Chapter 4
Cercidiphyllum japonicum

Masako Kubo and Hitoshi Sakio

Abstract The tertiary relict *Cercidiphyllum japonicum* is an important canopy tree species of riparian forests in Japan, despite typically occurring at low densities. Once mature, canopy individuals are typically 30 cm in diameter at breast height and have high annual seed production. Seedlings tend to germinate on steep slopes with exposed soil, but not in thick litter or gravel substrates. Annual seedling mortality is high at germination sites that are exposed to heavy rain and flooding. In contrast, *C. japonicum* has highly successful vegetative reproduction through basal sprouting (a product of endogenous [i.e., aging] and exogenous [i.e., gap formation and physical damage] factors), which leads to a multi-stemmed growth form. Sprouting allows *C. japonicum* to dominate stands over time, as it is longer lived than other coexisting species; this promotes the maintenance of its populations.

Keywords *Cercidiphyllum japonicum* · Life history · Riparian forest · Seedling traits · Seed production · Sprouting traits · Tertiary relict species

4.1 Introduction

Cercidiphyllum are known as tertiary relict species; fossils indicate that this angiosperm lineage arose during the Cretaceous period (Dosmann 1999). The genus comprises two genetically distinct dioecious tree species, *Cercidiphyllum japonicum* Siebold et Zucc. ex Hoffm. et Schult. and *Cercidiphyllum magnificum* (Nakai) Nakai (Fig. 4.1) (Li et al. 2002; Isagi et al. 2005). Although *Cercidiphyllum* was once distributed throughout the Northern Hemisphere (Crane and Stockey 1985;

M. Kubo (✉)
Faculty of Life and Environmental Science, Shimane University, Shimane, Japan
e-mail: kubom@life.shimane-u.ac.jp

H. Sakio
Sado Island Center for Ecological Sustainability, Niigata University, Niigata, Japan
e-mail: sakio@agr.niigata-u.ac.jp; sakiohit@gmail.com

Fig. 4.1 *Cercidiphyllum japonicum* and *Cercidiphyllum magnificum* at Ooyamazawa. (**a**) (photo by Kyoko Kato) and (**b**) show tree form; (**c**) and (**d**) show the leaves in spring and summer of *C. japonicum* and *C. magnificum*, respectively. The difference in leaf size between *C. japonicum* (right) and *C. magnificum* (left) is shown (**e**)

Skawińska 1986), *C. japonicum* is now found in only Japan and part of China, and *C. magnificum* is restricted to parts of Japan (Manchester et al. 2009). In Japan, *C. japonicum* mainly occurs in riparian areas in cool temperate forests on Hokkaido, Honshu, Shikoku, and Kyushu, and *C. magnificum* is found in subalpine forests on

Fig. 4.2 Multi-stemmed trunk and canopy of *Cercidiphyllum japonicum* in Hirogawara, Yamanashi

Honshu. There are no reports of varied morphology of *C. japonicum*, but the genotype is reported to vary between north-central and southwestern Japan (Qi et al. 2012). Populations of *C. japonicum* from north-central Japan have similar chloroplast DNA to *C. magnificum*, implying that some *C. japonicum* individuals may have had an advantage in severe climate conditions at northern latitudes, which could have facilitated the establishment and maintenance of northern populations (Qi et al. 2012).

Cercidiphyllum japonicum* is an essential canopy species in Japanese riparian forests (Ohno 2008), although it is mostly found in low abundance and pure stands are rare. Saplings are not often observed, implying that germination may be limited in forests. The species is long lived, often forming large canopies and multi-stemmed trunks (stools) through sprouting (i.e., producing shoots from the base or from roots) (Fig. 4.2). It is possible that vegetative reproduction may compensate for low sapling recruitment, allowing *C. japonicum* to coexist at low density with other canopy species.

This species, called "*Katsura*" in Japanese, is a sacred tree with ancient associations to moon, mountain, and water deities. Therefore, many large, multi-stemmed individuals are designated as natural monuments throughout the country (Fig. 4.3). Although *C. japonicum* is an important species both culturally and ecologically, its life history remains poorly understood. It is thought that populations are maintained

Fig. 4.3 *Cercidiphyllum japonicum* as a natural monument in Japan. (**a**) Katsura of Takezaki in Shimane Prefecture; (**b**) Oo-Katsura of Itoi in Hyogo Prefecture; (**c**) Katsura of Idoi Shrine in Shiga Prefecture; (**d**) Senbon-Katsura of Inari Shrine in Iwate Prefecture; (**e**) Senbon-Katsura of Oohora in Iwate Prefecture. The Japanese common name of *C. japonicum* is "*Katsura*"

on microtopography features created by various disturbances in riparian forests over long periods. However, such old-growth forests are now scarce due to extensive logging, and understanding the life history of *C. japonicum*, including germination traits and survivorship, may be confounded by this habitat loss.

An undisturbed population of *C. japonicum* occurs in a 1-km long preserved forest in the Ooyamazawa riparian area in central Japan. Here, *C. japonicum* is found as a canopy species, with most individuals distributed on steep slopes and exposed rocks. This population is small relative to those of other canopy species such as *Fraxinus platypoda* (Chap. 2) and *Pterocarya rhoifolia* (Chap. 3). In this chapter, we clarify the life history of *C. japonicum* using observations from the Ooyamazawa population. We investigated distribution patterns, size structure, flowering and seed production, seedling regeneration traits, and sprouting traits, and considered life history strategies in adapting to riparian disturbances. Additionally, we partially compared the life history of *C. japonicum* to that of the closely related *C. magnificum*.

4.2   Study Species

Cercidiphyllum japonicum is a tall, straight-stemmed species up to 30 m in height and 1 m in diameter (Fig. 4.1a). Associated canopy species within riparian forests include *F. platypoda*, *P. rhoifolia*, *Aesculus turbinata*, and *Acer* spp. Many individuals have multi-stemmed trunks, with wide, shoot-producing rootstocks (stools) and expansive individual canopies (Fig. 4.2). Leaves are borne on short and long shoots and are atypical in shape; those produced in spring are heart shaped, and those produced in summer are rhomboid (Fig. 4.1c).

Cercidiphyllum magnificum is distributed with *Betula ermanii*, *Acer shirasawanum*, and *Pterostyrax hispida* in riparian areas of subalpine forests in north-central Japan, where various disturbances occur, including spring avalanches. Its stems are usually creeping, growing on average to 5 m in height and 10 cm in diameter, although large specimens can reach 20 m in height and 40 cm in diameter (Fig. 4.1b). Their leaves are larger than those of *C. japonicum* (Fig. 4.1e).

4.3   Structure and Distribution

Our inventory recorded 2111 individual trees within a 4.71-ha study plot in Ooyamazawa riparian area. Of these, 59 were *C. japonicum* individuals (12.6 individuals/ha) (Table 4.1) with a main stem ≥ 4 cm diameter at breast height (DBH), measured from the main (largest) stem in multi-stemmed individuals. Most individuals were in the canopy layer ($n = 47$), with nine in the subcanopy layer, and three in the shrub layer. The DBH of main stems ranged from 5 to 153 cm (Fig. 4.4).

Most individuals were distributed within a V-shaped valley in the study area (Fig. 4.5), which had 30-degree slopes on the valley sides and roughly 12-degree slopes in sedimentary debris flow areas (Chap. 1). Alluvial fan and terrace debris flows in upstream areas contained rich soil with a litter layer, but there was little litter on terrace scarps, new landslide sites, old landslide slopes, and talus in downstream areas (Kawanishi et al. 2004). Various disturbances, including erosion and

Table 4.1 *Cercidiphyllum japonicum* trees in Ooyamazawa with a main stem DBH of ≥ 4 cm

	Number of trees			Mean number of sprouts
	Canopy	Subcanopy	Shrub	
Female	20	0	0	8.9 ± 9.5
Male	26	0	0	12.5 ± 15.5
Immature	1	9	3	2.9 ± 4.4
Total	47	9	3	9.1 ± 12.2

Canopy-layer trees reach the canopy and are >20 m in height and 20 cm in DBH. Subcanopy layer trees do not reach the canopy and are <20 m high. Shrub layer trees are <10 m high. The mean number of sprouts reflects the mean ± standard deviation per individual
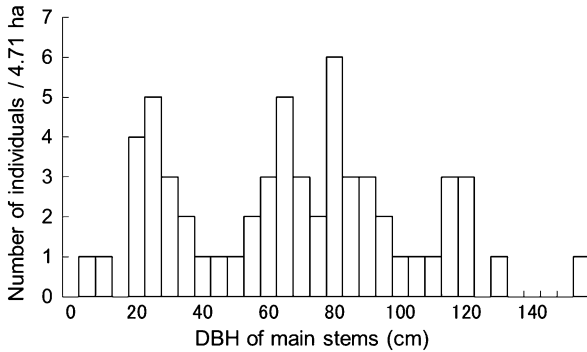
Fig. 4.4 Diameter at breast height size class distribution of main stems of *Cercidiphyllum japonicum* in Ooyamazawa. Individuals with a main stem DBH ≥4 cm are shown
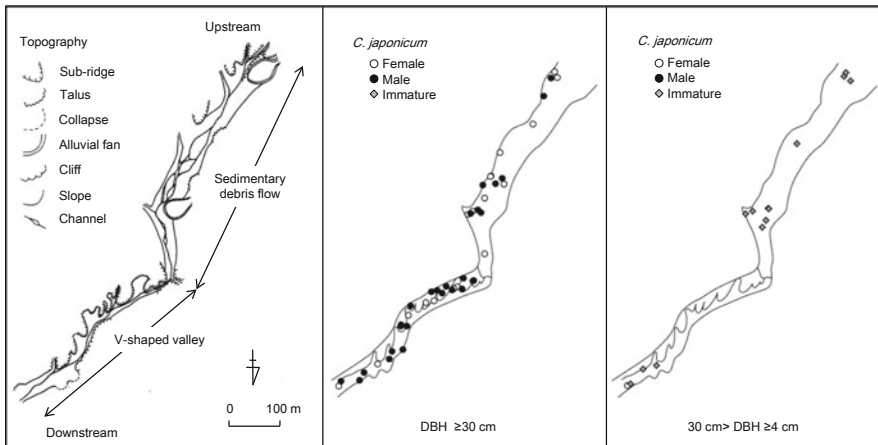

Fig. 4.5 Diagram of microtopography types and the distribution of *Cercidiphyllum japonicum* in Ooyamazawa. Individuals with a main stem DBH of ≥4 cm are shown

sedimentation of soil, sand, and/or gravel, were frequent in downstream valley areas due to stream flow and steep slopes. Upstream upland areas were less disturbed, whereas the valley bottom was filled in by previous large landslides and/or debris flows. Both the tree density and total basal area of *C. japonicum* were greater in the V-shaped valley than in the sedimentary debris flow areas upstream, and individuals were distributed over microtopography features such as sub-ridges, talus, and collapses (Kubo et al. 2001a). Only 46 of the 59 individuals, 20 females and 26 males (Table 4.1), were mature, and female and male trees were randomly distributed relative to each other (Fig. 4.5).

Individuals were distributed along a stream in the study area from 1200 to 1600 m in elevation, and were found co-occurring with *C. magnificum* on a talus slope next to a stream above 1600 m (Fig. 4.6). *Cercidiphyllum japonicum* was found at <1650 m in elevation, but *C. magnificum* was found at elevations ≥1600 m, extending to the ridge border at approximately 1720 m in elevation. The co-occurring
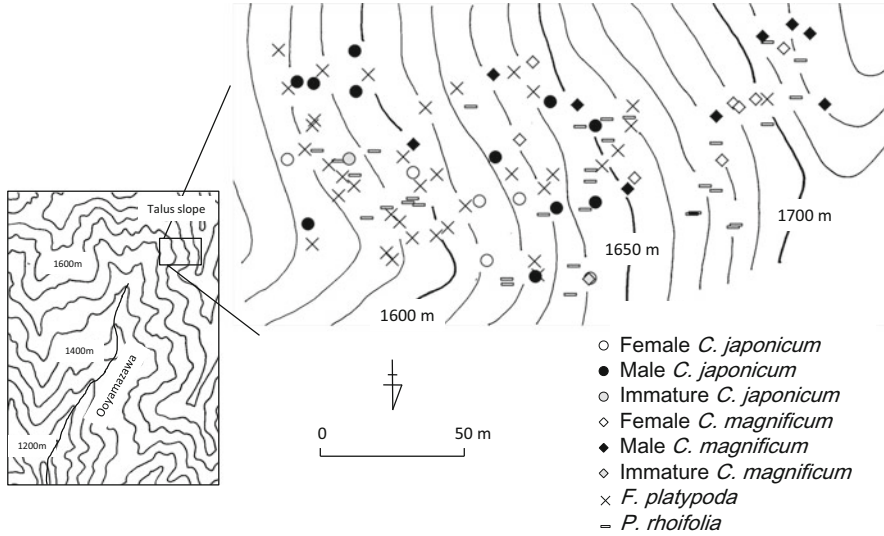
Fig. 4.6 Distribution of *Cercidiphyllum japonicum* and *Cercidiphyllum magnificum* on an upper stream talus slope at Ooyamazawa (Kubo et al. 2010, revised). Individuals with a main stem DBH of ≥4 cm are shown

canopy species *F. platypoda* and *P. rhoifolia* were distributed throughout the elevation range, with a greater number of *P. rhoifolia* individuals on the upper slopes of the study area.

4.4   Reproductive Traits

4.4.1   Flower

The canopy of *C. japonicum* turns purple-red at the time of blooming (Fig. 4.7), when individuals produce a large number of female or male flowers that lack a perianth at the tips of short shoots (Fig. 4.8). Blooming occurs in late April or early May in Ooyamazawa.

We categorized the 59 individuals of *C. japonicum* according to the DBH of their main stem (Fig. 4.9). All female and male trees reached the canopy layer, and except for one individual, all immature trees were found in the subcanopy and shrub layers (Table 4.1). All immature trees were < 26 cm in DBH, but one immature tree with a DBH of only 21 cm reached the canopy layer (Kubo and Sakio, unpublished data), implying that stem size may relate to reproductive maturity. Observations of the 46 reproductive individuals from 2000 to 2007 indicated that all mature trees with large main stems or many-stemmed trunks, including very old specimens, flowered and fruited heavily every year (Kubo and Sakio, unpublished data).

Fig. 4.7 Female *Cercidiphyllum japonicum* with purple-red flowers in late March in Shimane Prefecture (photo by Takuya Kashima)

The age of reproductive maturity varies widely among tree species. Many pioneer species begin flowering before 10 years, whereas late successional species such as beech and oak begin around age 60 (Thomas 2000). *Fraxinus platypoda* reaches reproductive maturity around age 50, and *P. rhoifolia* at age 20 (Sakio, personal observation). Although we cannot precisely determine the age of reproductive maturity for *C. japonicum*, four immature individuals in the subcanopy layer ranged from 16.9 to 22.0 cm in DBH and from 86 to 88 years in age (Sakio et al. 2002). By estimation, it may take up to 100 years for *C. japonicum* to reach a DBH of 30 cm.

4.4.2 Seed Production

Leaf-out occurs earlier in *C. japonicum* than in *F. platypoda* and *P. rhoifolia*, beginning in early May. Leaves appear soon after the very short blooming period, which generally lasts 10 days. Following flowering, banana-shaped follicles (fruits) are produced, each with approximately 20 samaras (seeds). These seeds are small, approximately 6 mm in length, including the wing, and 2 mm in width (Fig. 4.10). The dry weight of individual seeds collected from Ooyamazawa was 0.58 ± 0.14 mg ($n = 20$; Sakio et al. 2002).

Between late October and early November, *C. japonicum* leaves turn yellow (Fig. 4.11). This is followed by seasonal defoliation and seed dispersal (Fig. 4.12). Seed dispersal may begin as early as July, but it has been suggested that most seeds are immature at that time (Mizui 1993). Seeds are wind-dispersed, with larger dispersal events observed after seasonal defoliation. In the study area, the number

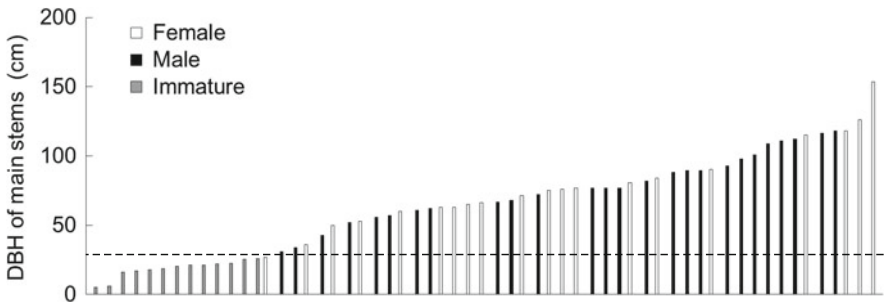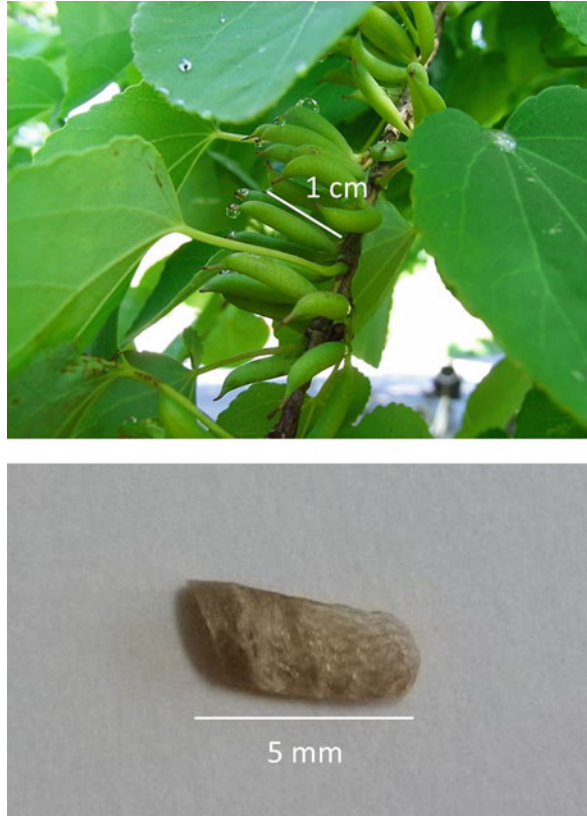**Fig. 4.8** Female and male flowers of *Cercidiphyllum japonicum* (photo by Yasuo Iizuka)

Fig. 4.9 Female, male, and immature *Cercidiphyllum japonicum* main stem DBH sizes at Ooyamazawa. The dotted line indicates a 26-cm DBH. Individuals with a main stem DBH of ≥4 cm are shown

Fig. 4.10 Fruit and seed of
Cercidiphyllum japonicum

of seeds was greatest from late October to mid-November and the dry weight of fallen leaves was greatest in October. Although seed production varied among years, *C. japonicum* produced seeds annually without an observed poor crop year (Fig. 4.13).

It is probable that the age of reproductive maturity of *C. japonicum* is later than those of other tree species; however, *C. japonicum* produces seeds annually after reaching maturity. Reproductive maturation at roughly 100 years old may be optimal in the context of the long lifespan of *C. japonicum*, as mature individuals can produce high annual volumes of seed over a long period.

4.5 Seedling Regeneration

4.5.1 Seedling Emergence

Although this species produces a large number of seeds annually, saplings are seldom observed in the understory of closed forests. Therefore, we wondered

Fig. 4.11 *Cercidiphyllum japonicum* leaves turning yellow in October at Ooyamazawa. (**a**) and (**b**) *C. japonicum*; (**c**) *C. magnificum*

when and where seedlings emerge, and investigated microhabitat conditions for *C. japonicum* seedlings. Numerous seedlings were recorded on the forest floor in
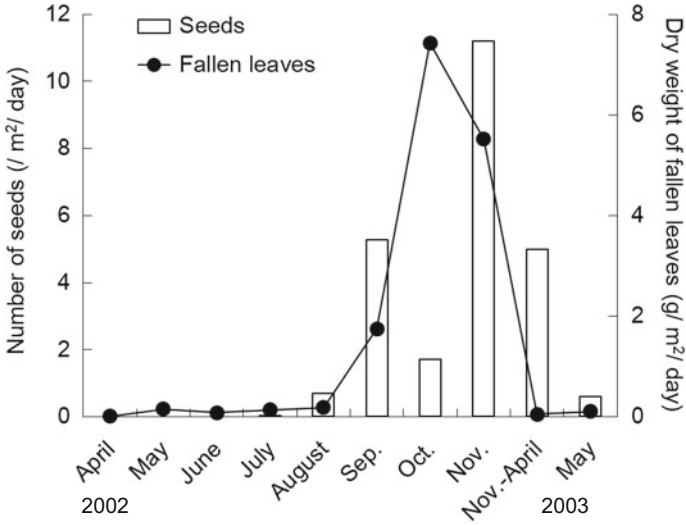
Fig. 4.12 Seasonal change in the amount of fallen leaves and dispersed seeds of *Cercidiphyllum japonicum*
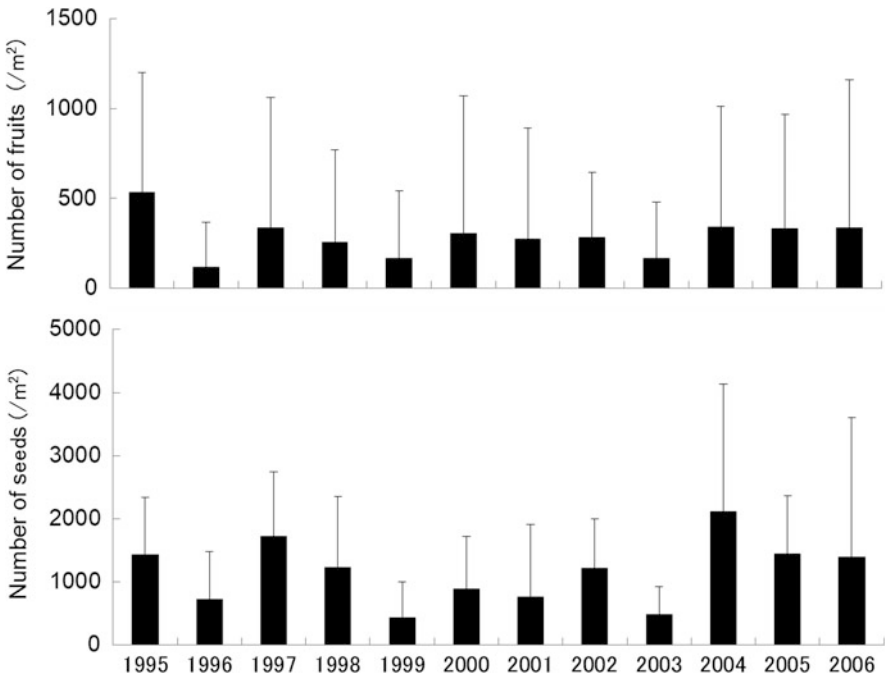

Fig. 4.13 Annual change in the number of dispersed seeds and fruits of *Cercidiphyllum japonicum*. Vertical bars indicate the standard deviation

Fig. 4.14 Seedling germination sites of *Cercidiphyllum japonicum*. (**a**) bare soil; (**b**) bare soil with small gravel; (**c**) a fallen log covered with moss; (**d**) a fallen log; (**e**) rock; and (**f**) first-year seedling size. Arrows and circles highlight *C. japonicum* seedlings and saplings

late May, after canopy trees had leafed out. Seedlings emerged on bare soil, rocky ground, and fallen logs (Fig. 4.14), but not on litter or gravel (Kubo et al. 2000). Such germination sites, where litter cannot accumulate and bare soil is exposed, occurred on steep slopes at small scales (Kubo et al. 2000), and saplings were frequently observed on rocks (Fig. 4.14e).

These observations are consistent with the results of a nursery experiment (Kubo et al. 2004). We investigated *C. japonicum* emergence and seedling survival in a nursery for 21 months, in which treatments of bare soil, soil with litter, and gravel under 3.0, 10.9, 22.7, 60.1, and 100.0% relative photosynthetic photon flux density (RPPFD) light conditions were tested. Seedling emergence was greatest in the bare-soil treatment (Fig. 4.15).

Some seeds at Ooyamazawa landed in areas appropriate for germination, i.e., bare soil on steep slopes. However, those which fell in areas with high litter or gravel accumulation were unlikely to survive after germination given the small size of the seedlings (approximately 1.5 cm high; Fig. 4.14f). Generally, seedlings from small seeds cannot penetrate a thick litter layer (Seiwa and Kikuzawa 1996). Furthermore, severe evaporation is more pronounced in gravel than in soil (Kayane 1980). In the nursery, seedlings preferentially emerged from gravel under the two lowest light conditions (3.0 and 10.9% RPPFD; Fig. 4.15), potentially because they were able to maintain moisture levels under those light conditions.

It is possible that *C. japonicum* has some form of seed dormancy (Kubo et al. 2008). We conducted germination tests using topsoil across three microhabitat conditions at Ooyamazawa, and although germination was observed, successful recruitment was very low (Table 4.2). Furthermore, under nursery conditions, four seedlings emerged in the second year after seeding (three seedlings and one seedling under 10.9 and 22.7% RPPFD, respectively, in bare soil; Fig. 4.15).

4.5.2 Seedling Survival

A good place for seedling emergence may not be a good place for seedling survival (Farmer 1997); forest conditions may be too severe for *C. japonicum* seedlings to survive. Although seedlings emerged under low light conditions (less than 10% relative illuminance), almost all were dead by summer (Fig. 4.16). The first-year survival rate of *C. japonicum* seedlings appeared to be greater under higher light conditions, although many individuals died by autumn. Seedling height and leaf size were reduced under lower light conditions (Kubo et al. 2000), and it is probable that smaller seedlings are more likely to die, be washed away, or to be covered by litter.

Cercidiphyllum japonicum seedlings emerged in bare soil under all light conditions in the nursery experiment, but seedling survival was greatest under moderate (10.9% RPPFD) and high light conditions (treatments of 22.7 and 60.1% RPPFD; Fig. 4.15). Extreme light conditions (3.0 and 100.0% RPPFD) were not optimal to survival. First-year seedlings grew poorly under high light (60.1% RPPFD), although most survived. After the second year, the seedlings appeared able to tolerate high light and grew tallest under this treatment (60.1% RPPFD; Fig. 4.17).

Slope may play a role in the observed differences in survival between nursery and forest conditions. The seedbeds in the nursery were flat, promoting seedling survival under moderate light conditions. Although *C. japonicum* seedlings likely have some shade tolerance, larger seedlings growing under bright light conditions would have a
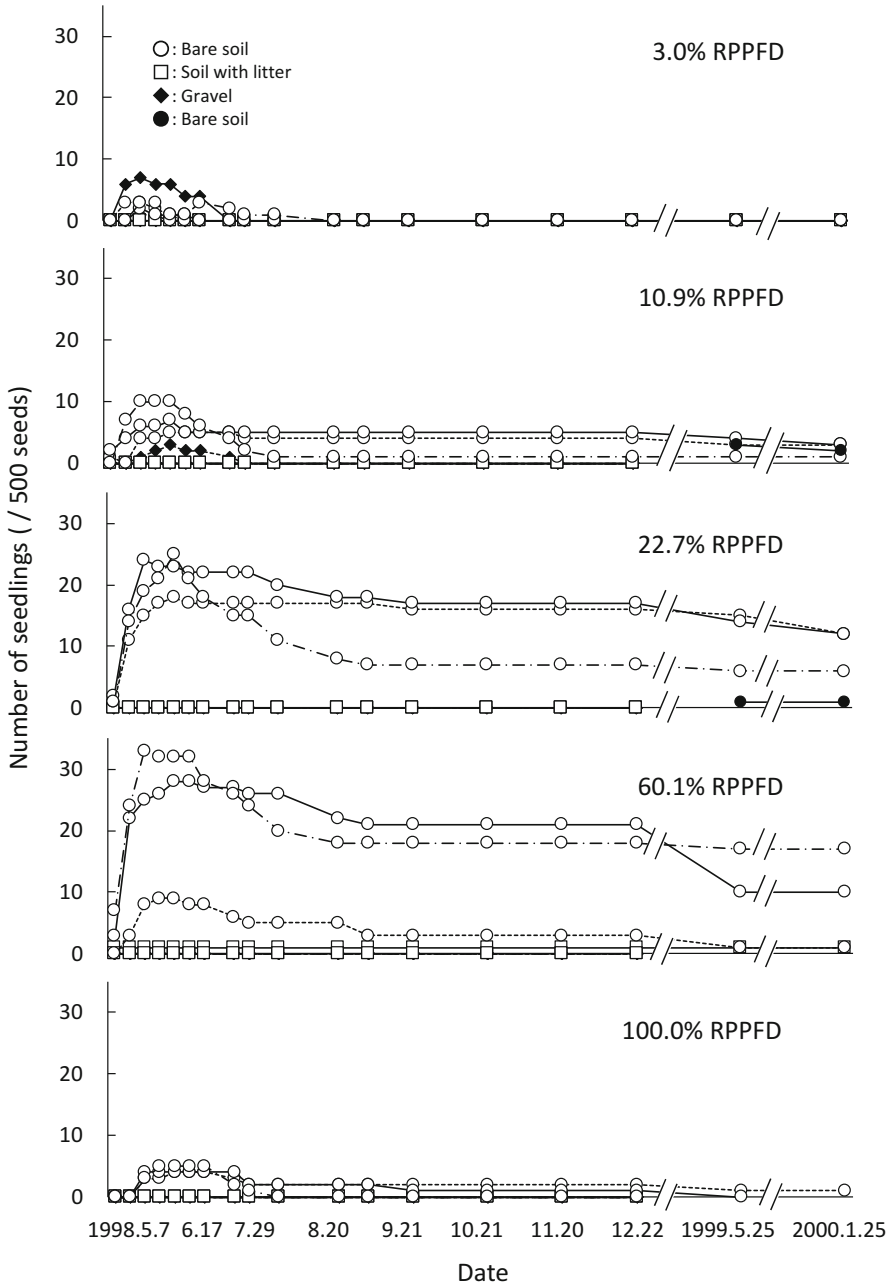
Fig. 4.15 Seedling germination and survival under experimental soil and light treatments (Kubo et al. 2004, revised). Open circles show seedlings grown on bare soil in 1998, open squares show seedlings grown on soil with litter in 1998, black rhomboids show seedlings grown on gravel in 1998, and black circles show new seedlings grown on bare soil in 1999

Table 4.2 Composition of seedlings emerging from topsoil and/or litter layers in Ooyamazawa (Kubo et al. 2008, revised)

	Topsoil			Litter layer		
	Upstream terrace of debris flow	Downstream terrace of debris flow	Downstream lower side slope	Upstream terrace of debris flow	Downstream terrace of debris flow	Downstream lower side slope
Woody plant						
Hydrangea macrophylla var. acuminata	30.2 ± 35.2 (151) *	0.2 ± 0.4 (1) *	5.4 ± 3.6 (27) *	3.6 ± 3.4 (18) *	0.0 ± 0.0 *	1.0 ± 0.8 (5) *
Buddleja japonica	0.8 ± 1.1^b (4)	8.2 ± 5.9^a (41)	0.0 ± 0.0^b	0.2 ± 0.3 (1)	0.6 ± 0.7 (3)	0.0 ± 0.0
Euptelea polyandra	0.0 ± 0.0^b *	4.8 ± 1.8^a (24) *	3.0 ± 1.9^a (15)	0.4 ± 0.4 (2) *	2.0 ± 1.7 (10) *	1.8 ± 1.3 (9) *
Betula grossa	5.8 ± 3.6^a (29) *	0.6 ± 0.9^b (3)	1.2 ± 1.1^b (6) *	4.2 ± 1.4^a (21) *	1.4 ± 0.8^b (7) *	0.8 ± 0.5^b (4) *
Actinidia arguta	2.2 ± 2.3 (11) *	0.4 ± 0.9 (2)	0.4 ± 0.5 (2) *	2.6 ± 1.6 (13) *	2.2 ± 1.9 (11)	0.0 ± 0.0 *
Cercidiphyllum japonicum	0.6 ± 0.9 (3) *	1.0 ± 1.2 (5) *	0.8 ± 0.4 (4) *	4.6 ± 4.5 (23) *	5.4 ± 3.0 (27) *	1.0 ± 0.7 (5) *
Rubus phoenicolasius	0.0 ± 0.0^b	2.2 ± 1.8^a (11)	0.2 ± 0.4^b (1)	0.0 ± 0.0	0.6 ± 0.7 (3)	0.2 ± 0.3 (1)
Pterocarya rhoifolia	0.2 ± 0.4 (1) *	0.0 ± 0.0 *	0.0 ± 0.0 *	0.0 ± 0.0 *	0.4 ± 0.4 (2) *	0.0 ± 0.0 *
Schizophragma hydrangeoides	0.0 ± 0.0 *	0.2 ± 0.4 (1) *	0.0 ± 0.0 *	0.0 ± 0.0 *	0.2 ± 0.3 (1) *	0.0 ± 0.0 *
Pterostyrax hispidus	0.2 ± 0.4 (1) *	0.0 ± 0.0 *	0.0 ± 0.0 *	– *	–	– *
Weigela decora	0.2 ± 0.4 (1) *	0.0 ± 0.0 *	0.0 ± 0.0	– *	–	–
Fraxinus platypoda	– *	– *	– *	0.8 ± 0.7 (4) *	0.8 ± 0.8 (4) *	0.4 ± 0.4 (2) *
Ericaceae spp.	–	–	–	0.2 ± 0.3 (1)	0.0 ± 0.0	0.0 ± 0.0
Unidentified species	0.0 ± 0.0	0.2 ± 0.4 (1)	0.0 ± 0.0	–	–	–
Herbaceous plant						
Carex spp.	0.0 ± 0.0	12.4 ± 17.0 (62)	0.4 ± 0.5 (2)	0.4 ± 0.4 (2)	2.4 ± 2.8 (12)	0.0 ± 0.0
Deinanthe bifida	0.0 ± 0.0^b	0.0 ± 0.0^b *	3.8 ± 2.3^a (19) *	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.5 (3) *
Poaceae spp.	1.4 ± 1.7 (7)	1.0 ± 0.7 (5)	0.2 ± 0.4 (1)	0.0 ± 0.0	0.2 ± 0.3 (1)	0.4 ± 0.4 (2) *

Species	Layer 1		Layer 2		Layer 3		Layer 4		Layer 5		Layer 6	
Macleaya cordata	1.4 ± 1.1 (7)		0.4 ± 0.5 (2)		0.6 ± 0.5 (3)		–		–		–	
Compositae spp.	0.4 ± 0.5 (2)		0.6 ± 0.9 (3)		0.4 ± 0.9 (2)		–		–		–	
Mitella pauciflora	0.0 ± 0.0	*	0.0 ± 0.0	*	0.6 ± 0.9 (3)	*	–	*	–	*	–	*
Urtica laetevirens	0.2 ± 0.4 (1)	*	0.2 ± 0.4 (1)	*	0.2 ± 0.4 (1)	*	–	*	–	*	–	*
Laportea macrostachya	0.2 ± 0.4 (1)	*	0.2 ± 0.4 (1)	*	0.0 ± 0.0	*	0.0 ± 0.0	*	0.2 ± 0.3 (1)	*	0.0 ± 0.0	*
Chrysosplenium macrostemon	0.0 ± 0.0	*	0.0 ± 0.0	*	0.4 ± 0.9 (2)	*	–	*	–	*	–	*
Elatostema umbellatum var. majus	0.0 ± 0.0	*	0.0 ± 0.0	*	0.4 ± 0.5 (2)	*	–	*	–	*	–	*
Laportea bulbifera	0.0 ± 0.0	*	0.0 ± 0.0	*	0.4 ± 0.9 (2)	*	–	*	–	*	–	*
Stellaria diversiflora	0.2 ± 0.4 (1)	*	0.0 ± 0.0	*	0.0 ± 0.0	*	–	*	–	*	–	*
Viola spp.	–		–		–		0.6 ± 0.7 (3)		0.2 ± 0.3 (1)		0.0 ± 0.0	
Cardamine flexuosa	–		–		–		0.0 ± 0.0		0.4 ± 0.4 (2)		0.0 ± 0.0	
Chrysosplenium spp.	–		–		–		0.2 ± 0.3 (1)		0.0 ± 0.0		0.0 ± 0.0	
Scopolia japonica	–	*	–	*	–	*	0.0 ± 0.0	*	0.2 ± 0.3 (1)	*	0.0 ± 0.0	*
Scrophularia duplicato-serrata	–		–		–		0.0 ± 0.0		0.2 ± 0.3 (1)		0.0 ± 0.0	
Meehania urticifolia	–	*	–	*	–	*	0.0 ± 0.0	*	0.0 ± 0.0	*	0.2 ± 0.3 (1)	*
Unidentified species	–		–		–		0.2 ± 0.3 (1)		0.0 ± 0.0		0.0 ± 0.0	
Total number of seedlings	44.0 ± 43.9 (220)		32.6 ± 20.3 (163)		18.4 ± 5.1 (92)		18.0 ± 9.8 (90)		17.4 ± 6.4 (87)		6.4 ± 2.9 (32)	
Total number of species	6.4 ± 2.1 (14)		7.4 ± 1.3 (15)		7.8 ± 1.1 (16)		7.4 ± 1.9 (12)		8.2 ± 2.5 (16)		4.8 ± 2.0 (9)	

Species composition was determined from five soil samples, each $20 \times 20 \times 5$ cm in depth, and five litter layer samples taken above the topsoil, and counting the number of seedlings emerging in each layer. Values indicate the mean number of seedlings ± standard deviation per sample from each layer. Numbers in parentheses show the total number of seedlings recorded for each species. Letters indicate significant differences between the layers (Kruskal–Wallis, Sheffe test, $P < 0.05$). *indicates that the species occurred in the above-ground vegetation in each microtopography layer

Fig. 4.16 Seasonal change in *Cercidiphyllum japonicum* seedling survival rate under different relative light intensities at Ooyamazawa (Kubo et al. 2000, revised)
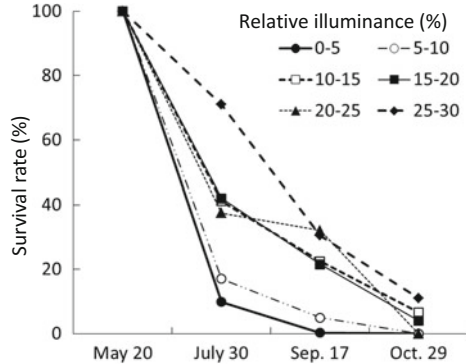
survival advantage in frequently disturbed riparian forests with steep slopes. Therefore, successful saplings are mostly likely to occur under bright light forest conditions (Kubo et al. 2000).
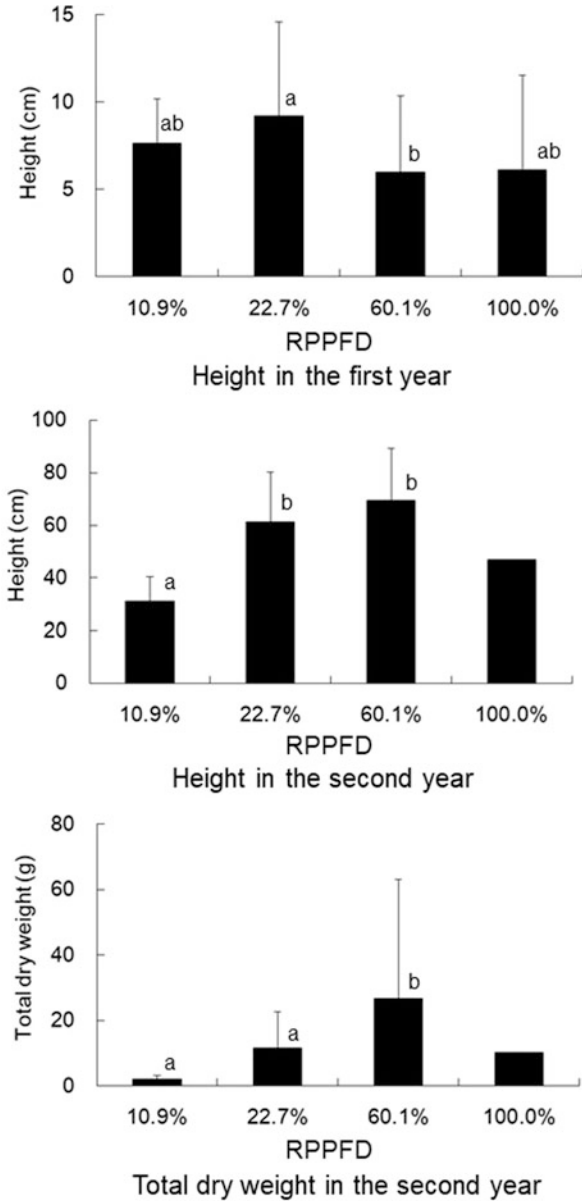
4.6 Sprouts

4.6.1 Structure of Multi-Stemmed Trunks

C. japonicum generally produces numerous sprouts (suckers), and it had the greatest mean number of stems (9.1 ± 12.2 per individual, $n = 59$) of all tree species in the Ooyamazawa study area (Table 4.1). Small sprout stems (shoot stems) occurred circularly around large (main) stems, although the distribution pattern of stems varied (Figs. 4.18 and 4.19). When considering stems arising from shoots, most *C. japonicum* stems are small in diameter ($n = 55$; Fig. 4.20), and individuals with larger main stems generally have a higher number of sprouts ($R = 0.37$, $n = 59$; Fig. 4.21; Kubo et al. 2001b). The mean number of sprouts per individual female, male, and immature tree was 8.9 ± 9.5, 12.5 ± 15.5, and 2.9 ± 4.4, respectively. Reproductive trees, both male and female, had a greater number of sprouts than did immature trees, although this difference was only significant between male and immature trees (Holm's method, $P < 0.05$). The sprout stem number was not significantly different between female and male trees (Holm's method, $P = 0.31$).

To clarify the dynamics of sprouts, we investigated age structure based on a growth-ring analysis of a *C. japonicum* stool (Kubo et al. 2005), which was harvested from between the slope and stream at the bottom of the study area valley. We cut all 29 associated stems at 50 cm high in autumn 2001. Across the study area, individual trees had large root systems from which many sprouts could originate. Sprouts frequently surrounded the main stems at the center of the stool (Fig. 4.22), and many individuals had coalesced stems (11 of 29 sprouts). The ages of coalesced stems tended to be similar (Fig. 4.22). Sprouts approximately 30 years old were usually clustered around main stems at the upstream slope site, whereas sprouts in

Fig. 4.17 Seedling height as influenced by light density (Kubo et al. 2004, revised). The upper and middle figures show the mean seedling height in their first year, November 1998, and their second year, January 2000. The lower figure shows the total dry weight of seedlings in the second year. Vertical bars indicate the standard deviation. Measurements were based only on seedlings that emerged in 1998, new seedlings germinating in 1999 were not included. Letters indicate significant differences between the light densities in each figure (*t*-test, $P < 0.05$). The level of significance was adjusted using the Holm's method. No seedlings survived the 3.0% RPPFD treatment over both years, and only one seedling remained in the 100.0% RPPFD treatment in the second year

Height in the first year

Height in the second year

Total dry weight in the second year

the downstream area tended to be older, around 80 years. Eighty-year-old sprouts from the slope site showed increased growth approximately 30 years ago, as determined by growth-ring analysis (Fig. 4.23). This suggests that light conditions may have improved around that time, allowing many shoots to sprout or grow rapidly, and potentially increasing stem coalescence. Growth patterns varied by

Fig. 4.18 Various multi-stemmed trunks (stools) of *Cercidiphyllum japonicum* in Ooyamazawa

individual and with age (Fig. 4.23) and sprout stem diameter was positively corre-
lated with age ($R^2 = 0.66$, $n = 45$; Fig. 4.24).

Most stems cut in 2001 produced new sprouts from their stools the following
September (Fig. 4.25). The number of current-year sprouts was positively correlated
with the age and diameter of the parent stems (Kubo et al. 2005). Smaller, younger
stems also produced new sprouts, and new sprouts would survive on the periphery of
the stand under favorable light conditions.
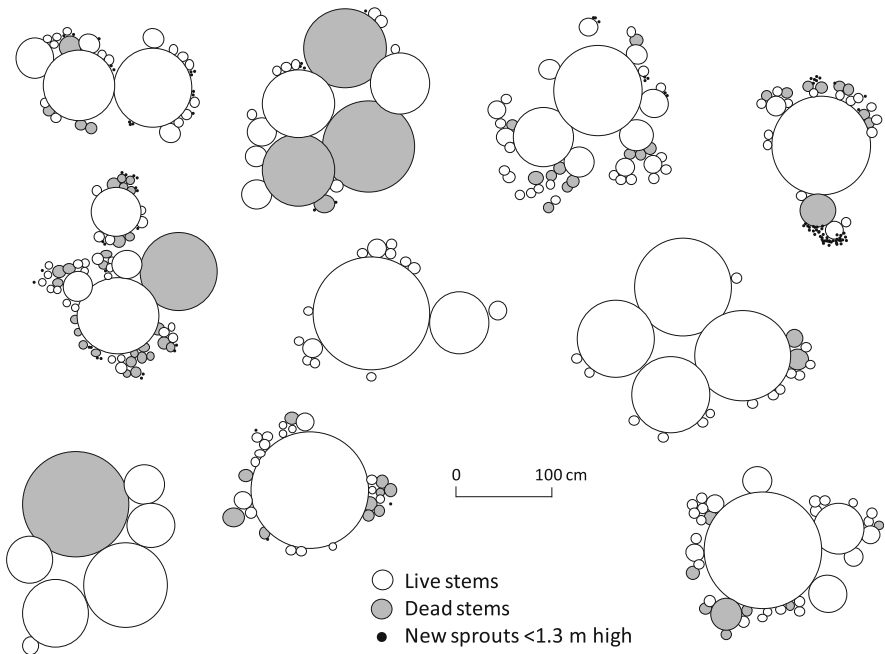
Fig. 4.19 Distribution patterns of stems for 10 typical, large *Cercidiphyllum japonicum* individuals in Ooyamazawa
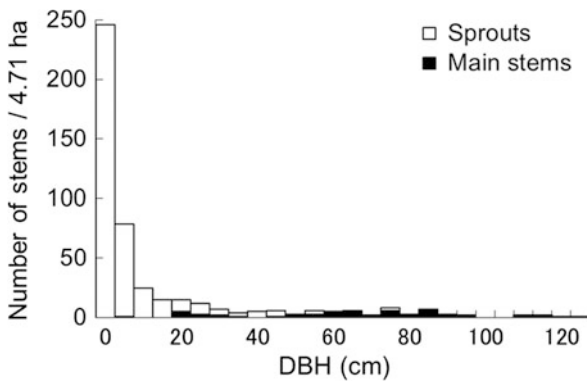
Fig. 4.20 DBH size class distribution, including main stems and sprouts, of *Cercidiphyllum japonicum* (Kubo et al. 2001b, revised)

4.6.2 Self-Maintenance by Sprouting

We show a proposed scheme for self-maintenance of *C. japonicum* by sprouting in Fig. 4.26. Following germination and growth, sprouts are produced as a result of
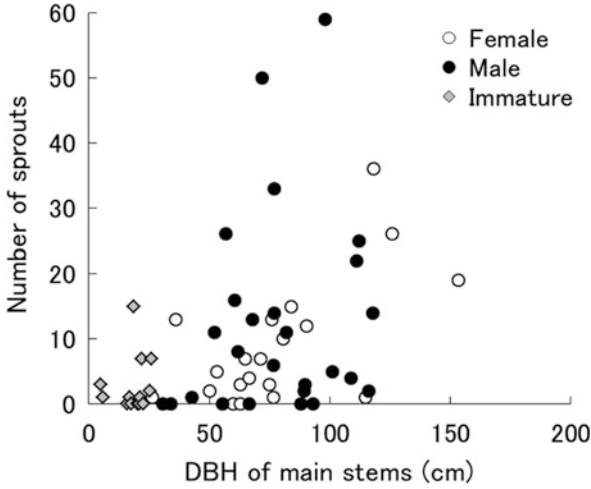
Fig. 4.21 Relationship between the DBH of main stems and number of sprouts of *Cercidiphyllum japonicum* (Kubo et al. 2001b, revised)
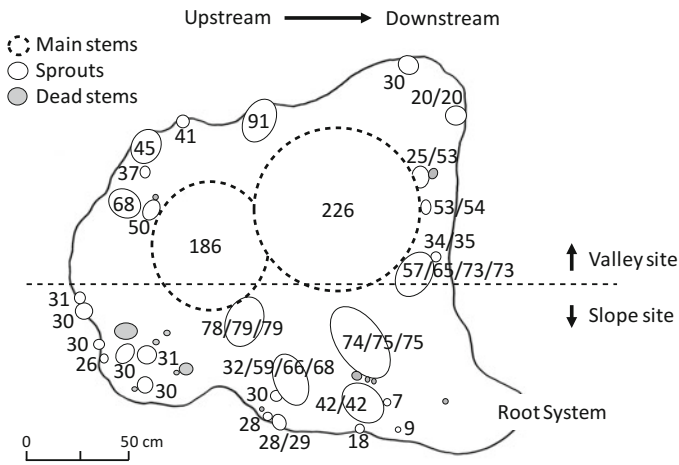
Fig. 4.22 Distribution of main stems and sprouts, denoted by age, of *Cercidiphyllum japonicum* (Kubo et al. 2005, revised). The upper site was in the valley, and the lower site was on the slope, as indicated

endogenous factors, such as aging, or in response to external factors, such as gap formation and physical damage. Following stem death, *C. japonicum* is able to fill in ensuing gaps by sprouting. Consequently, colonies containing sprouts of various ages are produced, which are circularly distributed around the stool. By this process, broad, extensive canopies and multi-stemmed individuals can be produced from a single main stem.
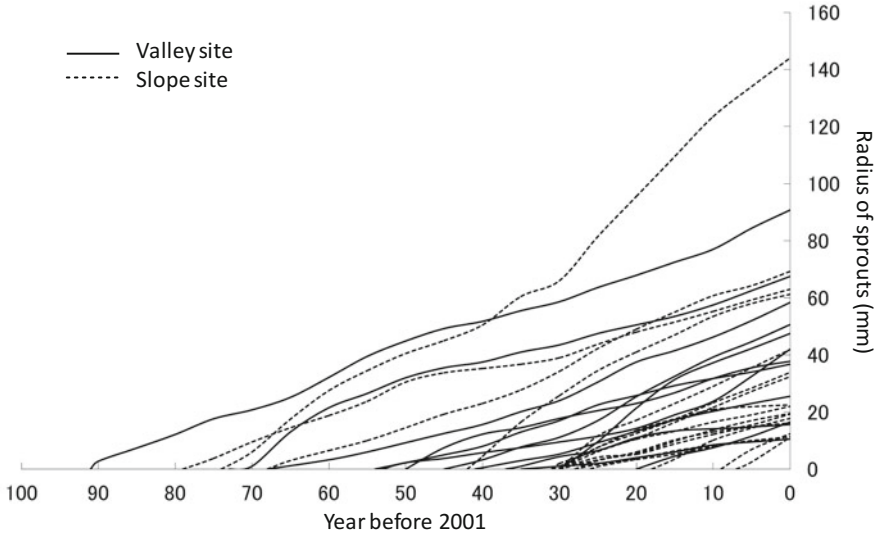
Fig. 4.23 Radial growth in *Cercidiphyllum japonicum* sprouts (Kubo et al. 2005, revised). Valley and slope sites are as indicated in Fig. 4.22
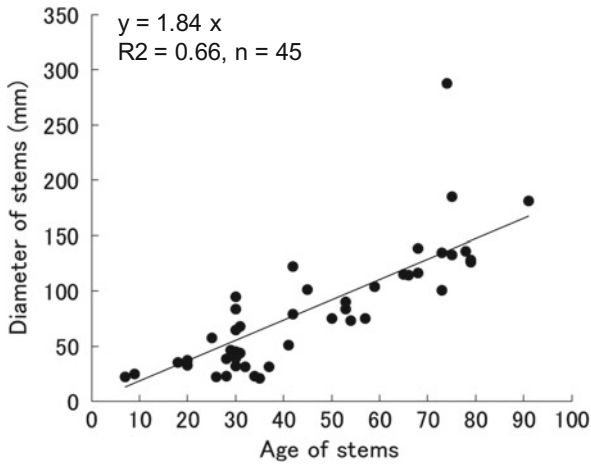

Fig. 4.24 Relationship between stem age and diameter (Kubo et al. 2005, revised). Age and diameter were measured 50 cm from the ground

4.6.3 Sprouting Traits of C. japonicum and C. magnificum

On the upper stream talus slope of Ooyamazawa (Fig. 4.6), almost all *C. japonicum* and *C. magnificum* produced numerous sprouts (Fig. 4.27); *C. magnificum* had a greater number of smaller stems and lower number of large stems relative to
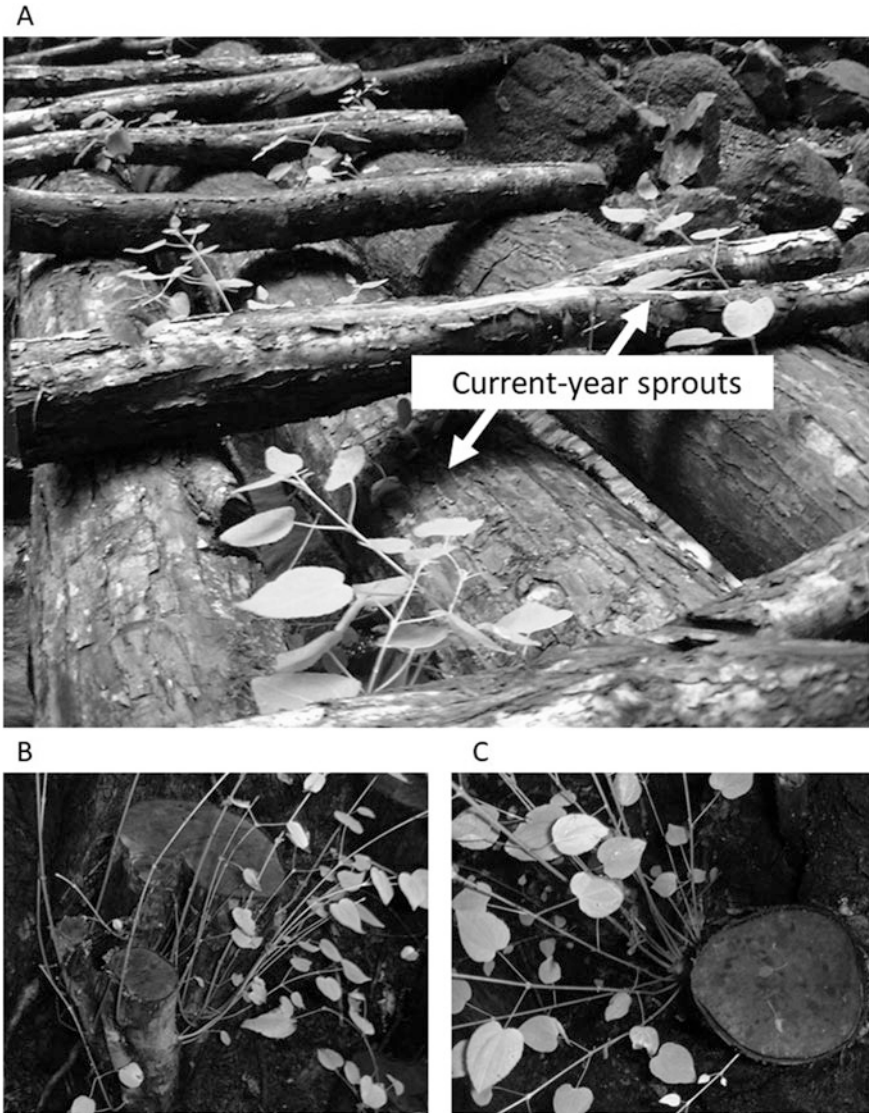
Fig. 4.25 Current-year sprouts from logged stems. (**a**) Bridge made from logged stems of *Cercidiphyllum japonicum*; (**b**) and (**c**) new sprouts arising from logged stumps

C. japonicum (Fig. 4.28). The average DBH of the main stems of *C. japonicum* was significantly larger than that of *C. magnificum* (*t*-test, $P < 0.01$). A number of *C. magnificum* individuals only reached the subcanopy layer, despite their being mature (Kubo et al. 2010). Dead stems in this species were numerous and often
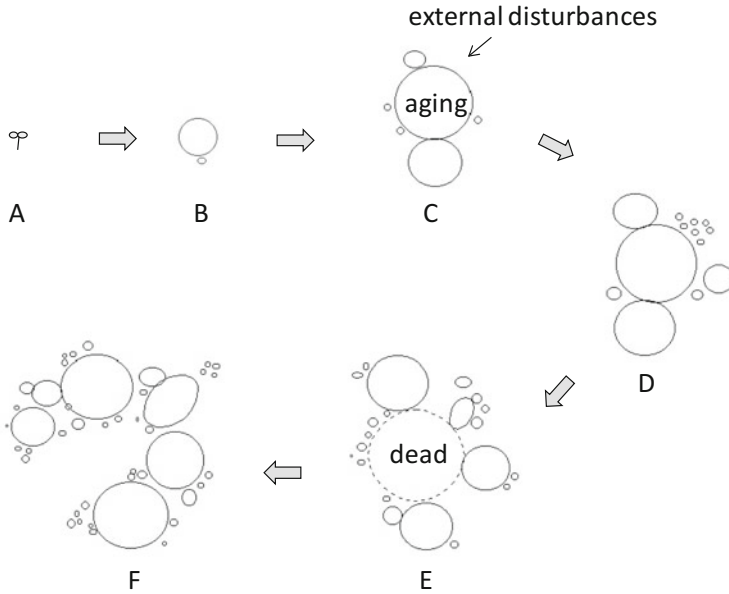
Fig. 4.26 Proposed scheme for the self-maintenance of *Cercidiphyllum japonicum* by sprouting (Kubo et al. 2005, revised). *Cercidiphyllum japonicum* germinates (**a**), grows to approximately 40 years of age (**b**), then produces sprouts as a function of aging at approximately 130 years (**c**), and in response to long-term external disturbances at approximately 230 years (**d**). Following the death of the parent stem, ensuing gaps fill with new sprouts at approximately 300 years (**e**). Consequently, *C. japonicum* creates colonies composed of sprouts of various ages (**f**). Age estimates were obtained from the individual shown in Fig. 4.22
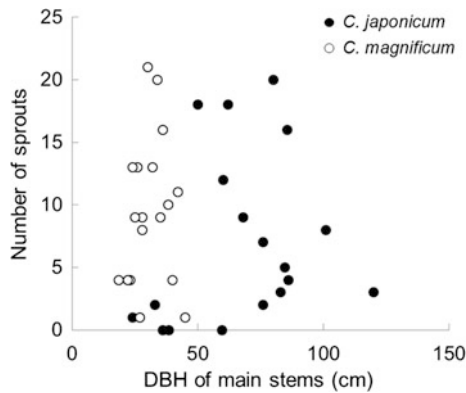

Fig. 4.27 Relationship between the DBH of main stems and number of sprouts of *Cercidiphyllum japonicum* and *Cercidiphyllum magnificum*, co-occurring on an upper stream talus slope at Ooyamazawa
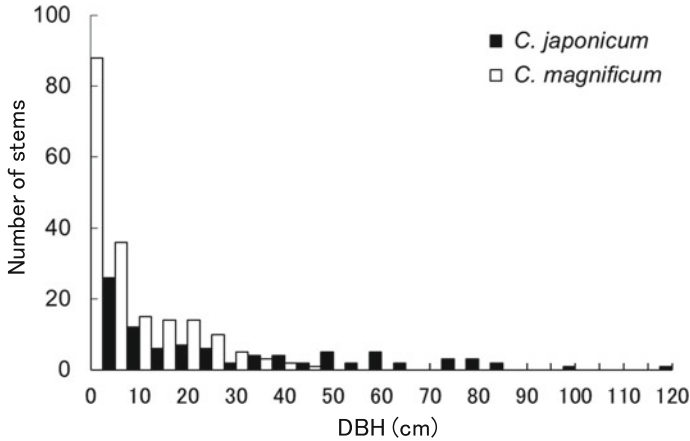
Fig. 4.28 DBH size class distribution of stems including main stems and sprouts of *Cercidiphyllum japonicum* and *Cercidiphyllum magnificum*, co-occurring on an upper stream talus slope at Ooyamazawa (Kubo et al. 2010, revised)

>30 cm DBH; the maximum recorded diameter of a live stem was 45 cm (Fig. 4.27). This suggests that stems are pressured to reach optimal size to ensure survival.

Cercidiphyllum are distributed in the montane and subalpine zones in Japan, and differences in stool structure between *C. japonicum* and *C. magnificum* reflect differences in the climatic conditions these species experience. Severe conditions such as wind and snowfall prevail in the subalpine zone in Japan (Shidei 1956; Yoshino 1973). One response to high disturbance severity and frequency is to reduce above-ground biomass and adopt a multi-stemmed, re-sprouting architecture (Bellingham and Sparrow 2000). Subalpine zone conditions may therefore require self-maintenance by *C. magnificum* by producing numerous sprouts with high mortality rates. In contrast, larger, taller individuals of *C. japonicum* indicate exposure to competition with co-occurring species for light in the canopy layer.

4.7 Conclusions

Cercidiphyllum japonicum reaches reproductive maturity at approximately 30 cm DBH (Fig. 4.9), which is estimated to occur after 100 years of growth. Larger individuals with many large sprouts flower heavily in early spring and then disperse a large amount of winged seeds following annual seasonal defoliation in autumn (Figs. 4.12 and 4.13). Suitable germination sites for *C. japonicum* seedlings include bare soil and fallen trees; sites with high litter accumulation or gravel are unsuitable for germination (Figs. 4.14 and 4.15) due to the small size of seeds and seedlings (Figs. 4.10 and 4.14). Germination does not imply survival for this species, given the high observed first-year mortality, which was likely a result of desiccation or stream

flow and precipitation events (Fig. 4.16). Larger seedlings growing under bright light conditions may have a survival advantage (Fig. 4.17).

Despite the expansive canopies and rootstocks of parent trees, saplings of *C. japonicum* are uncommon (Fig. 4.4). This species occurs at low density in its riparian habitat (Fig. 4.5), but produces many small stems per individual (Figs. 4.20 and 4.21). Sprouts are continually produced as a result of endogenous and external factors, and *C. japonicum* can self-maintain for several hundreds of years by sprouting (Fig. 4.26), potentially compensating for low sapling recruitment with high vegetative reproduction.

The oldest specimen of *F. platypoda*, a coexisting canopy species, is 254 years (Sakio 1997), and the lifespan of *P. rhoifolia* is approximately 120 years (Kisanuki et al. 1992). We found that *C. japonica* stands had live main stems dating to 226 years (Fig. 4.22). Many stools in Ooyamazawa contain the remains of previous main stems, meaning that many individuals are likely several hundred years old. It is possible, therefore, that *C. japonica* maintains its populations by outliving its competitors.

References

Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. Oikos 89:409–416

Crane PR, Stockey RA (1985) Growth and reproductive biology of *Joffrea speirsii* gen. et sp. nov., a *Cercidiphyllum*-like plant from the Late Paleocene of Alberta, Canada. Can J Bot 63:340–364

Dosmann MS (1999) Katsura: a review of *Cercidiphyllum* in cultivation and in the wild. New Plantsman 6:52–62

Farmer RE (1997) Seed ecophysiology of temperate and boreal zone forest trees. St. Lucie Press, Delray Beach

Isagi Y, Kudo M, Osumi K, Sato T, Sakio H (2005) Polymorphic microsatellite DNA markers for a relictual angiosperm *Cercidiphyllum japonicum* and their utility for *Cercidiphyllum magnificum*. Mol Ecol Notes 5:596–598

Kawanishi M, Sakio H, Ohno K (2004) Forest floor vegetation of *Fraxinus platypoda - Pterocarya rhoifolia* forest along Ooyamazawa valley in Chichibu, Kanto district, Japan, with a special reference to ground disturbance. Veg Sci 21:15–26. (in Japanese with English abstract)

Kayane I (1980) Physical geography course volume 5, hydrology. Daimei-do, Tokyo (in Japanese)

Kisanuki H, Kaji M, Suzuki K (1992) Structure and regeneration process of ash (*Fraxinus spaethiana* Ling.) stands in Chichibu Mountains. Bull Tokyo Univ For 88:15–32. (in Japanese with English summary)

Kubo M, Shimano K, Sakio H, Ohno K (2000) Germination sites and establishment conditions of *Cercidiphyllum japonicum* seedlings in the riparian forest. J Jpn For Soc 82:349–354. (in Japanese with English summary)

Kubo M, Shimano K, Ohno K, Sakio H (2001a) Relationship between habitats of dominant trees and vegetation units in Chichibu Ohyamasawa riparian forest. Veg Sci 18:75–85. (in Japanese with English summary)

Kubo M, Shimano K, Sakio H, Ohno K (2001b) Sprout trait of *Cercidiphyllum japonicum* based on the relationship between topographies and sprout structure. J Jpn For Soc 83:271–278. (in Japanese with English summary)

Kubo M, Sakio H, Shimano K, Ohno K (2004) Factors influencing seedling emergence and survival in *Cercidiphyllum japonicum*. Folia Geobot 39:225–234

Kubo M, Sakio H, Shimano K, Ohno K (2005) Age structure and dynamics of *Cercidiphyllum japonicum* sprouts based on growth ring analysis. For Ecol Manag 213:253–260

Kubo M, Kawanishi M, Shimano K, Sakio H, Ohno K (2008) The species composition of soil seed banks in the Ooyamazawa riparian forest, in the Chichibu Mountains, Central Japan. Jpn For Soc 90:121–124. (in Japanese with English summary)

Kubo M, Shimano K, Sakio H, Isagi Y, Ohno K (2010) Difference between sprouting traits of *Cercidiphyllum japonicum* and *C. magnificum*. J For Res 15:337–340

Li J, Dosmann MS, Tredici PD (2002) Systematic relationship of weeping Katsura based on nuclear ribosomal DNA sequences. Hort Sci 37(3):595–598

Manchester SR, Chen ZD, Lu AM, Uemura K (2009) Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere. J Syst Evol 47:1–42

Mizui N (1993) Ecological studies on reproduction in deciduous broad-leaved tree species. Bull Hokkaido For Res Inst 30:1–67. (in Japanese)

Ohno K (2008) Vegetation-geographic evaluation of the syntaxonomic system of valley-bottom forests occurring in the cool-temperate zone of the Japanese Archipelago. In: Sakio H, Tamura T (eds) Ecology of riparian forests in Japan. Springer, Tokyo, pp 49–72

Qi X-S, Chen C, Comes HP, Sakaguchi S, Liu Y-H, Tanaka N, Sakio H, Qiu Y-X (2012) Molecular data and ecological niche modelling reveal a highly dynamic evolutionary history of the East Asian Tertiary relict *Cercidiphyllum* (Cercidiphyllaceae). New Phytol 196:617–630

Sakio H (1997) Effects of natural disturbance on the regeneration of riparian forests in a Chichibu mountains, central Japan. Plant Ecol 132:181–195

Sakio H, Kubo M, Shimano K, Ohno K (2002) Coexistence of three canopy tree species in a riparian forest in the Chichibu mountains, Central Japan. Folia Geobot 37:45–61

Seiwa K, Kikuzawa K (1996) Importance of seed size for the establishment of seedlings of five deciduous broad-leaved tree species. Vegetatio 123:51–64

Shidei T (1956) A concept about the reason why coniferous forest zone is partially lacking in sub-alpine zone along the sea of Japan. J Jpn For Soc 38:356–358. (in Japanese)

Skawińska K (1986) Some new and rare pollen grains from Neogene deposits at Ostrzeszów (South-West Poland). Acta Palaeobotanica 25:107–118

Thomas P (2000) Trees: their natural history. Cambridge University Press, Cambridge (Kumazaki M, Asakawa S, Sudou S (2001) Trees: their natural history. Tsukiji-shokan, Tokyo (in Japanese))

Yoshino M (1973) Studies on wind-shaped trees: their classification, distribution and significance as a climatic indicator. Climatological Notes 12:1–52