Effects of Defoliation, Bud Removal and Girdling Treatments on Sprouting of Quercus acutissima Carr.

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Effects of defoliation, bud removal and girdling treatments on sprouting in adult trees and seedlings of *Quercus **acutissima*** Carr. were investigated in order to clarify the mechanism of sprouting and the ecological significance of sprouts. Both in adult trees and seedlings, sprouts flushed below the positions of girdling. In seedling experiments, numerous sprouts also flushed in bud removal treatment. These results suggest that inhibitors of sprouting, formed in terminal or axillary buds, are translocated through phloem, thereby inhibiting sprouting from suppressed buds. In defoliation treatments, seedlings flushed new shoots from current axillary buds after treatment, although only a few sprouts flushed. As a consequence, a shortage of photosynthetic organs were not assumed to be directly related to sprouting. From these results, it is suggested that trees recover their assimilative architecture by flushing new shoots from current terminal or axillary buds when they lose foliage as a result of disturbance such as predation. On the other hand, sprouts flushed from suppressed buds are thought to contribute to the recovery of canopy caps or the maintenance of seedlings when the growth points on upper sections are lost due to disturbance. It is also suggested that differences in sprouting vigor caused by age, size and species should be discussed in relation to the balance between inhibition from terminal or axillary buds, and stimulation from lower parts of plants.

INTRODUCTION

Sprouting is the most important type of vegetative propagation for woody plants (Kramer and Kozlowski, 1960), and has been utilized in the practical management of coppice forests (Blake, 1983). For this reason, there are many studies on sprouts from an ecological and silvicultural viewpoint (e.g., Blake, 1983; Mroz *et al.,* 1985; Kamitani, 1986; Ito *et al.,* 1989). These studies reported the differences in sprouting vigor in relation to age, size, species and cutting season. It is of course useful to investigate the growth of flushed sprouts in order to understand sprouting vigor. However, for a clear understanding of differences in sprouting vigor, it is necessary to analyze the flushing mechanism of sprouts and to investigate how conditions such as age and size modify inhibiting and stimulating factors.

On the other hand, there are many studies on the significance of sprouting ability as means of regeneration or a strategy for species propagation in the natural process of forest regeneration (e.g., Powell and Tryon, 1979; Higo, 1987; Ohkubo, *et al.,* 1988; Putz and Brokaw, 1989; Peters and Ohkubo, 1990). In natural forest regeneration with

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little disturbance, sprouts have the same role as seedlings in the recovery of canopy gaps (Ohkubo et al., 1988). However, the formation of gaps is generally irregular (Grime, 1979). Thus, temporal and spatial distribution of disturbance resulting in gap formation should coincide with the presence of sprouts for successful recruitment of advance reproduction. Therefore, the influence of changes in endogenous and exogenous factors of trees, due to disturbance, on the sprouting mechanism is important when discussing the contribution of sprouts to natural forest regeneration.

As indicated above, it is necessary to clarify the sprouting mechanism to understand the characteristics and the significance of sprouts and for efficient utilization in actual forest management. In this study, we examined effects of defoliation, bud removal and girdling treatments on sprouting in adult trees and seedlings of *Quercus* **acutissima** Carr., (the most common coppice forest species in Japan) in order to clarify mechanisms and the ecological significance of sprouts.

MATERIALS AND METHODS

Definition of terms

In studies concerning sprouts, classification of and terms for sprouts and their primordia differ according to the researcher. Therefore it is necessary to define terms used in this paper. In many papers, sprouts are classified according to the flushing position (e.g., Kramer and Kozlowski, 1960; Kamitani, 1986). Generally, sprouts flushed from the upper part of trunks are called 'epicormic branch' (Zimmermann and Brown, 1971), and sprouts flushed from the lower parts are called 'stump sprout'(Kramer and Kozlowski, 1960). The term 'root sucker' is used for sprouts flushed from roots or underground parts of trees (Kormanik and Brown, 1967). This classification of sprouts in terms of the flushing position is very useful when discussing ecological significance. However, classification by primordia is more appropriate for discussion of the sprouting mechanism. In previous studies, both adventitious buds (e.g., Jones and Raynal, 1986; 1987) and definite buds (e.g., Kormanik and Brown, 1967) were reported as the primordia of sprouts. The primordia of sprouts of Q. **acutissima** flushed from both above – and underground parts are definite buds originated from axillary buds (Gyokusen, 1987a; 1987b; 1988). Several terms has been proposed for these definite buds originated from axillary buds. Kauppi **et al.** (1987) used the term of 'dormant buds' for these definite buds as the primordia of sprouts. Zimmermann and Brown (1971) proposed that definite buds embedded in the periderm of branch and stem should be defined by the term 'suppressed buds'. They are active during much of the growing season in laying down new leaf and scale primordia and in keeping pace with the radially expanding cambium. Hasegawa (1987) also reported that the primordia of sprouts in Q. **dentata** are severely suppressed shoots, but he used the term 'latent buds'. The primordia of Q. *acutissima* are also assumed to be severely suppressed shoots (Gyokusen, 1987a). In this paper the term of 'suppressed buds' is used for the primordia of sprouts in Q. **acutissima.**

In this study, the following terms are used for shoots and their leaves flushed after treatments according to the classification of their primordia. Shoots, flushed from suppressed buds formed the previous year and which did not burst, are defined by the term 'sprouts'. Shoots flushed from current terminal or axillary buds after treatment

are defined by the term 'new shoots'. In seedling experiments, leaves which had already expanded at the beginning of treatment and which remained alive to the end of the experiment are referred to as 'remaining leaves' and are distinguished from 'sprout leaves' and 'new shoot leaves'.

Adult tree experiments

Plant materials used for adult tree experiments consisted of five 16-year-old Q. *acutissima* trees grown under field conditions in the nursery of Kyushu University, located in southwestern Japan. On April 17 1989, bark and cambium from the trunks of three sample trees were removed by girdling (bark stripping) treatment 80cm above the ground surface and 2cm in width (Fig. 1A). The lowest limb of another sample tree was girdled in the same way 30cm above the branch junction from their trunk on the same day (Fig. 1C). On August 7, the trunk of further sample tree was girdled half of its circumference in the same way 110cm above the ground surface (Fig. 1B). In October, five sample trees were cut down and the positions of suppressed buds and sprouts recorded by removing the bark.

Seedling experiments

Plant materials used for seedling experiments were 1 year old Q. *acutissima* seedlings grown in a container. Seedlings were grown under full sunlight conditions, and irrigation was carried out frequently to maintain the field capacity of the soil in the container. On June 7 1989, four groups of six seedlings were selected and used for defoliation treatment, bud removal treatment, girdling treatment and control. In the defoliation treatment, all leaves which had already expanded were removed from the base of their petioles. In the bud removal treatment, all current terminal and axillary buds were removed by their base. In the girdling treatment, bark and cambium of trunks were removed by girdling 5mm in width at a height of 15cm from the ground surface, approximately coinciding with half the average seedling height at the time of treatment. Seedlings were harvested in September, and positions of suppressed buds and sprouts, and the length of sprouts and new shoots recorded. Leaves were divided into sprout leaves, new shoot leaves and remaining leaves. The dry weight of leaves was measured after drying in a oven (85°C, 48hrs.).

RESULTS

Adult tree experiments

Figure 1 shows typical examples of the distribution of suppressed buds and sprouts of sample trees. In the tree girdled the whole circumference of the trunk (Fig. 1A), sprouting was observed from the girdling position to 60cm below girdling. Most suppressed buds to 40cm below the girdling position were flushed. No sprouts were observed above the girdling position. In the tree which was girdled half the trunk circumference (Fig. 1B), sprouts flushed just below the girdling position (90-110cm). There were no sprouts below the ungirdled parts. The number of sprouts decreased in the lower part of the trunk, and no sprouts were observed more than 40cm below the girdling. In the tree girdled on the lowest limb (Fig. 1C), sprouts flushed from the junction of the limb to the girdling position.

Seedling experiments

Figure 2 shows the number of sprouts and sprouting rates for each treatment. The number of sprouts was higher in the bud removal and the girdling treatments than in the defoliation treatment and the control. Sprouts in the girdling treatment were observed only below the girdling position. This result corresponded with results from the adult tree experiments. The primordia of sprouts of Q. *acutissivnu* are the suppressed buds, with numbers differing depending the individual tree. Therefore, the sprouting response should be compared in terms of sprouting rates, i.e., the ratio of sprouts to the total suppressed buds. Comparison of sprouting rates between treatments shows more clearly that sprouts flushed more vigorously in bud removal and girdling treatments than in defoliation treatment or control (Fig. 2).

Figure 3 shows the length of sprouts and new shoots per individual seedling in each treatment. The sprout length was longer in bud removal and girdling treatments
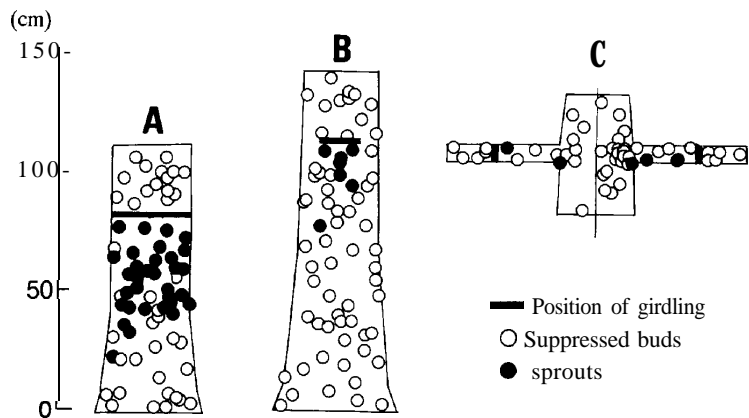

Fig. 1. Typical examples of distribution of suppressed buds and sprouts in *Quercus acutissima* adult trees used for girdling treatments. Distribution of buds and sprouts are shown on flattened out surfaces of trunks.
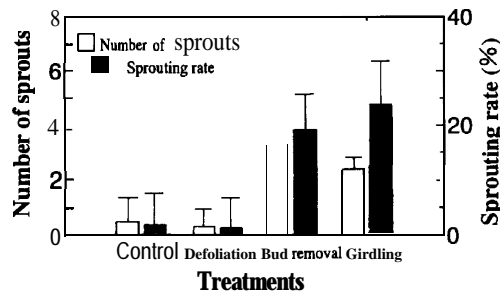

Fig. 2. Number of sprouts and sprouting rate per individual seedling of *Quercus acutissima* in each treatment. Bars indicate standard deviations.

showing the same tendency as for the number of sprouts (Fig. 2). The new shoot length was longer in defoliation treatment and control than in bud removal and girdling treatments. The longest new shoot length was observed in defoliation treatments.

Figure 4 shows the dry weight of sprout leaves, new shoot leaves, remaining leaves and total leaves for each treatment. The sprout leaf mass was larger in bud removal and girdling treatments where the number of sprouts was larger (Fig. 1) than in defoliation treatment and control. Conversely, the new shoot leaf mass was larger in defoliation treatments and control. As there were no remaining leaves in defoliation treatments, total leaf mass registered the highest value in control and the lowest value in defoliation treatment.

DISCUSSION

As indicated in results from adult tree experiments (Fig. 1), sprouts were stimulated by girdling treatment. This phenomenon was also observed in seedling experiments (Fig. 2). Sprouting from the lower part only of girdling indicated the possibility that sprouts were stimulated from the lower parts, and were inhibited by substances translocated through phloem from the upper parts. In the sample tree girdled half the
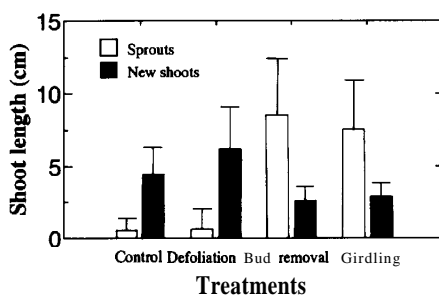

Fig. 3. Total sprout length and new shoots length per individual seedling of *Quercus acutissima* in each treatment. Bars indicate standard deviations.
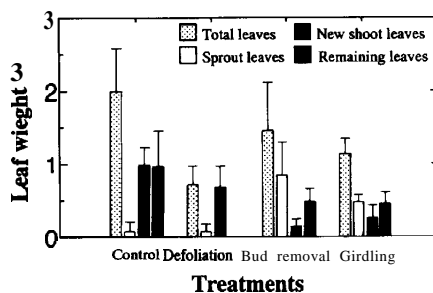

Fig. 4. Dry weight of sprout leaves, new shoot leaves, remaining leaves and total leaves per individual seedling of *Quercus acutissima* in each treatment. Bars indicate standard deviations.

circumference, sprouts were not observed more than 40cm below the girdling position (Fig. 1B). In the sample tree girdled on the lowest limb, no sprouts flushed from the trunk (Fig. 1C). These results suggest the lateral movement of inhibitors within the phloem. On the other hand, sprouting was observed in bud removal treatment in seedling experiments (Fig. 2). Raese (1975) reported that sprouts of pruned *Malus domestica* Borkh. and *Pyrus communis* L. were inhibited by panting Naphthaleneacetic acid (NAA) on the pruned ends of branches, From the results of this experiment, it is suggested that some inhibitors which have the same role as NAA formed in the terminal or axillary buds were translocated through phloem, and inhibited sprouting from suppressed buds.

In bud removal treatment, seedlings developed new shoots and expanded new leaves (Fig. 3 and 4). These shoots were thought to flush from the subsidiary meristem of terminal or axillary buds which were not completely removed by treatment. There was less development of new shoots in bud removal and girdling treatments than in defoliation and control (Fig. 3 and 4), in spite of their high sprouting rate (Fig. 2). This result suggested a difference in the mechanism between sprouting from suppressed buds and flushing from terminal or axillary buds. This difference in the flushing mechanism should be confirmed in further studies in relation to hormonal effects and phtosynthate allocation characteristics.

Generally, epicormic branches are thought to flush when light conditions are improved as a result of thinning (Zimmermann and Brown, 1971). However, in this experiment, seedlings in defoliation treatment and control showed quite low sprouting rates compared with the two other treatments (Fig. 2) though the experiment was carried out under fully sunlit conditions. Therefore, it is assumed that the light environment does not directly stimulate sprouting. In defoliation treatment, only a few sprouts were observed though seedlings developed a great number of new shoots from terminal and axillary buds (Fig. 3 and 4). This result indicated that a shortage of photosynthetic organs also did not have a direct effect on sprouting.

In natural forest dynamics, sprouts contribute greatly to the recovery of canopy gaps formed by stem or limb breakage through with wind damage (Putz and Brokaw, 1989). On the other hand, sprouts play an important role in the seedling stage as a surviving strategy against loss of above ground parts due to predation or stress (Grime, 1979; Powell and Tryon, 1979; Okano *et al.,* 1987). From results in this study, it is estimated that plants attempt to recover their assimilative architecture by developing new shoots from current terminal and axillary buds when they lose foliage due to predation or other reasons. In contrast, sprouting from suppressed buds is assumed to be stimulated and contribute to recovery when growth points of upper parts are lost through disturbance such as stem or branch breakage in canopy trees or as predation of above ground organs of seedlings.

Ohkubo *et al.* (1988) and Peters and Ohkubo (1990) reported that *Fagus japonica* trees have several sprout stems which flush constantly from the base of the main stem. These sprouts contribute to recovery of gaps after the main stem dies. In species such as *F. japonica* which have constantly sprouting stems independent from any distur-bance, inhibition of sprouting from buds is thought to be weak. These characteristics result in the positive utilization of sprouts in the regeneration process.

In this study, only the inhibition of sprouting was demonstrated. However, since

sprouts flushed only below the girdling position in girdling treatments, some stimula-
tion mechanism from lower parts can be also inferred. Therefore, differences in
sprouting vigor in relation to age, size and species should be discussed in terms of the
balance between intensity of inhibition from the terminal or axillary buds and of
stimulation of the lower parts.

   The experiments were carried out in order to investigate the flushing mechanism
of sprouts. However, flushing of sprouts consists of two developmental steps; the burst
of buds and their elongation. Kauppi et *al*.(1987) observed that dormant buds at the
trunk base of *Betula pubescens* seedlings burst every year. He reported that those burst
buds which maintained elongation became sprouts, and those which did not elongate
died and became dormant buds again. Burst buds which do not become sprouts can be
observed in *Q. acutissima* adult trees. Therefore, in order to understand the sprouting
mechanism more clearly, it is necessary to clarify the bursting mechanism of suppres-
sed buds and conditions for survival or elongation of burst buds.

ACKNOWLEDGEMENTS

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