The effect of duration of burial on the breakage of seed dormancy in a Japanese *Rubus* species, *Rubus illecebrosus.*

By

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Summary: To clarify the adaptive significance of seed dormancy, the effect of duration of burial was examined for a deciduous *Rubus* species, *R. illecebrosus*, which is widely distributed in western Japan. In early summer, just ripened seeds were buried in soil, and germination tests were carried out for the seeds retrieved from the soil litter 0 (not buried), 1, 2, 3, 5 and 8 months later. Almost no seeds germinated without light and at constant temperature in light regardless of burial duration. The percentage of seeds germinating under light and alternating temperature conditions increased with increasing duration of burial for this *Rubus* species. After 8 months of burial, 71% of seeds germinated with light under temperature alternation. The percentages of dormant seeds (no germination even with light and alternated temperature) and conditional dormant seeds (germination only with light and alternated temperature) were about 30% and 70%, respectively in the next germination season. Thus, *R. illecebrosus* is mostly adapted to germinate in safe sites which are subjected to temporally unpredictable disturbances.

1. Introduction

Most *Rubus* species, which are typical pioneer shrubs, form dense populations rapidly and predominate in forest openings after disturbances such as logging or fire (Grime et al., 1988; Suzuki, 1990). The seed germination traits of these species as well as vigorous clonal growth with underground branching, contribute to this rapid spread of the population (Nybom, 1987; Suzuki, 1990). In general, *Rubus* seeds are dormant just after dispersal, and are stored in the soil as a seed bank (Grime et al, 1988). Buried seeds gradually break their dormancy and germinate during favorable conditions for growing in response to seasonal changes or disturbances (Suzuki, 1997). However, *Rubus* species vary widely in germination characteristics due to their adaptation to various kinds of growing habitats (Suzuki, 1997). It is very useful to clarify germination traits in genus *Rubus* to understand their evolutionary strategy and specialization.

The *R. illecebrosus* examined in this study are deciduous shrubs which are mostly distributed in western Japan, having a wide vertical distribution range from 500-1500m above sea level (Naruhashi & Satomi, 1972) , and sprouting annual above-ground canes which produce seeds and die back each year (Suzuki, unpubl.data). *R. illecebrosus* is an integrated clonal plant which produces subterranean suckers on new perennial underground runners, and form a clonal structure with dense above-ground canes by underground branching at gaps or forest edges (Suzuki, 1990).

This paper will examine the effects of seed burial duration and breakage of seed dormancy of *R. illecebrosus*. It will also discuss the adaptive significance of seed dormancy regarding seed bank formation and germination response to environmental changes, by comparing with some other *Rubus* species.

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2. Materials and Methods

Ripened berries were collected from plants growing in the nursery of the Tohoku Research Center of the Forestry and Forest Products Research Institute in Morioka (Lat. 39°45', Log. 141°15', Alt. 200m) in July 1992. Mother plants of *R. illecebrosus* were transplanted from the Kiso district (Lat. 35°80', Log. 137°60', Alt. 800m) of Nagano Prefecture. After washing with running water, the seeds which sank in water were assumed to be viable and subjected to germination tests. A portion of the collected seeds was subjected to germination tests immediately as non-buried (0th month) seeds. For burial treatments, more than 2,000 viable seeds in this species were put into a fine-mesh nylon bag, and five seed bags were buried in the forest floor litter layer of a 150-year-old *Pinus densiflora* S. et Z. forest at the Institute. Seeds were buried in the order of fruit maturation. *R. illecebrosus's* seeds were buried on 1 August 1992. The buried seed bags were extracted from the ground after 1, 2, 3, 5 and 8 months of burial. The fifth month of seed burial corresponds to the winter season, and the last month (8th month) corresponds to the beginning of the next spring.

Germination tests on seeds from each burial treatment were carried out under four diurnal conditions: (a) alternating temperature in light, (b) alternating temperature in darkness, (c) constant temperature in light, and (d) constant temperature in darkness. The seeds were placed under diurnal conditions of an alternating temperature of 20℃ for 16 h, followed by 30℃ for 8 h, or at a constant temperature of 23℃. The seeds were exposed to cool white fluorescent light for 8 h a day. The photosynthetic photon flux density (700 nm) at seed level was adjusted to 36 μ mol $m^{-2}s^{-1}$. The high temperature period of the temperature alternation was synchronized with the light period. To achieve dark conditions, Petri dishes were put in black plastic bags. However, the seeds subjected to dark treatment were exposed to cool white fluorescent light for a very short time, when they were placed on the Petri dishes at the beginning of the experiment, and when the germinating seedlings were counted. Five replicates of 100 seeds of this *Rubus* species for each burial treatment were incubated on sheets of filter paper placed on 0.8% agar in 8.5 cm diameter plastic Petri dishes. The germination tests were performed for two months.

It is well known that the populations of seeds in many plant species constitute sub-populations of seeds with three different dormancy states: dormant, conditional dormant and non-dormant (Baskin & Baskin, 1985; Washitani & Takenaka, 1987; Suzuki, 1997). In this paper, seeds which do not germinate at alternating temperature in light are regarded as dormant seeds, while those which can germinate at alternating temperature even in darkness are regarded as non-dormant seeds. The seeds which cannot germinate in the dark, but can germinate in light can be regarded as conditional dormant seeds (Suzuki, 1997).

3. Results

3.1 Responses to light and temperature regime

Light had a positive effect on the germination of *Rubus illecebrosus*. Almost no seeds of this species germinated without light, regardless of temperature regime and burial time (Fig.1). Seeds that were either not buried or were buried for just a short duration also did not germinate at constant temperature, either in light or darkness. Even after eight months of burial, the final

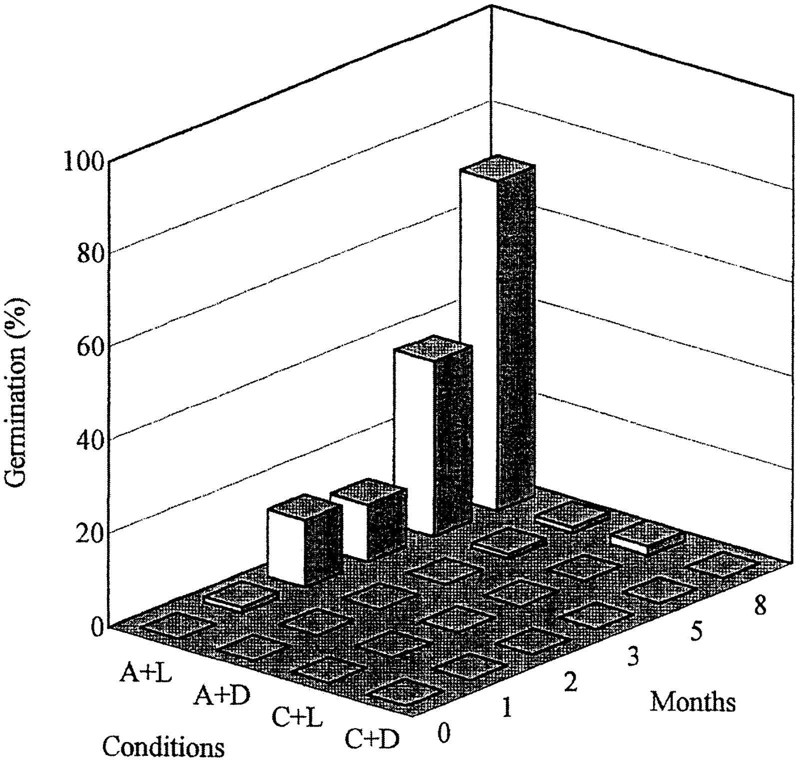

Fig. 1. Effects of the length of the buried duration on the seed germination percentage after 2 months of incubation in *Rubus illecebrosus*. A+L, alternating temperature under light; A+D, alternating temperature under darkness; C+L, constant temperature under light; C+D, constant temperature under darkness.

germination percentage of *R. illecebrosus* seeds was only 2 % at constant temperature in light (Fig.1).

3.2 Effects of burial on germination traits

Final germination percentages increased with increased seed burial time (Fig.2). These tendencies were conspicuous with the alternating temperature in light. For *R. illecebrosus*, non-buried seeds did not germinate even with the alternating temperature in light. Final germination percentages gradually increased with extended time of burial; the final germination percentage and the rate of germination ($1/t_{50}$) were 1.2 % and 0.022 day^{-1} after one month of burial, and 70.7 % and 0.053 day^{-1} after eight months of burial, respectively (Fig.2). Germination of the seeds buried for one month started 32 days after incubation, while it Germination took ten days for the seeds that had been buried for eight months (Fig.2).

3.3 Changes in dormancy states of seed

The seed dormancy state changed with buried duration (Fig.3). Although all non-buried seeds of this *Rubus* species were dormant just after ripening, the percentage of dormant seeds gradually decreased with increasing burial time. The percentage of non-dormant seeds was very low (<5%), until three months after the experiment began. During the next spring, after 8 months of burial, the percentage of dormant and conditional dormant seeds was 30% and 70%, respectively (Fig.3).

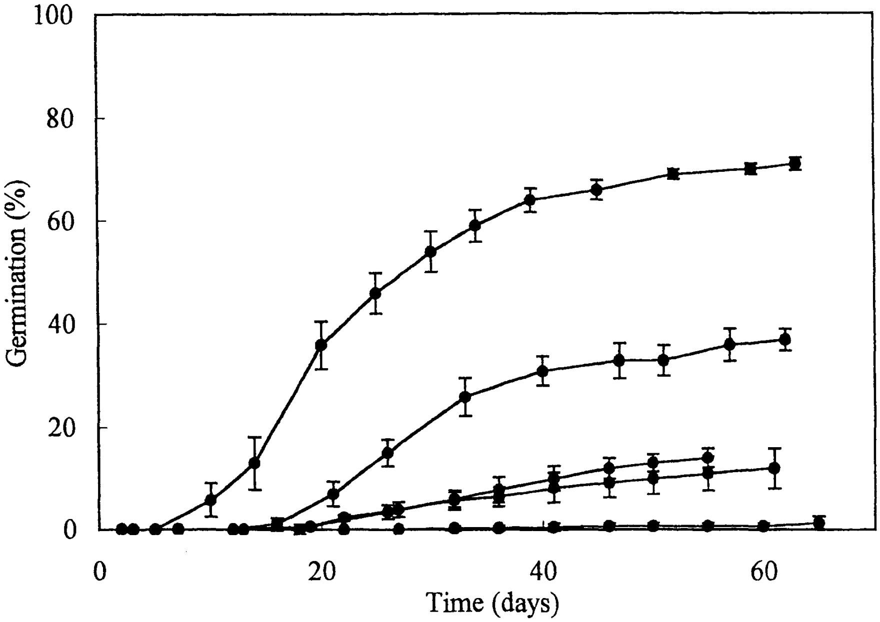

Fig. 2. Time courses of the germination of *Rubus illecebrosus* seeds retrieved after burial of one, two, three, five and nine months in soil litter, under the alternating temperature of 20℃(16h)-30℃(8h) in light. The seeds were illuminated for 8h (at higher temperatures in the case of alternating temperatures). The mean and standard error (vertical bar) are also represented.

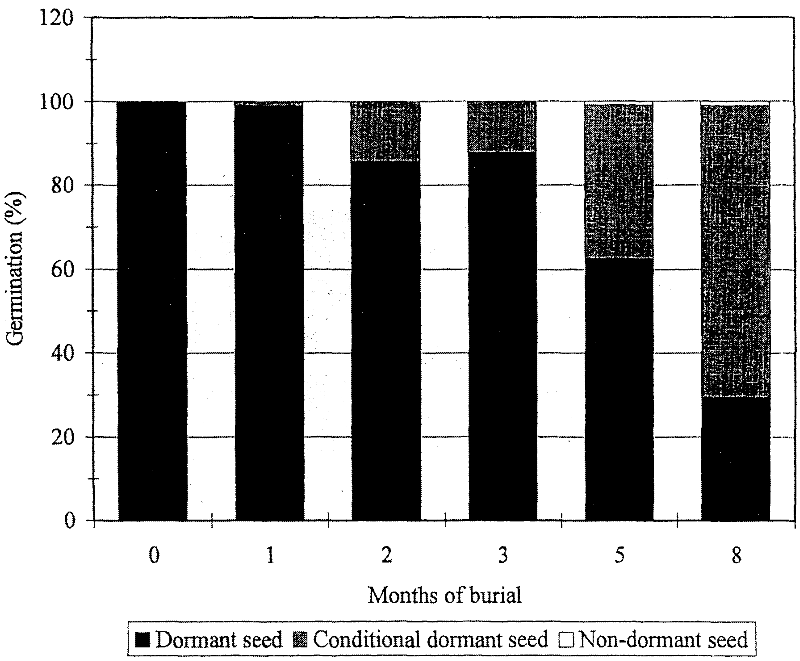

Fig. 3. Changes in the proportion of seed dormancy states of *Rubus illecebrosus*.

4. Discussion

The seeds of most *Rubus* species of cool temperate zones, including *R. illecebrosus*, do not germinate under any germination conditions just after ripening, because of their dormancy (Suzuki, 1997; Suzuki, unpublished data). Seed dormancy is broken gradually with increasing burial duration in soil (Yokoyama & Suzuki, 1986; Suzuki, 1997). However, the seeds buried for 8 months did not germinate in darkness and constant temperature (Figs.1 and 3). These results suggest that *R. illecebrosus* seeds are dormant just after ripening, and this dormancy is broken by light exposure, and that the seeds also require alternating temperature for germination. After 8 months of burial, the final percentage of germination at alternating temperature in light was 71% (Fig.2), and almost all germinated seeds may be regarded as conditional dormant seeds which could germinate only under this temperature and light regime (Fig.3).

Dormancy of the seeds just after ripening helps them to avoid unfavorable conditions for seedling survival and growth, and promotes seed bank formation (Harper, 1977; Cook, 1980). On the other hand, high requirements for light and alternating temperature for seed germination are supposed as the mechanism for detecting safe sites for regeneration provided by disturbances (Washitani & Takenaka, 1987).

R. illecebrosus, which is a shade-intolerant species, is distributed in higher elevations, and grows under more severe site conditions, even in canopy gaps and/or forest edges (Naruhashi and Satomi, 1972). This species certainly forms a persistent seed bank, since its seed dormancy will be maintained in soil. Therefore, this *Rubus* species does not only avoid competitive growing conditions just after seed dispersal, but also seems to have adapted to the favorable conditions created by unpredictable and infrequent disturbances. Thus, this species may be one of the so-called "seed bank types".

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バライチゴ種子の休眠解除における埋土期間の効果

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摘　要

西日本に広く分布するバライチゴの種子休眠の適応的な意義と埋土期間の発芽に及ぼす影響を明らかにするための試験を行った。初夏，成熟直後の種子を採取し，直ちに発芽試験を行うとともに，採取種子をシードバックに入れ土中に埋蔵した。埋土した種子は，１，２，５，８か月後に取り出し，それぞれについて，明・暗の光条件と変温・定温の温度条件を組み合わせて，発芽試験を行った。バライチゴの種子は，埋土期間の長短に関わらず，暗条件下，明条件の定温下では，ほとんど発芽しなかった。明条件の変温下における最終発芽率は，埋土期間が長くなるに従って高くなり，８か月後には71％になった。明条件の変温下という最適発芽条件でも発芽しない休眠種子とこの条件でのみ発芽する条件休眠種子の全体に占める割合は，８か月埋土後の翌発芽期で，それぞれ30％と70％であり，非休眠種子はほとんど見られなかった。こうしたことから，バライチゴは，種子散布後も長期に渡って種子の休眠体制を維持し，土壌中に永続的種子バンクを形成，その後の時間的に予測出来ない撹乱によって形成されるセーフサイトでの発芽に適応した種といえる。

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