

**Age structure and dynamics of *Cercidiphyllum japonicum* sprouts based on growth ring analysis**

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## Abstract

We investigated the factors that encourage sprouting by *Cercidiphyllum japonicum*, as well as its ability to sprout after cutting, by analyzing the age structure, distribution, and growth of sprouts in one stool of this species. *C. japonicum* produced numerous sprouts in various age classes, ranging from 7-92 years old; the main stem was 226 years old. Sprouts that were relatively close in age (e.g., 30 or 80 years old) tended to form clusters. Based on an increase in the width of annual growth rings, we estimated that gap formation occurred about 30 years ago. This encouraged existing sprouts to grow more, and many sprouts were produced on the periphery of the stand to take advantage of the improved light conditions. After cutting, larger stems produced more simultaneous sprouts; therefore, sprout occurrence probably depends on the biomass of parent stems, although smaller stems were also able to produce some simultaneous sprouts. In the absence of physical damage, *C. japonicum* produced more sprouts as a function of increased age as a means of self-maintenance. *C. japonicum* sprouted simultaneously in response to external disturbances, such as gap formation and cutting, and it sprouted sequentially with increasing age. Therefore, although *C. japonicum* seedlings are rarely found in forests, *C. japonicum* can maintain its populations over long periods by sprouting, which compensates for sparse seedling regeneration.

Key words: Age structure; Gap formation; Growth process; Light; Self-maintenance; Tree sprouting

## 1. Introduction

*Cercidiphyllum japonicum* Sieb. et Zucc. is a common tree species in riparian forests of Japan, and it maintains its populations over long periods of time by sprouting (Kubo et al., 2001a; Sakio et al., 2002). Since the sprouts of this species are often found in unstable areas, e.g., on steep slopes, small disturbances such as soil erosion probably provide a stimulus for sprouting (Kubo et al., 2001a). In addition, it is thought that *C. japonicum* sprouts to compensate for its sparse seedling regeneration (Kubo et al., 2001a), since its seedlings rarely regenerate more than those of coexisting tree species, including *Fraxinus platypoda* Oliv. and *Pterocarya rhoifolia* Sieb. et Zucc. (Kubo et al., 2000; Sakio et al.,

2002).

The ability to encourage sprouting varies by species (Basnet, 1993; Bellingham et al., 1994; Zimmerman et al., 1994), stem size and age (Kamitani, 1986; Ito and Gyokusen, 1996), and the intensity of and interval between damage events (Malanson and Westman, 1985; Crow, 1988; Keeley, 1992). Generally, sprouting is very common in non-coniferous trees in coppice forests following overstory removal for human use (Negreros-Castillo and Hall, 2000; Rydberg, 2000; Luoga et al., 2004). On the other hand, in the absence of human activities, tree species that produce many sprouts are mostly found in areas that experience disturbances, such as heavy snowfall (Okitsu, 1991; Tanimoto, 1993), coastal winds (Ito, 1993; Ito and Gyokusen, 1996), and steep slopes (Sakai et al., 1995), where conditions are generally too severe for seedlings to regenerate. Therefore, sprouting likely compensates for sparse seedling regeneration (Hara, 1987; Ohkubo, 1992; Kruger et al., 1997). Even in stable forests, sprouting plays an important role in the maintenance of forest vegetation by repairing the forest canopy after gap formation (Koop, 1987; Ohkubo et al., 1988, 1996; Peter and Ohkubo, 1990).

Certain stimuli probably encourage *C. japonicum* to sprout, although this species can produce numerous sprouts even in the absence of direct physical damage. However, few studies have investigated sprouting by *C. japonicum* (Kubo et al., 2001a; Sakio et al., 2002), and little is known about the age structure and dynamics of sprouts or about the ability of this species to sprout after experiencing physical damage. Extended longevity by sprouting is essential to the species composition of a particular area (Malanson and Westman, 1985); therefore, it is important for conservation and/or management of riparian forests to understand the sprouting capability of *C. japonicum*. In this study, we investigated the age structure, distribution, and growth processes of *C. japonicum* sprouts, as well as its ability to sprout after cutting. Specifically, we discuss the factors that encourage sprouting by *C. japonicum*, and what traits characterize *C. japonicum* sprouts.

## **2. Study site and methods**

Our study site was located along a small stream (Ooyamazawa) of the Nakatsugawa branch of the Arakawa River, in the Chichibu Mountains of central Japan (35° 57' 30" N,

138° 45' 32" E). This deciduous riparian forest is native forest that has no history of cutting (harvesting) or fire. The canopy in this area was over 30 m high and was dominated by *F. platypoda*, *P. rhoifolia*, and *C. japonicum* (Sakio, 1997). *F. platypoda*, which was the dominant tree, grew up to 40 m tall and 150 cm in diameter at breast height (DBH, approximately 130 cm above ground) and produced no sprouts; *P. rhoifolia*, which was the secondarily dominant pioneer species, grew up to 30 m tall and 100 cm in DBH and produced few or no sprouts. The age-class distribution of *F. platypoda* had a mode at the 200- to 220-year class, and the oldest tree was 254 years old (Sakio, 1997). *P. rhoifolia* grew in patches of even-aged trees (ca. 90 years old) based on measurements of core samples (Sakio et al., 2002). On the other hand, *C. japonicum* was the third most dominant species and grew up to 40 m tall and 150 cm in DBH, and almost all individuals of this species produced numerous sprouts. The topography in the forest included a site with muddy sediment upstream, which was formed by exposing the bottom of a V-shaped valley, and a V-shaped valley downstream, which was characterized by a steep slope of about 30 degrees, a cliff, and a talus (Kubo et al., 2001b). There were many disturbances including erosion, and sedimentation of soil, sand, and gravel occurred frequently by stream flow in the area near the active channel. The maximum snow depth in this area was about 30 cm from January to March.

The *C. japonicum* stool that we investigated was located between the slope and the stream at the bottom of the V-shaped valley (Fig. 1), and included many sprouts that had originated from the root system or base of larger stems. All 29 sprouts were cut at about 50 cm from the base of the stem in the fall of 2001, and stem disks, which were brought to the laboratory for analysis, were sliced from the standing stems. The two largest stems in this stool were not cut, as they were considered main stems; their ages were measured by increment coring. Since the borer did not reach the center, the number of missing rings was estimated from the mean radial growth. We were also unable to determine the ages of sprouts smaller than <1 cm in diameter, because they had been eliminated completely by the clearing of the stems. However, because we needed to clarify how many of these small sprouts *C. japonicum* produced naturally, we referred to data from 1998, when the last survey was conducted, and we presumed these stems were age 0-1.

We counted the annual rings on the stem disks under a stereoscopic microscope.

We often observed two to five sprouts that had coalesced, so we measured the ages of each sprout separately because of their different origins. Next, we surveyed the widths of growth rings (in sets of five) as a function of age by measuring the stem disks in four directions (or in one to three directions for sprouts that had merged). To clarify the relation between the age and the diameter of sprouts, we measured sprout diameter. We used the double average radius of the measurements in one to four directions to estimate sprout diameter, which was measured separately for coalesced sprouts.

We mapped the distribution of sprouts in the stand and defined the center of the stool as the center of the largest main stem. We then used a ruler to measure the distance from the center of the stand to the center of each sprout and measured the exact size of each. The number of new sprouts in September 2002 (i.e., current-year sprouts) was counted for each parent stem.

### **3. Results**

#### 3.1. Age structure

*C. japonicum* produced many sprouts, ranging in age from 7-92 years, with varying numbers of stems in each age class (Fig. 2). Based on measurements from increment cores, we determined that the main stems had diameters of 70 and 55 cm and were 226 and 186 years old, respectively. For each age class, there was a variable number of sprouts, although sprouts around 30 years old were the most numerous and sprouts aged 74-80 years were the second most numerous. Six sprouts measured <1 cm in diameter.

#### 3.2. Sprout distribution

The two main stems stood at the center of the stool, and many sprouts occurred around these main stems (Fig. 3). *C. japonicum* has large root systems from which many sprouts can originate. In the area around the stand (Fig. 1), we distinguished between slope and valley sites. The slope site had a steep slope on one side, while the valley site was on the other side near the stream in the V-shaped valley. Sprouts that were around 30 years old were clustered around the main stems at the slope site upstream, whereas sprouts around 80 years old tended to be downstream. Other sprouts were positioned randomly around the main stems. We observed a negative relationship between sprout age and the distance

from the center of the stool to each sprout ( $P < 0.01$ ), such that older sprouts were near the interior of the stool and younger sprouts were in the periphery (Fig. 4).

We found many coalesced sprouts (11 of 29 sprouts; Fig. 5), most of which consisted of two sprouts, and the maximum consisted of five sprouts. The original ages of the coalesced sprouts tended to be similar (Fig. 3).

We found no large dead sprouts, only small dead sprouts (Fig. 3). Although the stand was located along the banks of a stream, the stream did not affect sprout distribution. Moreover, the stand showed no trace of physical damage, with the exception of one fallen log in the slope site upstream.

### 3.3. Sprout growth

The sprout growth process is shown in Fig. 6, separated by site (slope and valley) according to the sprout distribution shown in Fig. 3. The growth process varied by individual sprout and changed with age, although sprout diameter was positively correlated with age ( $P < 0.01$ , Fig. 7). On the slope site, 80-year-old sprouts showed increased growth starting about 30 years ago. Sprouts ca. 30 years old showed vigorous growth soon after their inception; some of them had even outgrown older sprouts. In contrast, many sprouts in the valley site and those close to the main stems grew slowly, but consistently.

### 3.4. Sprouting after cutting

Most stems that were cut produced sprouts from the lower parts of the stems in September 2002. The number of current-year sprouts was positively correlated with the age and diameter of the parent stems (age:  $R^2 = 0.28$ ,  $P < 0.01$ ; diameter:  $R^2 = 0.43$ ,  $P < 0.01$ ; Fig. 8). Smaller, younger stems also produced sprouts. In total, we counted 181 current-year sprouts: 150 from live stems, 18 from the root system, and 13 from dead stems. Main stems produced no current-year sprouts.

## 4. Discussion

### 4.1. Sprout occurrence and growth in relation to light conditions

We showed that *C. japonicum* produced numerous sprouts in various age classes, and

sprouts of similar age tended to cluster together (Figs. 2 and 3). Eighty-year-old sprouts on the slope site showed increased growth approximately 30 years ago (Fig. 6), when a large tree may have fallen down as a result of windthrow or soil erosion. A number of sprouts were apparently produced around this same time. This suggests that light conditions improved at this site, allowing many sprouts to occur simultaneously.

Many species can sprout under the brighter light conditions following overstory removal for human use (Rydberg, 2000; Louga et al., 2004), and even in undisturbed stable forests, light conditions are also important for sprouting (Koop, 1987; Ohkubo et al., 1988, 1996; Peter and Ohkubo, 1990). Sonoyama et al. (1997) reported that sprouting by *Fraxinus lanuginosa* Murata is encouraged by brighter light conditions following gap formation. This suggests that the effects of sprouting on population dynamics are regulated secondarily by light conditions. Crow (1992) reported that under brighter light conditions, when seedlings of red oak, *Quercus rubra* L., received sufficient light to fix enough CO<sub>2</sub> to offset respiration, they showed increased growth and produced numerous sprouts. Recently, several researchers have reported a relationship between sprouting ability and carbohydrate or CO<sub>2</sub> levels (Sakai et al., 1997; Bond and Midgley, 2001). Therefore, simultaneous sprouting by *C. japonicum* may have been facilitated in part by certain chemical reactions, e.g., the production of some material(s) that encouraged sprouting as soon as light conditions improved. However, we did not investigate these reactions in this study.

*C. japonicum* sprouts may be encouraged by small disturbances, since stools with numerous sprouts were found more often in the V-shaped valley than in the muddy sediment of the riparian forest (Kubo et al., 2001a). Gracia and Retana (2004) investigated a number of variables at different sites and showed that position on a slope is a key factor for size differentiation of sprouting holm oak (*Quercus ilex*). In our study site, light conditions in the V-shaped valley may change more frequently (Kubo et al., 2001b) when various low-intensity, high-frequency disturbances occur (Akamatsu and Aoki, 1994), including windthrows, soil erosion, and/or annual flooding. If gap formation is one of the factors that cause sprouting, this may be why *C. japonicum* produced so many sprouts at that site.

Within a stand, sprouts must avoid impeding their own growth. Stems of *Euptelea polyandra* Sieb. et Zucc. gradually become inclined with increased size,

allowing younger sprouts to become established underneath (Sakai et al., 1995). Sprouts under a canopy of *Fagus japonica* Maxim. continue to grow after the death of the main stem (Peter and Ohkubo, 1990), and the stand expands and disconnects (Ohkubo, 1992). Ohkubo et al. (1996) suggested that these sprouts play a role in ‘sprout banks’, analogous to seedling banks (Bellingham et al., 1994). *C. japonicum* may therefore produce similar ‘sprout banks’. Once a gap has been formed, pre-existing sprouts of *C. japonicum* can grow, and some may coalesce. New sprouts will occur on the periphery of the stand under more favourable light conditions. Therefore, *C. japonicum* has the potential to produce a vast canopy and a large stand from only one main stem.

#### 4.2. Traits of *C. japonicum* sprouts

Sprout formation by *C. japonicum* is dependent on the age and size of a stand, since larger stands typically produce more sprouts (Kubo et al., 2001a). The *C. japonicum* stands that we investigated in this study had no sprouts in the age class between the main stems (226 and 186 years old) and the oldest sprout (92 years old), but had produced sequential sprouts since then (Fig. 2). If sprouts are encouraged only by small disturbances (Kubo et al., 2001a) or by light conditions, these parent trees may not have had an opportunity to sprout if the ground and light conditions around them did not change. In addition to the surrounding conditions, an additional factor that causes sprouting is age. Younger *C. japonicum* may have invested their energy only toward enhancing their own growth. Producing more sprouts with age is advantageous for self-maintenance when faced with multiple external stresses (Peter and Ohkubo, 1990; Ito and Gyokusen, 1996).

A number of studies have investigated sprouting ability resulting from physical disturbances, such as cutting (Kamitani, 1986; Ito 1996; Negreros-Castillo and Hall, 2000; Rydberg, 2000; Luoga et al., 2004), fire (Malanson and Westman, 1985; Crow, 1988; Keeley, 1992), and hurricanes (Basnet, 1993; Bellingham et al., 1994; Zimmerman et al., 1994). Kamitani (1986) reported that the patterns of sprouting after cutting (expressed in numbers of sprouts over time) could be classified as convex, increasing, or constant. This suggests that sprouting ability for the purposes of maintaining individuals and populations is related to the cycle of disturbances. After cutting, the number of *C. japonicum* sprouts that is produced depends on the size of the parent stem; sprout occurrence might initially depend on the production of the parent stem to repair damage,

although even small stems could have this capacity (Fig. 8).

Koop (1987) pointed out that trunk suckers can replace stems that are aging or dying from endogenous damage resulting from senescence or caused by disease and mechanical damage that has resulted in partial uprooting or stem breakage. Ohkubo (1992) observed both of these scenarios in *F. japonica*. *C. japonicum* also produced sequential sprouts as a result of endogenous factors such as aging, as it reached the canopy, and it produced many sprouts simultaneously as a result of external factors, such as gap formation and physical damage, in response to long-term environmental changes (Fig. 9). Moreover, following the death of a stem, *C. japonicum* is able to fill the ensuing gap with sprouts, thereby preventing other species from replacing it. Consequently, *C. japonicum* can create colonies by producing sprouts of various ages, which changes the age make-up of a stand. *C. japonicum* juveniles are more rare than those of coexisting tree species in riparian forests (Sakio et al., 2002), because most seedlings die in the current year as a result of desiccation or washing away despite their shade-tolerance (Kubo et al., 2000; Kubo et al., 2004). However, *C. japonicum* can maintain its populations by sprouting over long periods, thereby compensating for sparse seedling regeneration.

## 5. Conclusion

We showed that *C. japonicum* sprouts may have been produced as a result of gap formation, which might have allowed more sprouts on the periphery of the stand to gain light, as older sprouts showed increased growth around that time. In the absence of disturbances, *C. japonicum* produces sprouts as a function of increased age after investing energy into the main stem. Therefore, *C. japonicum* is able to maintain its populations and dominate a stand by producing many sprouts over a longer time than the life span of coexisting species.

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## Figure Captions

Figure 1. The investigated *C. japonicum* stand, which was located at the bottom of a V-shaped valley between a slope and a stream.

Figure 2. Number of sprouts per age class in the *C. japonicum* stand. Hatched bars indicate the main stems, solid bars indicate sprouts, and the open bar indicates sprouts <1 cm in diameter in 1998.

Figure 3. Distribution of main stems and sprouts by age class in the *C. japonicum* stand. Circles with a dotted line indicate the main stems; circles with a solid line indicate sprouts; solid circles indicate dead sprouts. The stand was located near a stream at the bottom of a V-shaped valley; the upper site was in the valley and the lower site was on a slope.

Figure 4. Relationship between sprout age and distance from the center of the stand.

Figure 5. Cross-section of a stem disk of three coalesced sprouts, showing the three centers and partial remnants of bark.

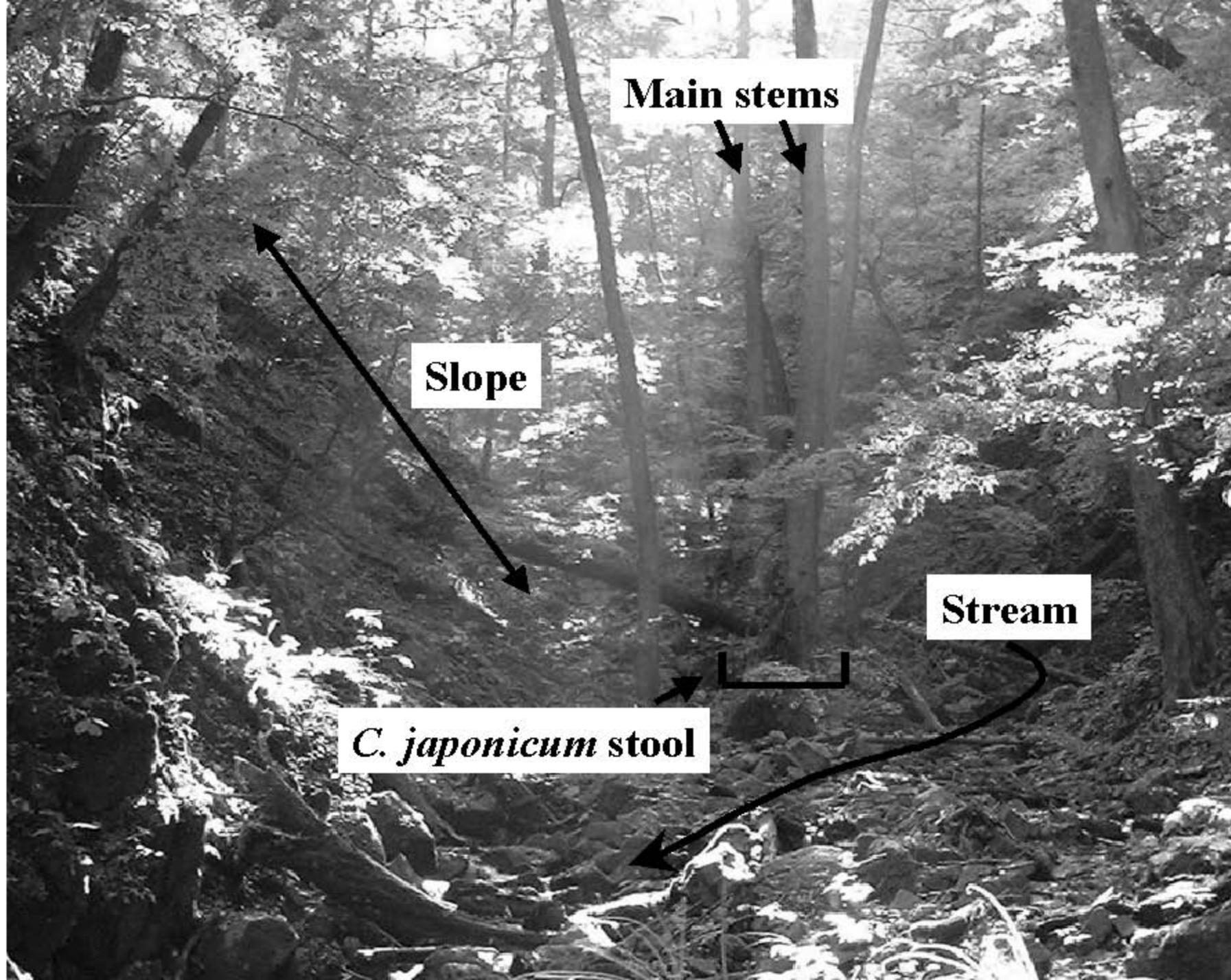
Figure 6. Radial growth in *C. japonicum* sprouts. Open circles with a solid line indicate sprouts in the valley site and solid circles with a dotted line indicate sprouts at the slope site. The two sites were distinguished as indicated in Figure 3.

Figure 7. Relationship between sprout age and diameter.

Figure 8. Relationship between the number of current-year sprouts and the age (top panel) and diameter (bottom panel) of the parent stem.

Figure 9. Proposed scheme for the self-maintenance of *C. japonicum* by sprouting. *C. japonicum* regenerates from seedlings, reaches the canopy, and then produces sprouts

as a function of aging and in response to long-term external disturbances. Moreover, following the death of the parent stem, it is able to fill the ensuing gap with sprouts. Consequently, *C. japonicum* can create colonies composed of sprouts at various ages.



**Main stems**



**Slope**



**Stream**



*C. japonicum* stool

