Is the Janzen-Connell Hypothesis Valid in Temperate Forests?

Symposium Paper

Is the Janzen–Connell Hypothesis Valid in Temperate Forests?

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Abstract

Although degradation of biodiversity is a worldwide concern, relatively little evidence is available on the mechanisms of biodiversity. If sustainability of forest ecosystem is closely related to species diversity, recovery of species diversity is important for forest managers. Thus, it is important to understand the mechanisms of biodiversity in forest ecosystems. The Janzen–Connell hypothesis is one of the most important hypotheses explaining species diversity in tropical forests. To examine whether this hypothesis is also valid in temperate forests, we investigated the density, growth, mortality, and agents of mortality of seedlings, and the density, size, and age of saplings of *Prunus grayana* at three distances (0–3, 6–10, and 16–26 m) from conspecific adults in a temperate forest in Japan. The probability of mortality was highest at 0–3 m during the first 2 years of growth. Mortality mainly resulted from distance-dependent attack by two types of pathogen that caused damping-off epidemics and spot symptoms on leaves. Vertical and diameter growth was lowest at 0–3 m and highest at 16–26 m in both seedlings and saplings. The results suggest that seed dispersal enhances the probability of survival by distancing offspring from adults because natural enemies reduce recruitment near conspecific adults in a distance-dependent manner, freeing space for other plant species. Such phenomena affect species diversity within plant communities. The traits demonstrate that the Janzen–Connell mechanism also operates in a temperate forest in Japan. Knowledge of the mechanisms of species diversity and of ecosystem functioning will encourage forest mangers to create mixed hardwood–coniferous forests rather than monocultures.

Loss of species diversity in forest ecosystems

Humans are altering the composition of biological communities through a variety of activities that increase rates of species invasion and species extinctions from local to global scales. These changes in components of Earth's biodiversity lead to ethical and aesthetic concerns, but also have a strong potential to alter ecosystem properties and the goods and services that biodiversity provides to humanity (Hopper et al. 2005).

Increasing evidence is available on the effects of biodiversity on ecosystem properties such as productivity, carbon storage, hydrology, and nutrient cycling (e.g., Tilman et al. 1996; Hopper et al. 2005). Although degradation of biodiversity is a worldwide concern at both global and local scales, relatively little evidence is available on the mechanisms involved. If biodiversity is a consequence of biotic interactions, linkage between biodiversity and ecosystem functioning (services for humans) is inevitable.

In Japan, a large area of the natural virgin forest has been clear-cut and converted to monoculture, such as in Japanese cedar plantations established after World War II. Now, conifer plantations occupy one-quarter of the total area of Japan (10 million ha; Forestry Ag., 2006). Even-aged conifer forests generally have low value for wildlife, are susceptible to pests and strong winds, and may create a more acid soil. If sustainability of forest ecosystems is closely related to species diversity, recovery of species diversity is an important management goal for forest managers, and it is essential that they understand the mechanisms of forest ecosystems.

Hypotheses explaining species diversity

A substantial number of hypotheses have been presented to explain species diversity in forest communities (Fig. 1). In temperate forests, it was thought that species diversity is mainly created by abiotic factors such as heterogeneity of light, water, and nu-

trients, which are closely related to topography and gap creation. In tropical forests, increasing evidence has demonstrated the effects of biotic agents such as pathogens and herbivores, each of which has an important role in maintaining species diversity. One of the most important hypothesis regarding tropical forests is the Janzen–Connell hypothesis.

Janzen (1970) and Connell (1971) proposed that spatial patterns of juvenile mortality caused by natural enemies (i.e., pathogens and herbivores) could be a key factor in maintaining high tree diversity. They predicted that seed dispersal enhances the probability of survival by distancing offspring from adults because host-specific natural enemies reduce recruitment near conspecific adults in a density-dependent and/or distance-dependent manner, freeing space for other plant species (Fig. 2). Such phenomena affect species diversity within plant communities. In a large number of tree populations, density- and distance-dependent analyses of microbial pathogens and invertebrate or vertebrate herbivores support the Janzen–Connell hypothesis for tropical forests (e.g., Augspurger 1983; Gilbert 2005; Bell et al. 2006). Recent community-level studies have also shown that the density- or distance-dependent mortality of progeny plays an important role in the maintenance of plant
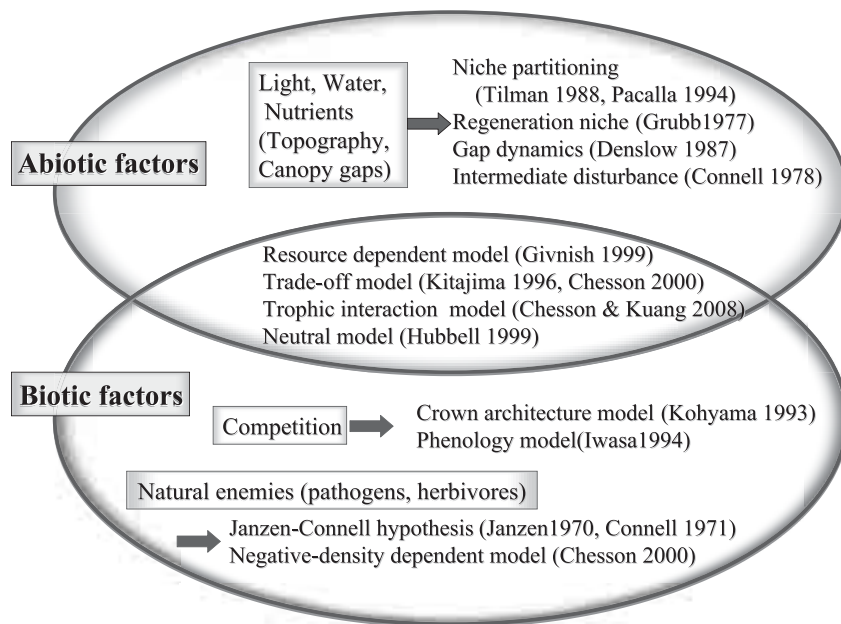

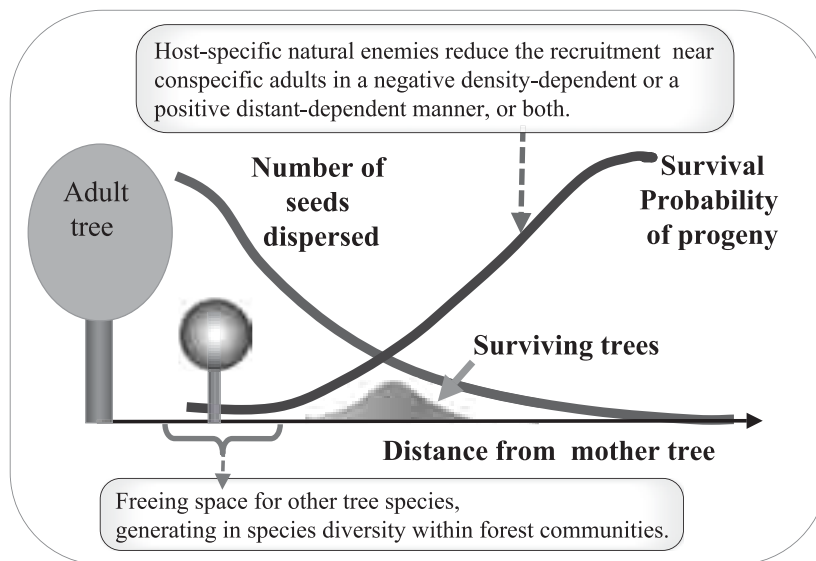**Fig. 1.** Hypotheses explaining species diversity in forest communities.

Fig. 2. Janzen–Connell hypothesis

alpha diversity in tropical moist forests (Wills et al. 1997; Harms et al. 2000; reviewed by Wright 2002), but several previous studies found density- or distance-dependent trends in half or fewer of the species examined (Connell et al. 1984; Condit et al. 1992).

Fewer studies have tested the Janzen–Connell hypothesis in temperate forests than in tropical forests. Although several studies in temperate forests have reported the density and distance dependence of tree seed and seedling mortality (e.g., Lambers and Clark 2003), little evidence is available regarding the causes of mortality and the consequent spatial patterns of progeny (but see Packer and Clay 2000; Masaki and Nakashizuka 2002; Tomita et al. 2002; Kotanen 2007). Recently, Seiwa et al. (2008) clearly demonstrated that the Janzen–Connell hypothesis is valid for a deciduous broadleaf tree, *Prunus grayana*, in a temperate forest of northern Japan. In this review, I explain how the cause of seedling mortality changes in type and intensity with distance from the parent and how the relationship between age and juvenile size changes with distance from the parent in a temperate hardwood forest.

Distant- and density-dependent mortality

Although seedling density was highest beneath (0–3 m) and lowest far (16–26 m) from an adult, the mortality of *Prunus grayana* seedlings decreased with increasing distance from conspecific adults. However, the percentage mortality was higher at 0–3 m than at 6–10 m or 16–26 m at the end of both growing seasons examined. These results indicate the distance-dependent mortality of seedlings of *Prunus grayana* in a temperate forest.

Causes of mortality

Distance-dependent mortality was caused mainly by pathogen activity on seedlings beneath adult conspecifics (Fig. 3). The percentage mortality from the pathogens that cause damping-off and from *Phaeoisariopsis pruni-grayanae* was greater at 0–3 m than at 6–10 m and 16–26 m, whereas few effects were observed for vertebrate herbivores, invertebrate herbivores, and physical damage (Fig. 3, 4). In *P. grayana*, damping-off accounted for a much greater proportion of seedling mortality than did other factors and was higher close to parent trees. Bell et al. (2006) found that seedling death of a tropical tree was not directly affected by the density itself, but by
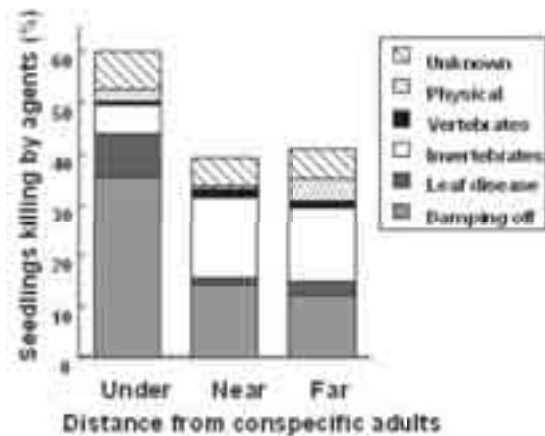

Fig. 3. Seedlings killed by individual agents of mortality during the first growing season: differences among distances from conspecific adults (under, 0–3 m; near, 6–10 m; far, 16–26 m). (Seiwa et al. 2008)
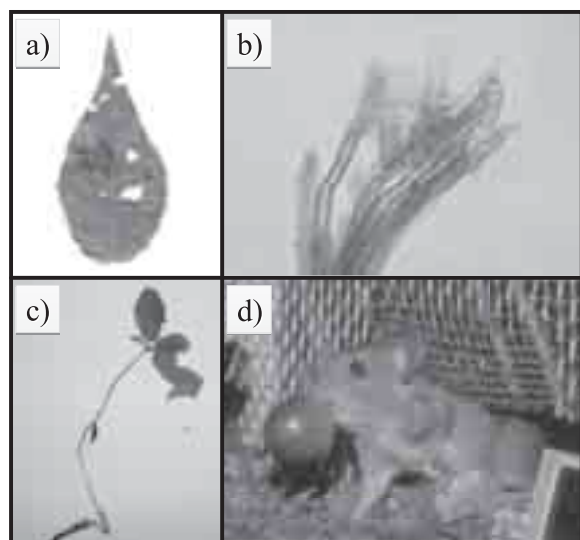

Fig. 4. Kiling agents for the current-year seedlings of *Prunus grayana*. Spot symptoms on the leaves caused by the leaf pathogen, *Phaeoisariopsis pruni-grayanae* Sawada, which infected many more seedlings of *P. grayana* than seedlings of the two other tree species tested in inoculation experiments (a; Seiwa et al. 2008). Conidia and conidiophores characteristic of *Phaeoisariopsis* (b). Damping off epidemics caused by soilborne pathogens such as *Colletotrichum*, *Phoma*, *Cladosporium*, and *Fusarium* (c). Vertebrate herbivore, *Apodemus speciosus*.

the density-mediated infection of damping-off pathogens. They conducted a manipulation experiment in which the effect of density was clearly separated

from that of pathogens (Bell et al. 2006). Therefore, heavy seed rain may not overwhelm the effects of pathogens, but rather reinforce them. We also found that the leaf pathogen *P. pruni-grayanae* attacked *P. grayana* seedlings in a distance-dependent manner, although the effects were much lower than were those of damping-off pathogens.

In temperate forests, similar traits of distance-dependent morality by pathogens were observed for *Prunus serotina* in North America (Packer and Clay 2000) and *P. grayana* in Japan. Furthermore, in a seed-sowing experiment of eight species co-occurring within a forest community, we found that six species (i.e., *Castanea crenata*, *Cornus controversa*, *Fraxinus lanuginosa*, *Magnolia obovata*, *P. grayana*, *Fagus crenata*) showed distance- and/or density-dependent mortality caused by pathogenic fungi (Yamazaki et al. 2009). These traits, together with evidence of distance-dependent mortality by pathogens for *C. controversa* (Masaki and Nakashizuka 2002) and *F. crenata* (Tomita et al. 2002), suggest that the effects are not specific to the genus *Prunus*, but are more general for tree species in temperate as well as tropical forests.

Reduction of vertical growth beneath the adults

The height of saplings increased with age, and this increase was most at 16–26 m from the adult and slowest at 0–3 m (Fig. 5). What is the most important cause of the reduction of vertical growth beneath conspecific adults? Little difference among the three
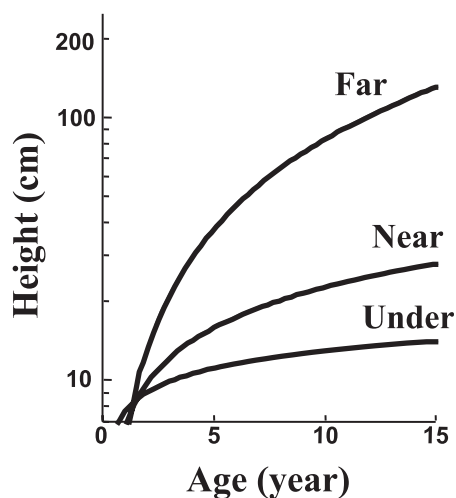

Fig. 5. Relationships between age and height of saplings at three distances from conspecific adults.

distances was observed for either relative PPFD or soil water potential, suggesting only slight influence of abiotic factors on sapling growth. Although pathogens that cause damping-off epidemics can affect plants of any age, damage caused by their infection is usually highest during the early stages of seedling growth and decreases with increasing maturity (Sahashi et al. 1995; Martin and Loper 1999). Furthermore, infection of large and old plants is often limited to the fine roots, suggesting that damping-off pathogens become less important growth-inhibiting agents as plants increase in size. In contrast, the pathogen *P. pruni-grayanae* strongly reduces plant performance (growth and survival), irrespective of plant size, because it usually causes early shedding of leaves with necrotic spots. We observed this pathogen over a large area of individual leaves for seedlings, saplings, and adults (Miwa and Seiwa personal observation; see also Kobayashi et al. 1992). Furthermore, a higher number of diseased leaves fall onto conspecific juveniles, particularly in the vicinity of adults. This suggests that continued distance-dependent reduced sapling performance (mortality and growth) could result from pathogen activity, especially that of this leaf pathogen.

Consequences of distance- or density-dependent seedling mortality

An exploration of the consequences of distance- or density-dependent seedling mortality is also needed. Even though density-dependent seedling mortality is observed, the highest density of survivors occurs in the vicinity of adults when most seeds land close to these adults (Nathan and Casagrandi 2004). The full extent of recruitment reduction near fruiting conspecifics has been systematically underestimated in short-term studies focused on the very early stages of regeneration because distance- and density-dependent reductions in performance accumulate as juveniles grow (Wright 2002). Therefore, the spatial distribution of saplings is more important than the spatial distribution of seedlings for determining species diversity within a community.

In *P. grayana*, the smallest and youngest saplings were distributed at 0–3 m, whereas a higher number of larger and older saplings were observed at 16–26 m. *P. grayana* saplings can survive gap-forming events, grow more rapidly in gaps than below the canopy, and reach the canopy in a single gap cycle

(Hara et al. 1991). These characteristics suggest that the larger saplings at 16–26 m have a higher probability of recruitment to the canopy than do smaller saplings at 0–3 m or 6–10 m because larger plants usually out-compete smaller neighbors for resources (i.e., light) under crowded conditions after canopy gap formation. In contrast, competitor-free space near adults of *P. grayana* should promote recruitment of other tree species. As a result, the adults are distributed randomly in the studied forest (Fig. 6).

Implications for forest management

   If the Janzen–Connell hypothesis is valid in temperate forests, replacement of individual tree species would occur at a fine scale, generating species diversity in the forest communities even in temperate forests. Knowledge of the mechanisms of species diversity and of ecosystem functioning would encourage forest mangers to create mixed hardwood–coniferous forests instead of monocultures because diversity becomes increasingly important as a management goal, from both economic and ecological perspectives.

Fig. 6. Spatial distribution pattern of the adults of *Prunus grayana*.

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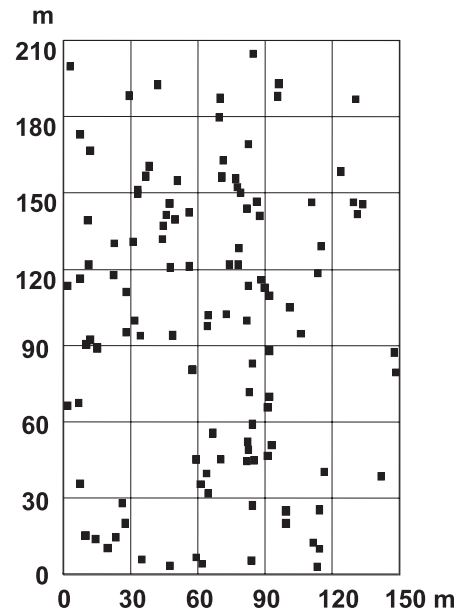Gilbert, G. S. (2005) Dimensions of plant disease in tropical forests. In: Biotic interactions in the tropics: their role in the maintenance of species diversity. Ed. by D. F. R. P. Burslem, M. A. Pinard and S. E. Hartley. Cambridge University Press, Cambridge, UK. pp. 141-164.

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