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Succession of abandoned coppice woodlands weakens tolerance of ground-layer vegetation to ungulate herbivory: A test involving a field experiment

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ABSTRACT

Ground-layer vegetation of abandoned woodlands is threatened by excessive shading and increasing pressure from ungulate herbivores. Although these issues are studied separately, they are presumed to be interactive because decreasing energy input into ground layer seems to limit herbivory tolerance in plants. To separately estimate impacts of succession, herbivory, and their interactions, I conducted a 2-by-2 factorial experiment (creating canopy gaps, setting deer exclosures, their combinations and controls) in abandoned woodlands, where ground-layer vegetation had nearly vanished from deer herbivory. Changes of plant community were monitored three times since half a year before the start of experiment. Rapid increases in foliar cover, plant height, and species richness were found in plots under gaps within half a year from the beginning of the experiment. The major cause of this rapid increase was reestablishment of light-demanding and fast-growing species, whose compensation growth exceeded consumption by deer. In contrast, no significant change was found in ground-layer vegetation under a closed canopy, where only shade-tolerant and slow-growing species existed. These results suggested that limits in light resulting from the progress of forest succession is a primary factor inhibiting recovery of ground-layer vegetation from herbivory damage. In the short term, a combination of gap creation and the removal of herbivores is necessary to restore ground-layer plants in abandoned woodlands.

1. Introduction

The secondary woodlands around human residential areas, which had been under traditional management for millennia, are now threatened with significant loss of biodiversity (Rackham, 2008). The special fauna and flora of secondary woodlands, which had developed through long-term interactions with human activities (Nagaike et al., 2003, 2005; Rackham, 2008; Fujii et al., 2009), are declining with the abandonment of management activities (Fukamachi et al., 2001; Hédl et al., 2010; Takeuchi, 2010). Among the issues resulting from abandonment, two factors are most prominent: excessive shading from forest succession and excessive ungulate herbivory (Rackham, 2008). Excessive shading has caused significant loss of shade-intolerant plants, which are rare in dark, matured forests (e.g., Keith et al., 2009; Hédl et al., 2010). This issue is especially significant in woodlands traditionally utilized for coppicing, where cyclic harvesting of fuel wood between long intervals had maintained many light-demanding and fast-growing plants (Nagaike et al., 2003, 2005; Fujii et al., 2009). Loss of these "pioneer" plants is rapidly decreasing diversity of woodland vegetation so that most dominant species are shade-tolerant and slow-growing plants (Keith et al., 2009). In addition to stopped cutting, excessive pressure by ungulate herbivory, especially deer, is also threatening forest vegetation (Rooney et al., 2004; Rackham, 2008). Extinction of natural enemies and the decline of hunting pressure have freed deer populations from top-down control and caused unprecedented impacts from herbivory (Côté et al., 2004; Rooney and Waller, 2003). Herbivory from overabundant deer has significantly decreased biomass and species richness, and drastically changed the species composition of plant communities (e.g., Gill, 1992; Hester et al., 2000; Côté et al., 2004; Rooney and Waller, 2003) resulting in a loss of functional diversity (Rooney, 2009). The long-lasting impact of deer may change seedbank composition (Gill and Beardall, 2001; Chaideftou et al., 2009, 2011) and soil properties (Wardle et al., 2001; Singer and Schoenecker, 2003), and eventually bring the system to an alternative stable state (e.g., Augustine et al., 1998; Coomes et al., 2003).

These two threats had been studied separately, but they seem to be dependent on each other because the plants' strategy for herbivory defense is largely limited by light environment (Coley et al., 1985). Plants can tolerate herbivory damage using two kinds of defensive tactics: increase "resilience" with compensation growth; and be "resistant" or avoid herbivory using chemical and physical defenses (Fornoni, 2011). Both defensive tactics require a supply of photosynthates, which are extremely limited in conditions of

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excessive shading. Additionally, light-demanding species, which exhibit compensatory growth after herbivory, have nearly disappeared from the ground layer of abandoned woodlands. For reasons stated above, ground-layer vegetation of abandoned woodlands might be becoming more sensitive than ever to herbivory. This expectation is supported by the fact that herbivory damage on ground-layer vegetation tend to lasting for a long period under closed canopies of old-growth forests (e.g., Anderson and Kats, 1993; Webster et al., 2005; Tremblay et al., 2006; Tanentzap et al., 2009), but it can be easily recovered under gaps (e.g., Castleberry et al., 2000; Nomiya et al., 2003; Joys et al., 2004; Holladay et al., 2006; Tremblay et al., 2006; Naaf and Wulf, 2007). If the above expectation is valid, improvement of the light environment, as well as the elimination of deer, would be necessary to restore degraded ground-layer vegetation.

The secondary woodlands of the Boso Peninsula, Japan, is severely threatened by the above two problems. Herbivory by Sika deer (*Cervus nippon*) is prominent in this region: foliar cover of ground-layer plants sharply decreases as deer density increases; and at the core area of the deer population, ground-layer vegetation has nearly vanished except for a few shade-tolerant and herbivory-resistant species (Suzuki et al., 2008, in press). This high sensitivity to herbivory might be attributable to species composition of dark, abandoned woodlands. Because traditional coppicing was stopped, these woodlands have lost their light-demanding and fast-growing species, which had been common until the 1980s (Miyawaki, 1986). These light-demanding plants remain at the forest edges, providing food to overabundant deer (Miyashita et al., 2008) and keeping the potential to recruit into new gaps. Here, I attempted to restore ground-layer vegetation of these woodlands by creating artificial gaps in the canopy layer and eliminating deer. I predicted that plant biomass would increase under the gaps, where plants' productivity exceeds consumption by deer. In contrast, ground-layer plants under a closed canopy would not increase in biomass even if deer were eliminated. I also predicted that plant species richness would be increased under the gaps through recruitment of light-demanding species; a biased food habit of deer would slightly decrease species richness, but this decrease would be much smaller than that caused by limits in light under a closed canopy. These hypotheses were examined with a 2×2 factorial experiment (gap creation and deer exclosures, and combination and control plots of both) in heavily damaged vegetation in the Boso Peninsula.

2. Methods

2.1. Study sites

Boso Peninsula exhibits a humid, warm-temperate climate. Three study sites were set in The University of Tokyo Chiba Forest located in southern Boso Peninsula (Table 1). Study sites were 2–5 km apart (35.8–11 N, 140.7–9 E). Hinokio (HNK) and Hiratsuka (HRT) sites were located 300 m above sea level (a.s.l.), about 7 km from the nearest shoreline. Mean, minimum, and maximum annual air temperatures were 14, −4.7, 34.3 °C, respectively, and mean annual precipitation was 2389–2479 mm from 2007 to 2009 (The University of Tokyo Forests, 2009, 2010, 2011). Kotsubosawa (KBS) site was 2.0 km from the nearest shoreline, with an altitude of 50 m a.s.l., having a somewhat milder climate than HNK and HRT. Mean, minimum, and maximum annual air temperatures were 16, −1.3, 33.3 °C, respectively, and mean annual precipitation was 1893 mm (The University of Tokyo Forests, 2009, 2010, 2011).

Coppicing had been common in the three sites until the 1950s and, in those days, local residents had repeatedly clear-cut canopy trees (mainly oaks) at 30- to 40-year intervals for fuel-wood harvesting. This management was abandoned approximately 50–60 years ago. At the beginning of this study, the vegetation of the study sites was characterized by a high diversity of toll trees. The canopy layer in KBS was dominated by evergreen trees such as *Quercus glauca* and *Castanopsis sieboldii*, *Eurya japonica* at the subcanopy layer, and a mix of other evergreen woody species (e.g., other oaks, *Myrsine seguinii*, and *Camellia japonica*). Vegetation in HRT was dominated by *Q. acuta* in the canopy layer, *E. japonica* and *Camellia. japonica* in the subcanopy layer, and a mix of other evergreen trees (e.g., *Quercus* spp., *Ilex integra*, *Dendropanax trifidus*) and deciduous trees such as maples and cherries. The canopy layer of HNK was dominated by *Q. glauca*, with *Cleyera japonica* and *E. japonica* as the subcanopy dominants, and a mix of *C. sieboldii* and *Q. myrsinifolia*. Many lianas were also observed at the canopy layer. A few sparse evergreen shrubs and lianas, which might be tolerant to deer herbivory, were observed at the ground layer of three sites.

Deer populations in the Boso Peninsula increased in density from early 1970s, damaging forestry and farming in this region (Chiba Prefecture, 2004). The ecological impact is also significant, especially on forest-floor vegetation (Kabaya, 1988; Suzuki et al., 2008), net-building spiders (Miyashita et al., 2004; Takada et al., 2008), and the physical properties of topsoil (Yanagi et al., 2008). The study sites are located at the core areas of the deer population, where deer density has been fairly constantly high in these two decades (Table 1).

2.2. Experimental treatments

Eight 10-by-10-m plots were established at each of the three study sites (Fig. 1). Species names of trees of DBH > 1 cm in these plots were recorded in November 2006. From February to March 2008, the canopy layers of the three sites were cut to create an artificial gap of approximately 20 by 20 m, which included four of the eight experimental plots. Cut stems and branches were moved to outside the plots. In HNK and KBS sites, plots under gaps and those under a closed canopy were more than 10 m apart; however, they were adjacent to each other in HRT because of topographic limitations. In each study site, two plots under a closed canopy and two plots under gaps were fenced using a polyethylene net 1.5 m high to avoid deer herbivory. In total, 2×2 treatments with two replications each were set for each study site: plots in deer exclosures under a closed canopy (plot E), those in deer exclosures under gaps (plot EC), those under gaps but outside deer exclosures (plot C), and the control plot (Ctrl).

Table 1
Summary of study sites.

Site name (abbreviation)	Years from last cutting event	Topography	Altitude (m)	Slope inclination (°)	Recent deer density (km^{-2})[a]
Kotsubosawa (KBS)	58	Lower part of west-facing slope	50	34.5	2–13
Hiratsuka (HRT)	53	Upper part of concaved south-facing slope	300	35.8	4–24
Hinokio (HNK)	60	Top of south-facing ridge	300	28.3	2–15

[a] Monitoring data 1986–2008 based on the block-counting method (Maruyama and Nakama, 1983). Cited from Yamanaka (2007).