

# Changes in size of soil seed bank in *Robinia pseudoacacia* L. (Leguminosae), an exotic tall tree species in Japan: Impacts of stand growth and apicultural utilization

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## ABSTRACT

This study examined the factors that influence the size of a soil seed bank in *Robinia pseudoacacia* stands. We proposed two hypotheses: the amount of buried seeds of *R. pseudoacacia* is proportional to stand biomass rather than stand age, and apicultural utilization influences the size of the soil seed bank. *R. pseudoacacia* generally produces seeds with various degrees of physical dormancy. In addition, this tree is short-lived, and fecundity declines after 30–40 years in relation to tree vigor. However, *R. pseudoacacia* is intensively used in apiculture as an important honey source, and supply of honeybees by beekeepers could influence seed crops. We investigated 25 plantations in Hokkaido (Central, Hidaka, and Oshima) and in Nagano, Japan, where many naturally regenerated *R. pseudoacacia* stands occur. We found great variation in the size of the soil seed bank among stands, ranging from 13,757 to 6.4 seeds m<sup>-2</sup> per plot. A generalized linear mixed model revealed that both basal area (BA<sub>RP</sub>) and apicultural utilization best explained the size of the soil seed bank. Both the positive effect of BA<sub>RP</sub> and small contribution of stand age to the model implied that the soil seed bank is transitory, and will not persist for very long time. The large contribution of apicultural utilization to the size of the soil seed bank implied pollinator limitation under natural conditions. *R. pseudoacacia* often has large flower crops, and native pollinators can not keep up with the demand for pollination. Thus, the supply of honeybees by beekeepers should improve the pollination success of *R. pseudoacacia*. From these results, we conclude that we must consider stand history with respect to apicultural utilization if the land is harvested or a stand declines.

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## 1. Introduction

Many invasive plant species form soil seed bank, and the character causes one of the major difficulties to control the species. If an invasive plant has a soil seed bank, removing it can be very difficult because complete seed removal from the soil is almost impossible. Even if the vegetative organs of the invasive plants are removed, seeds in the soil may remain a source of re-infestation for many years (Cavers and Benoit, 1989). Therefore, we must understand the processes involved in the growth of soil seed bank size of invasive plant species.

*Robinia pseudoacacia*, a tall leguminous species native to the Appalachians in the United States, is considered an invasive plant

worldwide (Cronk and Fuller, 1995), although it has been used for variable purposes such as the control of land erosion, forest restoration, wood production, and apiculture (Groninger et al., 2006; Keresztesi, 1980; Lee et al., 2004; Panagopoulos and Hatzistathis, 1995; Rédei et al., 2002; Tamura et al., 2007). Seeds of this species show physical dormancy, and are difficult to germinate without treatments such as scarification, heat shock, or sulfuric acid (Huntley, 1990; Strode, 1977). Hence, *R. pseudoacacia* forms a soil seed bank (Takahashi et al., 2008; also see Hille Ris Lambers et al., 2005; Keresztesi, 1980; Kostel-Hughes et al., 1998), but the processes in the formation of this soil seed bank are not well understood.

Recently, some seeds of *R. pseudoacacia* were reported to show weak or little physical dormancy, and the argument was made that polymorphisms exist regarding the ecological significance of dormancy (Masaka and Yamada, 2009; Takahashi et al., 2008). According to Masaka and Yamada (2009), it is difficult for seeds with little physical dormancy to remain viable in the soil, and such seeds do not survive even one winter. Hence, some seeds of *R. pseu-*

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*doacacia* show short longevity while others can survive for about 40 years in the soil (Toole, 1946). In addition, the growth rate and fecundity of *R. pseudoacacia* trees decline after 30–40 years (Strode, 1977), implying that the abundance of buried seeds is also reduced during stand decline, which in turn implies that the abundance of *R. pseudoacacia* seeds in the soil is proportional to fecundity rather than stand age (Hypothesis 1). Fecundity will be proportional to stand biomass.

Furthermore, we need to consider apiculture because *R. pseudoacacia* is a very important honey source for honey production industry (Keresztesi, 1980; Rédei et al., 2002). Even though *R. pseudoacacia* has large flower crops, trees in general cannot produce seeds without pollinators. The significance of honeybees supplied by beekeepers is well-known in agriculture and horticulture (Jacobsen, 2008), but little is known of their importance for wild plants. Many honeybees supplied by beekeepers could also contribute to increased pollination success in *R. pseudoacacia*, and consequently, the trees would produce more seeds. We therefore propose that apiculture influences the size of the soil seed bank in *R. pseudoacacia* stands (Hypothesis 2).

In the present study, we address Hypotheses 1 and 2 to examine what factors influence the change in the size of a soil seed bank in *R. pseudoacacia* in Japan. If we could demonstrate the factors, the information would contribute to the development of a manual to control *R. pseudoacacia*.

## 2. Materials and methods

### 2.1. Study species

*R. pseudoacacia* has been widely planted throughout the world's temperate zone for soil improvement at nutrient poor sites, control of erosion in road cuts, revegetation at stripped area (e.g., Groninger et al., 2006; Keresztesi, 1980; Lee et al., 2004; Panagopoulos and Hatzistathis, 1995; Tamura et al., 2007) due to its drought-tolerance and ability of nitrogen fixation (Boring and Swank, 1984; Bormann et al., 1993). Besides, this species has been used intensively by apiculture for honey source (Keresztesi, 1980; Rédei et al., 2002). However, *R. pseudoacacia* rapidly spreads in flood plains, coastal forests, suburban forests, and abandoned fields (e.g., Elliott et al., 1997; Fukuda et al., 2005; Gyokusen et al., 1991; Jung et al., 2009; Larsen, 1935; Lee et al., 2004; Luken et al., 1992; Maekawa and Nakagoshi, 1997a,b; Rice et al., 2004; Sakio, 2003; Takahashi et al., 2008; von Holle et al., 2006; Yamada and Masaka, 2007). The fragrant, whitish flowers, borne in showy racemes, appear after leaf emergence. In central Hokkaido, northern Japan, we can observe flowers in June. The perfect flowers originate in the axils of current year leaves and are pollinated by insects, primarily bees. The fruit is a flattened, oblong pod that ripens during September and October. These pods contain 1–20 seeds, and the number of seeds is 36,000–65,000 kg<sup>-1</sup> (Chapman, 1936). Some pods open on the tree, some other pods disperse by wind. Seeds and pods are shed from September to April. Pods remained on the crown may show an aerial seed bank (Masaka and Yamada, 2009). Some seeds can survive at least 39 years in the soil (Toole, 1946), but the survival curve of buried *R. pseudoacacia* seed in the soil is still unknown. Seed predators, such as bean beetles, are not reported in Japan.

### 2.2. Study sites

We focused on *R. pseudoacacia* plantations to examine the effect of stand age on size of the soil seed bank. We selected eight stands in central Hokkaido in mid-May 2007 (hereafter Central), seven stands Hidaka in mid-May 2008 (hereafter Hidaka), eight stands in Oshima Peninsula in mid-May 2009 (hereafter Oshima), with a total

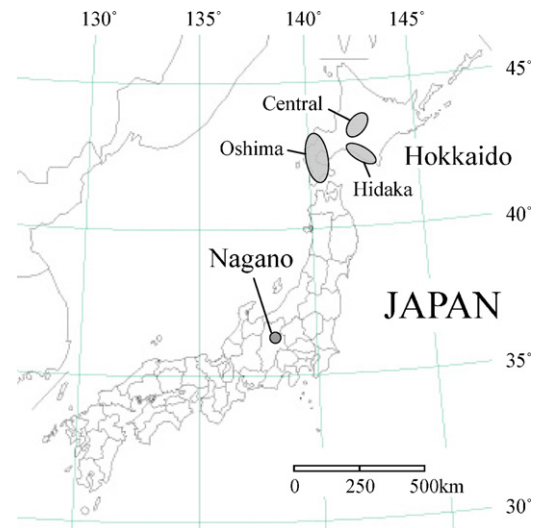


Fig. 1. Location of the study sites at the regional level.

of 23 stands (Fig. 1). We paid attention to the selection of study sites to prevent bias in stand age distribution, and both the youngest and oldest stand in each region (34–94 years old for Central, 33–72 years old for Hidaka, and 32–64 years old for Oshima) were included. The forest procedures for Hokkaido suggest planting 3000 *R. pseudoacacia* saplings per hectare. Climatic conditions, vegetation type, and availability for apiculture differ markedly among regions. Heavy snowfall occurs in Central and Oshima, whereas little winter snow falls in Hidaka, leading to the development of seasonal soil frosts in this region. The forest floor is covered by dense dwarf bamboo (*Poaceae*) of a height similar to that of the snow depth; *Sasa kurilensis* and/or *S. senanensis* are found in Central and Oshima, and *S. nipponica* in Hidaka. The former two species often reach heights of 1–2 m, whereas the latter is only 0.5 m high. Many *R. pseudoacacia* stands in Central are used by beekeepers for honey production because large stands develop on ex-coal mine sites, failed *Larix leptolepis* sites, and abandoned crop fields in this region (cf. Yamada and Masaka, 2007).

We also selected two plantations in Nagano, central Japan, in mid-May 2008 (Fig. 1). The forest floor was dominated by *Adoxa moschatellina* (*Adoxaceae*) and *Chelidonium majus* (*Papaveraceae*) in the oldest (60-year-old) and youngest (30-year-old) stands, respectively. In Nagano Prefecture, *R. pseudoacacia* has been planted for soil erosion control since the early twentieth century. Since climatic conditions in Nagano are suitable for *R. pseudoacacia*, it has invaded into mainly floodplains (Maekawa and Nakagoshi, 1997b), and can now be found all over Nagano (Shimizu, 1997). Beekeepers target *R. pseudoacacia* stands particularly the older stands in the present study (Koyama, personal communication).

A 20 m × 20 m plot was established in each stand, and 10 soil samples (0.1 m radius × 0.10 m deep) were collected from the forest floor: at nine lattice points (center of the plot and 2 m from the edge of the plot) and one point at the center of four adjacent sampling points. Fresh litter on the surface was removed from the soil samples in the field before samples were taken to the laboratory. The direct seed counting method consisted of sieving the soil sample, separating soil particles and other debris, and counting only *R. pseudoacacia* seeds. We did not test seed viability or germinability at all in the present study, since we did not obtain enough seeds for the test in some plots. According to Takahashi et al. (2008), *R. pseudoacacia* seeds obtained from the soil seed bank showed high germinability (approximately 70–90%). Morimoto et al. (in press) also reported that more than 90% of buried seeds could germinate

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