-recovery mechanisms.

Carbon allocation to growth, defense and storage

Imaji and Seiwa (2010) examined the pattern of carbon allocation to defense, storage, and growth in seedlings of two temperate broadleaf tree species with contrasting shade tolerance (shade-intolerant species: *Castanea crenata*; shade-tolerant species: *Quercus mongolica* var. *grosseserrata*). RGR (relative growth rate) in gaps was higher in the light-demanding species, *C. crenata*, compared to the shade-tolerant species, *Q. mongolica* var. *grosseserrata* (Fig.3). In contrast, concentrations of defense compounds (condensed tannins and total phenolics) were higher in *Quercus* than *Castanea* at both sites (Fig. 4a,b). TNC (total non-structural carbohydrate) pool sizes did not differ between the two species (Fig.4c). Thus, interspecific trade-offs between growth and de-

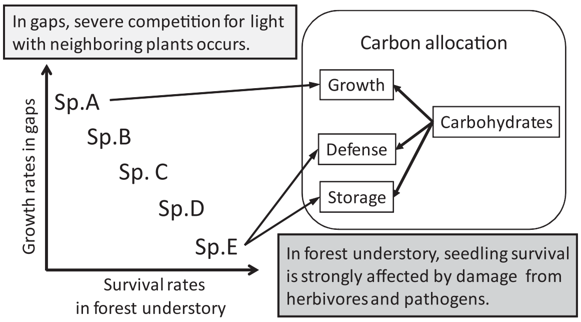

Fig. 2. Relationship between growth–survival trade-off and carbon allocation.

fense were observed in species differing in shade tolerance. These results suggest that *Castanea* allocates more carbon to shoot elongation at the expense of defense, which enables seedlings to regenerate under high-light conditions where rapid vertical growth is required to compete with neighboring plants for light. In contrast, *Quercus* puts more carbon into defense, rather than growth and storage, which enables seedlings to persist in the shaded understory where activity of natural enemies (herbivores and pathogens) is high. From the results of relationships in carbon allocation to defense and storage (Fig. 5a,b), relative allocation to defense against storage was usually higher in *Quercus* compared to *Castanea*. This suggests that *Quercus* preferentially allocates carbon to defense rather than to storage. Therefore, the optimal

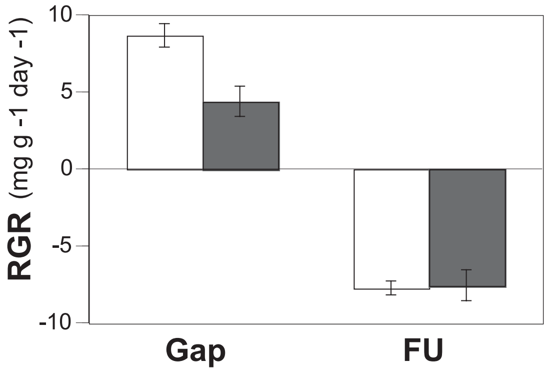

Fig. 3. Relative growth rate (RGR) of the light-demanding species *Castanea crenata* (white bars) and shade-tolerant species *Quercus mongolica* var. *grosseserrata* (shaded bars) in gaps and the forest understory (FU) (Imaji and Seiwa 2010).

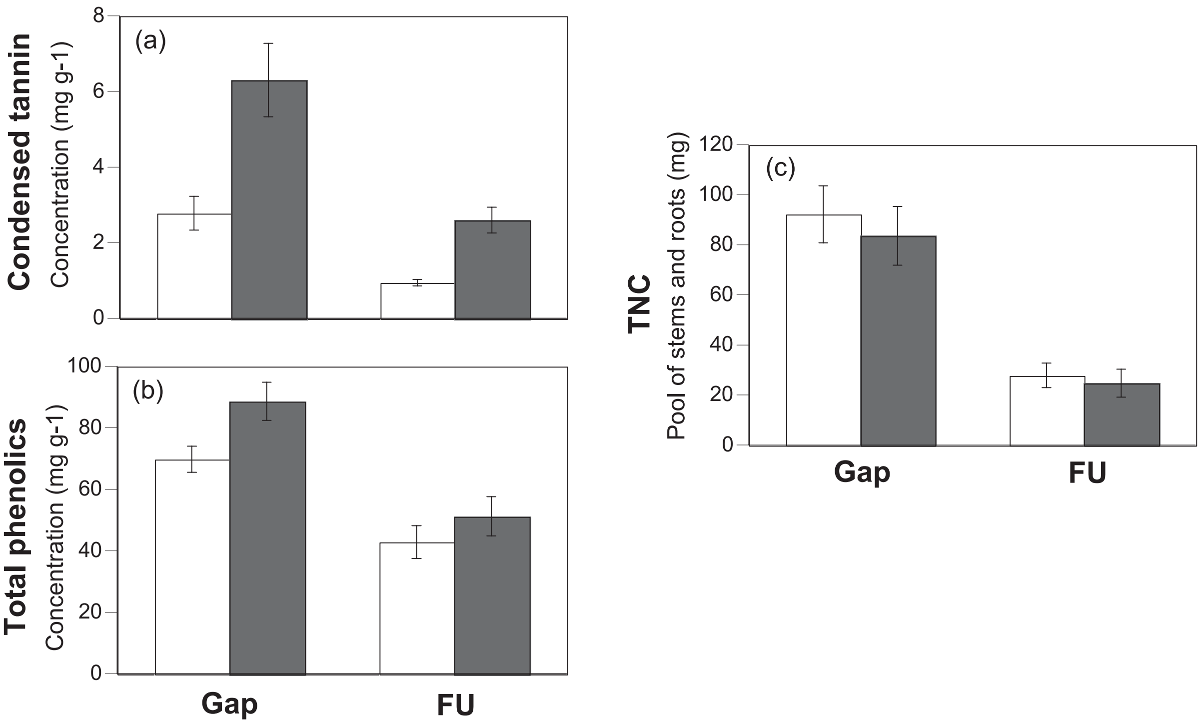

Fig. 4. Concentration of condensed tannins (a), total phenolics (b), and pool of TNC in stems and roots (c) of the light-demanding species *Castanea crenata* (white bars) and the shade-tolerant species *Quercus mongolica* var. *grosseserrata* (shaded bars) in gaps and the forest understory (FU) (Imaji and Seiwa 2010).

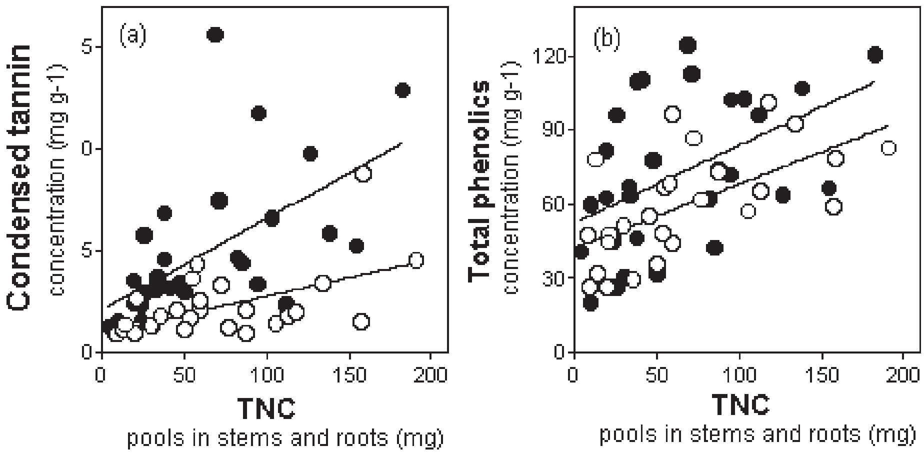

Fig. 5. Relationships between pool of TNC and concentration of condensed tannins (a), and pool of TNC and concentration of total phenolics (b) for the light-demanding species *Castanea crenata* (open circles) and the shade-tolerant species *Quercus mongolica* var. *grosseserrata* (solid circles) (Imaji and Seiwa 2010).

carbon allocation pattern is inherent to individual tree species, and may contribute to persistence in their respective habitats. To understand the carbon allocation strategy more generally in an ecological context, further comparative studies of a large number of species are needed.

Conclusion

Recent studies, especially in tropical forests, have provided evidence for the prediction that differences in carbon allocation underlie species differences in growth and the survival of seedlings, resulting in a trade-off between growth and survival in spatially heterogeneous environments. Our study (Imaji and Seiwa 2010) also supported the contribution of carbon allocation to the growth–survival trade-off in temperate forests. These studies suggest that growth–survival trade-offs, one mechanism of species diversity, are strongly associated with contrasting carbon allocation patterns. However, few studies have addressed carbon allocation patterns in relation to susceptibility to multiple seedling mortality agents. In particular, the relative importance of carbon allocation to defense and storage for survival remains poorly understood. Furthermore, empirical studies examining relationships between carbon allocation to growth, defense, and storage, together with causes of mortality across a large number of species, should lead to better understanding of mechanisms underlying growth–survival trade-offs. Because the trade-off model is based not only on abiotic conditions (i.e., spatially heterogeneous environments) but also on biotic conditions (i.e., interaction between plants and natural enemies), the integrated model should well explain the mechanisms shaping species diversity in forest communities.

References

Alverz-Clare, S. and K. Kitajima (2007) Physical defense traits enhance seedling survival of neotropical tree species. Functional Ecology, 21: 1044-1054.

Baraloto, C., D. E. Goldberg and D. Bonal (2005) Performance trade-offs among tropical tree seedlings in contrasting microhabitats. Ecology, 86: 2461-2472.

Chesson, P. L. (2000) Mechanisms of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics, 31: 343-366.

Coley, P. D. (1987) Interspecific variation in plant anti-herbivore properties: the role of habitat quality and rate of disturbance. New Phytologist, 106: 251-263.

Gilbert, B., S. J. Wright, H. C. Muller-Laudau, K. Kitajima and A. Hernandez (2006) Life history trade-offs in tropical trees and lianas. Ecology, 87: 1281-1288.

Imaji, A. and K. Seiwa (2010) Carbon allocation to defense, storage and growth in seedlings of two temperate broad-leaved tree species. Oecologia, 162: 361-369.

Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia, 98: 419-428.

Kitajima, K. and L. Poorter (2008) Functional basis for resource niche partitioning by tropical trees, Walter C, Schnitzer SA (Eds), Tropical forest community ecology, Wiley Blackwell, UK, pp. 160-181.

Kobe, R. K. (1997) Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. Oikos, 80: 226-233.

Kurokawa, H., Y. Kitahashi, T. Koike, J. Lai and T. Nakashizuka (2004) Allocation to defense or growth in dipterocarp forest seedlings in Borneo. Oecologia, 140: 261-270.

Myers, J. A. and K. Kitajima (2007) Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. Journal of Ecology, 95: 383-395

Myster, R. W. (1993) Tree invasion and establishment in old fields at Hutcheson Memorial Forest. Botanical Review, 59: 251-272.

Nakashizuka, T. (2001) Species coexistence in temperate, mixed deciduous forest. Trends in Ecology and Evolution, 16: 205-210.

Poorter, L. and K. Kitajima (2007) Carbohydrate storage and light requirements of tropical moist and dry forest tree species. Ecology, 88: 1000-1011.

Seiwa, K. (1998) Advantages of early germination for growth and survival of seedlings of *Acer mono* under different overstory phonologies in deciduous broad-leaved forests. Journal of Ecology, 86: 219-228.

Seiwa, K. (2007) Trade-offs between seedling growth and survival in deciduous broadleaved trees in a temperate forest. Annals of Botany, 99: 537-544.