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Combined effects of gap creation and deer exclusion on restoration of belowground systems of secondary woodlands: A field experiment in warm-temperate monsoon Asia

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ABSTRACT

Ground-layer vegetation in abandoned woodlands of the Northern Hemisphere is rapidly declining because of overshading and an overabundance of ungulate herbivores; these changes may be affecting belowground ecosystems. An effective countermeasure is to restore ground-layer vegetation by establishing deer exclosures immediately after creating canopy gaps. However, such measures disturb belowground processes (e.g., decelerate decomposition rates and decrease soil water content) and may cause further disintegration of the whole system. To estimate the combined effects of gap creation and exclosure installation, we established a 2×2-factorial experiment (including gap creation, exclosure installation, both methods, and a control) in warm-temperate secondary woodlands. After five years, we studied ground vegetation, litter cover, soil–water physics, abundance of litter-dwelling invertebrates, and litter decomposition in each experimental plot. A significant increase in ground vegetation was found in gap-and-exclosure plots and gap-and-deer plots, although the increase in the latter was limited to approximately half of that in the former; in contrast, no significant increase was found in the control or canopy-and-exclosure plots. The abundance of litter-dwelling invertebrates was significantly reduced by gap creation, although this effect was offset by installation of exclosures in gaps. Fine porosity and water holding capacity of topsoil were reduced by gap creation, but these negative effects were mitigated by exclosures installed in gaps. Meanwhile, coarse porosity and water permeability of topsoil were not affected by gap creation; they tended to be increased by exclosure installation both in gaps and under the canopy. Litter decomposition tended to be delayed in the gap-and-deer plot, although this effect was temporary; exclosure installation slightly increased decomposition rates, but this effect was limited. These results show the possibility of restoring belowground dynamics in abandoned forests by creating small canopy gaps and establishing ungulate exclosures. This mixture of interventions should increase habitat heterogeneity in these forests and help prevent biological homogenization while mitigating long-term negative effects of gap creation on belowground ecosystems.

1. Introduction

Human withdrawal from nature and underuse of natural resources are common social issues in forests of developed countries. These problems have had biological consequences in forest ecosystems, such as an overabundance of ungulate herbivores and increased shading by dense forest canopies, both of which cause a further loss of biodiversity and of the functioning of aboveground ecosystems (Rackham, 2008). Although the influence of ungulates is most pronounced on aboveground biota (e.g., plants, invertebrates, birds), their direct/indirect effects on belowground biota (e.g., microbes and invertebrates) has also been reported (Côté et al., 2004; Hédl et al., 2010; Rooney and Waller, 2003; Wardle, 2002, 2006). An overabundance of ungulates has negative effects on the decomposer community (Wallace, 1987; Sørensen et al., 2009; Gass and Binkley, 2011; Niwa et al., 2011), worsens topsoil physics (Yanagi et al., 2008; Gass and Binkley, 2011), reduces litter accumulation (Wakahara et al., 2008; Lessard et al., 2012; Heckel et al., 2010), and potentially changes litter decomposition rates (Wardle, 2002). In addition, succession of aboveground vegetation usually homogenizes the forest

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environment and tends to reduce the diversity of belowground biota (Pontegnie et al., 2005; Spitzer et al., 2008). The ultimate solution to these problems is a multidisciplinary challenge, but some forest ecosystems require urgent measures.

Simple but effective countermeasures are generally taken to address these problems, including creation of canopy gaps for improving understory light conditions (Shibuya et al., 2008; Spitzer et al., 2008) and exclusion of herbivores or reduction in their numbers (Wardle et al., 2001; Bressette et al., 2012). The effectiveness of these activities is widely accepted for some aboveground components, such as plants and herbivorous insects (e.g. Castleberry et al., 2000; Lessard et al., 2012; Brousseau et al., 2013; Suzuki, 2013). However, their effects on belowground systems are open to debate (Wardle, 2002, 2006; Suominen and Danell, 2006) in relation to the complex direct and indirect pathways underlying management of various components (Fig. 1).

Generally, exclusion of ungulates is thought to be effective for restoring belowground systems. When exclosures protect and facilitate recovery of aboveground flora (Fig. 1, arrow 1), these improvements also result in accumulation of the litter layer (Fig. 1, arrow 2). A thick litter layer promotes increases in litter-dwelling fauna including decomposer invertebrates (Fig. 1, arrow 3; Elia et al., 2010; Bressette et al., 2012; Lessard et al., 2012). Thick litter also protects topsoil from physical damage (e.g., trampling and raindrops) and from water loss, and prevents soil compaction that would degrade soil–water physics (Fig. 1, arrow 4; Yanagi et al., 2008; Heckel et al., 2010; Gass and Binkley, 2011). As a result, creation of exclosures may solve problems caused by soil compaction such as delayed growth of some plants (Kozlowski, 1999), a decline in soil fauna (Wardle et al., 2001; Wardle, 2002; Bressette et al., 2012), and water and nutrient loss from soil (Heckel et al., 2010; Gass and Binkley, 2011). Furthermore, installation of exclosures might alter the decomposition process via several pathways, including: (i) recovery of aboveground vegetation and a change in the quantity and quality of litter and of root exudates (Pastor et al., 1993; Kielland et al., 1997; Stark et al., 2003); (ii) prevention of the addition of soluble nutrients to the soil via feces and urine (Pastor et al., 1993; Wardle, 2002); and (iii) stimulation of decomposers such as microbes (Sankaran and Augustine, 2004; Sørensen et al., 2009; Stark et al., 2010; Niwa et al., 2011). Also, an increased abundance of litter-eating fauna is likely to accelerate decomposition (Fig. 1, arrow 5). Ground cover by plants and the litter layer, together with good soil–water conditions, is expected to keep the litter layer adequately moist and thus may increase decomposition rates (Fig. 1, arrow 6). Moreover, the exclosures themselves prevent trampling by ungulates. This protection of the soil may in turn prevent erosion of the litter layer (Fig. 1, arrow 7) and degradation of soil–water physics (arrow 8) and litter-dwelling invertebrate communities (Fig. 1, arrow 9; Wardle et al., 2001). On the other hand, the effects of herbivores and exclosures are highly dependent on site conditions (Wardle, 2002, 2006; Sørensen et al., 2009; Stark et al., 2010) and on species groups as response nodes (Wardle et al., 2001; Pontegnie et al., 2005; Suominen and Danell, 2006; Lessard et al., 2012).

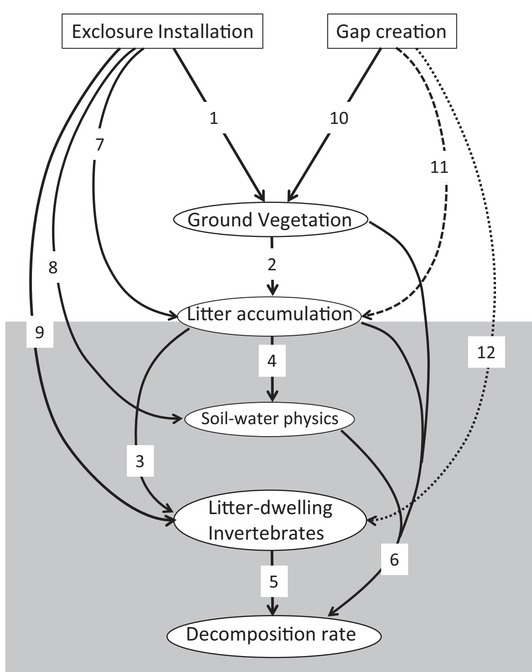

Fig. 1. Possible pathways underlying the management interventions, as predicted before the experiment. We have illustrated the paths tested in this study, which represent a subset of all possible paths. Positive, negative, and uncertain pathways are illustrated by solid, dashed, and dotted arrows, respectively. Both deer exclosures and gap creation are expected to facilitate establishment and growth of ground vegetation (arrows 1 and 10), which in turn will increase litter accumulation (arrow 2). Thick litter accumulation is expected to increase the population of litter-dwelling invertebrates (arrow 3). Litter accumulation should shelter topsoil from physical damage, preventing compaction and water loss (arrow 4). An increase in litter-dwelling invertebrates, including decomposer fauna, will accelerate litter decomposition (arrow 5). The litter decomposition rate should be increased by good moisture conditions, which are related to ground cover of vegetation, thickness of the litter layer, and water conditions of the soil (arrow 6). In addition, deer exclusion is expected to prevent trampling; this change will stabilize and thicken the litter layer on sloped ground (arrow 7), improve soil–water physics (arrow 8), and prevent reductions in litter-dwelling fauna (arrow 9). Meanwhile, direct effects of gap creation on litter accumulation should be negative because of decreased litter influx from the canopy layer (arrow 11). The population size of some groups of litter-dwelling invertebrates is expected to increase, but others will decrease, with the increase in light intensity after gap creation (arrow 12).

The interactive effects of exclosure installation and gap creation are expected to be more complex (Fig. 1). Gap creation itself is expected to have both positive and negative impacts on above- and belowground systems. Gap creation may increase forest floor vegetation (arrow 10 in Fig. 1) and thus may initiate a positive series of effects on the belowground systems (arrows 2–6 in Fig. 1). Also, increased light and temperature on the forest floor may activate microbial decomposition (Kim, 2000) and increase some groups of decomposing invertebrates (arrow 12 in Fig. 1; Spitzer et al., 2008). As negative effects, however, direct sunlight and decreased litter influx from the canopy layer would cause the litter layer to be dry and thin (arrow 11 in Fig. 1); this may be harmful for some groups of litter fauna including litter-eating invertebrates (arrow 12 in Fig. 1; Pontegnie et al., 2005; Grebenc et al., 2009) and microbial decomposers, thus potentially decelerating litter decomposition. Moreover, human activities related to the creation of gaps often cause additional soil compaction (Bouget et al., 2012). These negative effects of gap creation can usually be mitigated by reestablishing ground vegetation in the gap. Exclusion of ungulate herbivores helps in the establishment of ground vegetation, and thus is expected to mitigate the negative effects of gap creation (Suzuki, 2013). The results of exclosure installation and gap creation can be both positive and negative, according to the relative strength of the above-mentioned effects. Although forest managers in many regions would address herbivory and overshading problems simultaneously, the combined effects of such measures on belowground systems have rarely been examined (but see Spitzer et al., 2008; Dufresne et al., 2009).

Here, we report the results of an attempt to restore vegetation and belowground systems in a secondary woodland. The Boso Peninsula, our study site, belongs to a warm temperate region of monsoon Asia, where very high forest productivity has allowed for traditional recurring fuelwood harvests. Economic growth and industrialization after World War II, accompanied by a focus on