Chapter 9

Temporal Changes in Browsing Damage by Sika Deer in a Natural Riparian Forest in Central Japan

Motoki Higa, Motohiro Kawanishi, Masako Kubo, and Hitoshi Sakio

Abstract Over the last few decades, population increases of sika deer (*Cervus nippon*) have become a major issue in various forest ecosystems across temperate regions; however, the influences of deer browsing on riparian forests are less known. In this chapter, we illustrate the herbivore–forest vegetation relationships over a long term from the past when deer was absent to the current when deer became overabundant in an old-growth riparian forests of Ooyamazawa, the Chichibu Mountains of central Japan. We revealed that (1) the browsing activity of deer has a negative influence on riparian forests, (2) the damage of these species is mainly induced by easiness to browsing by deer resulting from small tree size structure, and (3) the resistance to the deer browsing differs among tree species. Thus, small mature trees (i.e., shrub species) with low browsing resistance should be primarily protected for effective management of riparian forests.

Keywords *Cervus nippon* · Debarking · Forest management · Mortality risk · Species preferences · Tree size

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H. Sakio (ed.), *Long-Term Ecosystem Changes in Riparian Forests*, Ecological Research Monographs, https://doi.org/10.1007/978-981-15-3009-8_9

9.1 Introduction

Browsing by large herbivores can drastically modify the structure, environment, and tree-species composition of forests (Gill 1992a, b). Over the last few decades, sika deer (*Cervus nippon*) populations have increased due to the absence of predators and a gradual decline in hunting, and have become a major issue for forest ecosystems in several regions of Japan (Uno et al. 2007; Takatsuki 2009; Kaji et al. 2010). In places where deer density is too high, plant-species diversity has decreased due to a drastic decline in forest-floor vegetation (Suda et al. 2001; Suzuki et al. 2008) and the increased mortality of palatable plant species (Akashi and Nakashizuka 1999; Yokoyama et al. 2001) caused by heavy browsing and debarking activities of deer. Thus, the adverse effects of these activities on the regeneration of tree species in natural forests have become a major concern (Takatsuki and Gorai 1994; Akashi and Nakashizuka 1999; Suda et al. 2001; Yokoyama et al. 2001). Previous studies have shown that increasing deer populations can also have other impacts on forest ecosystems and resources. For example, they may reduce the quality of timber resources (Kaji et al. 2000; Oi and Suzuki 2001; Ueda et al. 2002; Akashi and Terazawa 2005; Suzuki et al. 2008), decrease the diversity of insect communities (Kanda et al. 2005; Ueda et al. 2009), alter the structure and function of soil microbial food webs (Niwa et al. 2011), and increase the risks of soil erosion and landslides in mountainous areas (Furusawa et al. 2003).

An understanding of herbivore–vegetation relationships is necessary for the assessment of potential risks and design of management plans. In Japan, deer consume forest-floor vegetation and tree leaves from spring to autumn and utilize tree bark and dead fallen leaves when facing food shortages, which usually occur in winter (Takahashi and Kaji 2001; Takatsuki 2009). Browsing damage from deer occurs intensively on certain plant species among a wide array of co-occurring species (Gill 1992a; Augustine and McNaughton 1998; Côté et al. 2004; Boulangera et al. 2009). Tree-species composition and food-resource availability in forests affect the dietary selections of deer (Gill 1992a; Moser et al. 2006; Jayasekara and Takatsuki 2000; Takahashi and Kaji 2001). Many researchers have proposed factors to explain differences in the plant-species preferences of deer, including the morphological and physiological traits of plants (Gill 1992a; Ando et al. 2003; Jiang et al. 2005; Moser et al. 2006; Sauvé and Côté 2006). For example, smaller trees are well known to be preferentially browsed by deer (Gill 1992a; Boulangera et al. 2009; Didion et al. 2009) because they have more leaves and branches at heights easily accessible to deer, as well as thin and soft bark. The trunk size of these trees is also suitable for antler fraying. Large-herbivore densities also affect the occurrence and intensity of browsing damage on plants (Gill 1992a). However, the temporal changes in dietary selection and browsing damage on plants associated with deer density changes have been poorly documented. In particular, information about the initial changes that occur when an area transitions from the absence to overabundance of deer is lacking.

Riparian forests are important and unique ecosystems that provide specialized habitats and resources for wildlife, support and maintain faunal and floral diversity, and prevent soil erosion in precipitous mountain terrain (Malanson 1993; Richards et al. 2002; Ward et al. 2002). The majority of riparian forests in Japan disappeared during the twentieth century due to increased industrial or agricultural land use and the construction of embankments for river management (Sakio 2008); several of the remaining forests are being subjected to heavy browsing pressure by deer. In an old-growth riparian forest dominated by *Ulmus davidiana* Planch. var. *japonica* (Rehder) Nakai in the district of Nikko in central Japan, heavy browsing and debarking by deer have resulted in the decline of forest-floor vegetation and dieback of mature trees (Nomiya et al. 2003). The deer population is expected to continue to increase and expand throughout the less-snowy regions of Japan. Hence, riparian forests are expected to be subject to increasingly serious damage due to deer browsing activity.

In this chapter, we illustrate long-term herbivore–forest vegetation relationships in an old-growth riparian forest of Ooyamazawa, in the Chichibu Mountains of central Japan, from the past, when deer were absent, to the present, when deer are overabundant. Using long-term tree-census data, we elucidated the temporal changes in the dietary selections of deer and species-specific differences in browsing damage. Finally, we discuss effective management plans for riparian forests.

9.2 Ooyamazawa Riparian Forest

In Ooyamazawa (35°57′30″N, 138°46′32″E, 1200–1620 m a.s.l.), an old-growth natural forest lies along a mountain stream of the Arakawa River in part of Chichibu-Tama-Kai National Park, Saitama Prefecture, central Japan (Fig. 9.1). The annual mean temperature, annual precipitation, and maximum snow depth in the nearest settlement (Nakatsugawa; 700 m a.s.l. and 4.6 km from the study site) are 10.7 °C, 1100 mm, and 30 cm, respectively (Sakio 1997). The estimated annual mean temperature at the study site (1450 m a.s.l.) is 6.5 °C, based on a temperature lapse rate of 0.6 °C per 100-m increase in elevation (Sakio 1997). The site lies in the upper part of a cool-temperate, deciduous broad-leaf forest zone (Sakio 1997). The dominant species of the forest canopy are *Flaxinus platypoda* Oliv., *Pterocarya rhoifolia* Siebold et Zucc., and *Cercidiphyllum japonicum* Siebold et Zucc. ex Hoffm. et Schult., which are more than 30 m in height (Table 9.1). The subcanopy is dominated by *Acer shirasawanum* Koidz. and *Acer pictum* Thunb. The understory is composed primarily of *Acer carpinifolium* Siebold et Zucc. and *Acer argutum* Maxim (Table 9.1). Before deer became abundant, the forest floor had dense vegetation cover with greater plant-species richness, including *Parasenecio tebakoensis* (Makino) H.Koyama, *Parasenecio delphiniifolius* (Siebold et Zucc.) H.Koyama, *Chrysosplenium macrostemon* Maxim. var. *macrostemon*, *Laportea bulbifera* (Siebold et Zucc.) Wedd., *Impatiens noli-tangere* L., *Dryopteris*

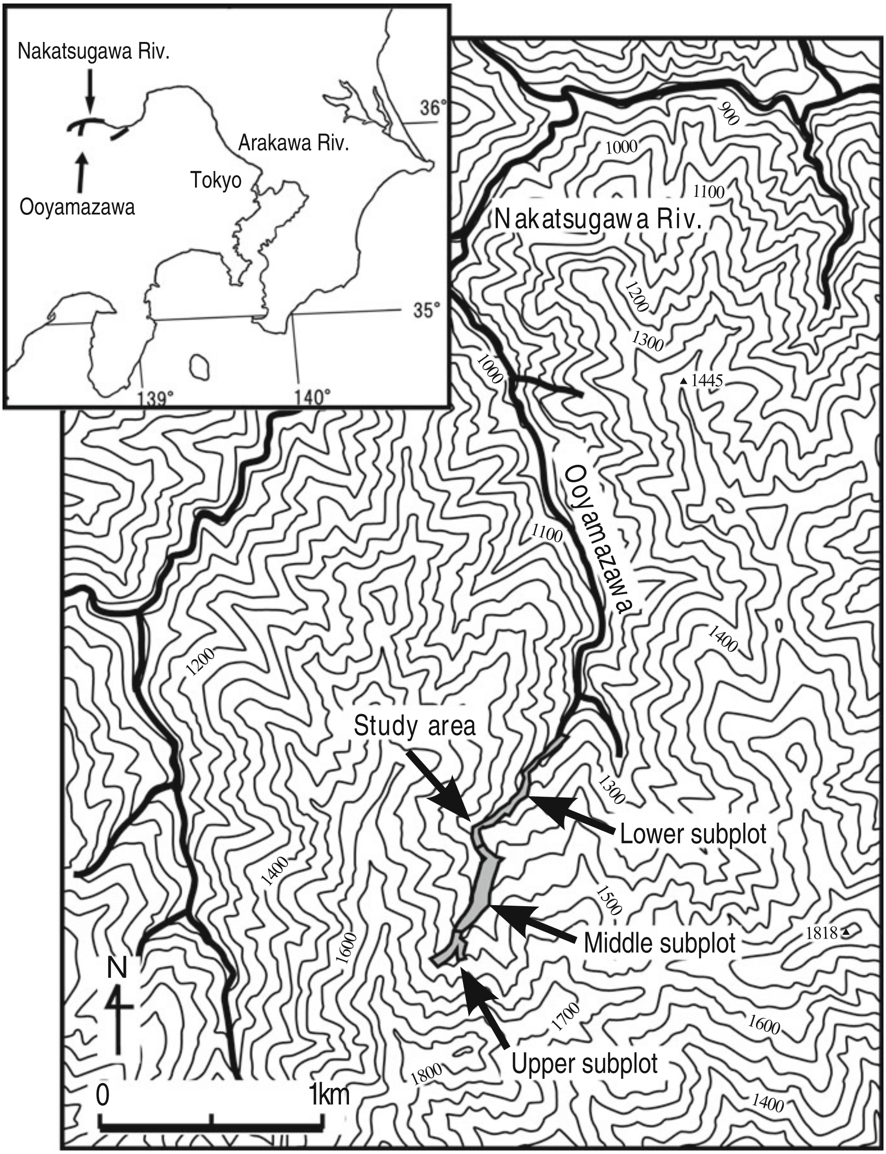

Fig. 9.1 Index and location maps of the study area

crassirhizoma Nakai, *Dryopteris polylepis* (Franch. et Sav.) C.Chr., and *Polystichum tripteron* (Kunze) C.Presl (Sakio et al. 2013).

In the Ooyamazawa riparian forest, a permanent study plot (4.71 ha; Fig. 9.1) consisting of three subplots (upper, middle, and lower) was established, and tree censuses were conducted at each subplot at 5-year intervals from 1991 to 2008. The upper and middle subplots (3.2 ha) were established in 1991, and the lower subplot

Table 9.1 Tree-species composition, life form, and size structure of the Ooyamazawa riparian forest (4.71 ha^2)

Species	LF	N. ind	N. tree	BA	RBA	Max. DBH
Fraxinus platypoda Oliv.	D, B, T	460	463	88.61	55.2	140.5
Cercidiphyllum japonicum Siebold et Zucc. ex Hoffm. et Schult.	D, B, T	59	59	25.02	15.6	153.4
Pterocarya rhoifolia Siebold et Zucc.	D, B, T	118	118	14.07	8.8	77.7
Acer shirasawanum Koidz.	D, B, T	428	428	7.33	4.6	62.8
Acer pictum Thunb.	D, B, T	271	272	6.16	3.8	92.0
Ulmus laciniata (Trautv.) Mayr ex Schwapp.	D, B, T	95	95	6.32	3.9	89.4
Acer carpinifolium Siebold et Zucc.	D, B, S	484	508	2.82	1.8	47.0
Tilia japonica (Miq.) Simonk.	D, B, T	9	9	1.92	1.2	93.9
Betula maximowicziana Regel	D, B, T	4	4	1.42	0.9	73.0
Abies homolepis Siebold et Zucc.	E, C, T	12	12	1.70	1.1	93.0
Carpinus cordata Blume	D, B, T	52	52	0.76	0.5	21.6
Kalopanax septemlobus (Thunb.) Koidz.	D, B, T	3	3	0.84	0.5	78.0
Fagus crenata Blume	D, B, T	6	6	0.52	0.3	62.6
Betula grossa Siebold et Zucc.	D, B, T	4	4	0.52	0.3	50.8
Padus buergeriana (Miq.) T.T.Yü et T.C.Ku	D, B, T	1	1	0.31	0.2	62.7
Acer argutum Maxim.	D, B, S	138	141	0.37	0.2	13.2
Acer palmatum Thunb.	D, B, S	6	6	0.11	0.1	23.9
Acer rufinerve Siebold et Zucc.	D, B, S	11	11	0.18	0.1	33.6
Pterostyrax hispida Siebold et Zucc.	D, B, S	89	89	0.38	0.2	16.5
Phellodendron amurense Rupr.	D, B, T	1	1	0.10	0.1	35.5
Actinidia arguta (Siebold et Zucc.) Planch. ex Miq.	D, B, L	13	13	0.10	0.1	16.2
Acer maximowiczianum Miq.	D, B, T	2	2	0.14	0.1	39.0
Fraxinus lanuginosa Koidz. f. *serrata* (nakai) Murata	D, B, T	2	2	0.03	<0.1	19.5
Aria alnifolia (Siebold et Zucc.) Decne.	D, B, T	4	4	0.07	<0.1	25.5
Schizophragma hydrangeoides Siebold et Zucc.	D, B, L	8	8	0.03	<0.1	10.1
Acer amoenum Carriére var. *amoenum*	D, B, S	3	3	0.03	<0.1	15.5
Carpinus japonica Blume	D, B, T	1	1	0.00	<0.1	7.0
Tsuga sieboldii Carriére	E, S, T	2	2	0.07	<0.1	24.5
Hydrangea petiolaris Siebold et Zucc.	D, B, L	1	1	0.01	<0.1	8.0
Acer nipponicum H.Hara	D, B, T	16	16	0.15	0.1	28.7
Trochodendron aralioides Siebold et Zucc. f. *longifolium* (Maxim.) Ohwi	E, B, T	2	2	0.02	<0.1	13.2
Acer japonicum Thunb.	D, B, T	3	3	0.00	<0.1	3.9
Acer tenuifolium (Koidz.) Koidz.	D, B, T	7	7	0.04	<0.1	15.0
Euptelea polyandra Siebold et Zucc.	D, B, S	10	10	0.08	<0.1	16.0
Euonymus sieboldianus Blume	D, B, T	7	7	0.05	<0.1	20.0

(continued)

Table 9.1 (continued)

Species	LF	N. ind	N. tree	BA	RBA	Max. DBH
Swida controversa (Hemsl. ex Prain) Soják	D, B, T	2	2	0.08	<0.1	23.9
Acer cissifolium (Siebold et Zucc.) K.Koch	D, B, T	1	2	0.03	<0.1	18.2
Acer tschonoskii Maxim.	D, B, T	1	1	0.00	<0.1	4.1
Fraxinus apertisquamifera H.Hara	D, B, T	9	9	0.05	<0.1	15.3
Vitis coignetiae Pulliat ex Planch.	D, B, L	4	4	0.02	<0.1	10.0
Clethra barbinervis Siebold et Zucc.	D, B, T	3	3	0.01	<0.1	6.4
Viburnum furcatum Blume ex Maxim.	D, B, S	7	7	0.01	<0.1	6.8
Stewartia pseudocamellia Maxim.	E, B, T	2	2	0.04	<0.1	17.6
Padus grayana (Maxim.) C.K.Schneid.	D, B, T	1	1	0.10	0.1	35.0
Acer distylum Siebold et Zucc.	D, B, S	1	1	0.02	<0.1	14.0
Celtis jessoensis Koidz.	D, B, S	1	1	0.00	<0.1	4.1

LF life form, *D* deciduous, *E* evergreen, *B* broad-leaf, *C* needle-leaf, *T* tall tree, *S* small tree or shrub, *L* liana. *N. ind* number of individuals, *N. tree* number of standing trees, *BA* basal area (m^2), *RBA* relative basal area (%)

(1.5 ha) was established in 1998. All living trees with diameters at breast height (DBHs) > 4 cm were numbered and identified to the species level. Tree DBHs, alive/dead status, and extent of browsing damage by deer were recorded. An initial survey was conducted at the upper subplot in 1991 and at the middle subplot in 1992; 1982 standing trees of 42 species were observed and measured, and the total basal area was 36.3 $m^2\ ha^{-1}$. A second survey was conducted in the upper, middle, and lower subplots from 1996 to 1998. The third and fourth surveys were conducted from 2001 to 2003 and 2006 to 2008, respectively. The second, third, and fourth surveys included 2396 standing trees of 46 species, 2335 standing trees of 45 species, and 2050 standing trees of 41 species, and the total basal areas were 34.2, 35.2, and 35.5 $m^2\ ha^{-1}$, respectively. The entire permanent plot was designated as an associate site of the Japan Long-Term Ecological Research Network in 2006, and the middle subplot has been a core site of the nationwide Japanese Monitoring Sites 1000 program since 2008.

9.3 Increase in Deer Density Around Ooyamazawa

Deer density has been monitored using the block-count method for more than 30 years as part of density monitoring for a protected species, Japanese serow (*Capricornis crispus*) (Saitama Museum of Natural History 1983; Gunma, Saitama, Tokyo, Yamanashi and Nagano Prefectural Boards of Education 1988, 2010). During the 1980s and 1990s, the deer density around the study site was 0–6.3 heads/km^2. This density began to increasing in the late 1990s, and had reached 20.9 heads/km^2 in the 2000s (Saitama Museum of Natural History 1983; Gunma, Saitama, Tokyo, Yamanashi and Nagano Prefectural Boards of Education 1988, 2010). The deer censuses were performed using the block-count method on only single days every few years. The visibility of the census site is well known to affect the accuracy of density estimation when using this method (Maruyama and Furubayashi 1983). In Ooyamazawa and its surroundings, the slope is very steep and the geomorphology is complex. Therefore, the actual densities may be greater than estimated. The deer are permanent, year-round residents of the forest.

9.4 Temporal Changes in Browsing Damage

Grazing and browsing of overabundant large herbivores drastically change the structure and species composition of forest vegetation (Ripple and Beschta 2008; Didion et al. 2009; Salk et al. 2011). By the 2010s, most herbaceous plants and the seedlings and saplings of all tree species had disappeared due to heavy deer foraging pressure (Sakio et al. 2013). On the forest floor, only unpalatable and poisonous plants, such as *Veratrum album* subsp. *oxysepalum* (Turcz.) Hultén, *Aconitum tonense* Nakai ex H.Hara, and *Scopolia japonica* Maxim., remain in low abundance (Sakio et al. 2013).

Many studies have shown that heavy browsing and debarking activities of deer result in failed regeneration of tree species and reduced plant-species diversity (Takatsuki and Gorai 1994; Akashi and Nakashizuka 1999; Suda et al. 2001; Yokoyama et al. 2001; Suzuki et al. 2008). Similar phenomena were observed in the Ooyamazawa riparian forest. In the first survey, no trace of browsing damage was found on any standing tree in the upper or middle subplot (Table 9.2). In the second survey, evidence of debarking was found on three trees of *U. laciniata* and one tree of *A. shirasawanum* (Table 9.3). Thereafter, evidence of deer browsing increased rapidly; it was observed on 170 trees of eight species in the third survey. Among the damaged species, *A. carpinifolium* and *A. argutum* showed considerably increased browsing damage, which affected approximately 20 and 25%, respectively, of the total number of trees of these species. The three dominant canopy species, *F. platypoda*, *C. japonicum*, and *P. rhoifolia*, exhibited no evidence of browsing damage. By the fourth survey, browsing damage had increased to 536 trees

Table 9.2 Temporal changes in browsing damage (ND: number of damaged trees) of sika deer on tree species in the Ooyamazawa riparian forest during 1991–2008

	First survey (1991–1992)		Second survey (1996–1998)		Third survey (2001–2003)		Fourth survey (2006–2008)	
Subplot	ND	TN	ND	TN	ND	TN	ND	TN
Upper	0	622	4 (0.7)	576	57 (11.5)	494	101 (25.3)	399
Middle	0	1361	0	1286	20 (1.7)	1183	267 (25.6)	1042
Lower	–	–	0	550	93 (13.8)	674	168 (27.5)	611

The percentage of damaged trees is shown in parentheses. *TN* total number of trees

Table 9.3 Temporal changes in browsing damage (number of damaged trees in 4.71 ha), mortality rate, and percentage of browsed trees among all dieback trees among the main 10 tree species in the Ooyamazawa riparian forest from the second through fourth surveys

	Second survey (1996–1998)							Third survey (2001–2003)									Fourth survey (2006–2008)								
	ND	S	B	SB	TN	*D*	*P*	ND	S	B	SB	TN	MR	PDD	*D*	*P*	ND	S	B	SB	TN	MR	PDD	*D*	*P*
Fraxinus platypoda	0	0	0	0	463	−1.00	<0.01	0	0	0	0	440	5.6	0	−1.00	<0.01	14	2	11	1	407	7.5	0	−0.75	<0.01
Cercidiphyllum japonicum	0	0	0	0	59	−1.00	<0.01	0	0	0	0	105	5.1	0	−1.00	<0.01	22	12	5	5	103	1.9	0	0.67	0.30
Pterocarya rhoifolia	0	0	0	0	118	−1.00	<0.01	0	0	0	0	108	9.3	0	−1.00	<0.01	12	8	2	2	92	14.8	6.3	0.52	<0.01
Acer shirasawanum	1	0	1	0	429	−0.98	<0.01	4	0	4	0	396	7.7	0	−0.90	<0.01	36	8	24	4	361	8.8	5.7	−0.32	<0.01
Acer pictum	0	0	0	0	272	−1.00	<0.01	0	0	0	0	257	6.3	0	−1.00	<0.01	4	3	1	0	242	5.8	0	−0.78	<0.01
Ulmus laciniata	3	0	3	0	95	−0.12	<0.01	15	1	14	0	84	17.9	17.6	0.71	<0.01	30	2	28	0	56	33.3	60.7	0.95	<0.01
Acer carpinifolium	0	0	0	0	510	−1.00	<0.01	119	118	0	1	586	5.9	16.7	−0.13	<0.01	343	264	12	67	529	9.7	17.5	0.68	<0.01
Carpinus cordata	0	0	0	0	53	−1.00	<0.01	0	0	0	0	51	7.5	0	−1.00	0.05	3	3	0	0	48	5.9	0	0.47	<0.01
Acer argutum	0	0	0	0	141	−1.00	<0.01	25	22	3	0	101	29.1	2.4	0.76	<0.01	39	12	10	17	52	48.5	42.9	0.98	<0.01
Pterostyrax hispida	0	0	0	0	89	−1.00	<0.01	3	3	0	0	67	30.3	3.7	0.23	0.63	14	13	0	1	40	40.3	33.3	0.93	0.21
Others	0	0	0	0	174			4	1	3	0	156					19	9	6	4	122				

ND total number of damaged trees, *S* feeding damage to leaves and stems, *B* debarking and fraying damage, *SB* both S and B, *TN* total number of standing trees, *MR* mortality rate (%), *PDD* percentage of browsed trees among all dieback trees, *D* Ivlev's modified electivity index (Jacobs 1974), *P* significance of the difference between the browsing-damage ratio for each species and the overall ratio (Fisher's exact test) of 19 species, including some trees of the dominant canopy species (Table 9.3). The likelihood ratio test indicated that browsing damage had increased significantly throughout the survey period ($P < 0.001$), and that the extent of damage varied among species ($P < 0.001$). However, the interaction between year and species was not significant ($P = 0.96$).

9.5 Species and Size Preferences, and Mortality

Among the browsed tree species, *U. laciniata* and *A. argutum* had significantly higher ratios of damaged trees among the total number of trees in the forest ($P < 0.01$), and higher Ivlev's modified electivity indices (D values) in all surveys (Table 9.3). The index D_i (Jacobs 1974) for species i was calculated as follows:

$$D_i = \frac{r_i - P_i}{r_i + P_i - 2r_iP_i},$$

where r_i is the ratio of the number of damaged trees of the ith species to the total number of damaged trees, and P_i is the ratio of the total number of trees of the ith species to the total number of trees (Jacobs 1974). The index D is 1 for preferred species and -1 for non-preferred species. The D values for *P. hispida* and *A. carpinifolium* increased gradually throughout the survey period, reaching 0.93 and 0.68, respectively, by the fourth survey. By contrast, *F. platypoda* and *A. pictum* had lower proportions of damaged trees among the total number of trees ($P < 0.01$) and lower D values. Initially, browsing damage was found primarily on trees with smaller DBHs (4–20 cm); its distribution then expanded gradually to include larger trees (DBH > 20 cm; Fig. 9.2). The likelihood ratio test indicated that the DBH correlated negatively with browsing damage caused by the deer ($P < 0.01$). This correlation was particularly strong for *U. laciniata*, *A. argutum*, and *A. carpinifolium* (Fig. 9.3). Exceptionally, the DBH showed no obvious relationship to browsing damage to trees of *P. rhoifolia* and *C. japonicum*. During the tree census, we recorded browsing-damage levels and divided them into three categories: (1) feeding on leaves and stems; (2) debarking, including the fraying of bark; and (3) a combination of feeding and debarking damage (Fig. 9.4). Evidence of feeding on leaves and stems, debarking, and combined feeding and debarking damage was found on almost all dominant and abundant species in 2006–2008 (Table 9.3). Among the excessively browsed species, debarking damage occurred more frequently than feeding damage on *U. laciniata* and *A. shirasawanum*. By contrast, *A. carpinifolium* and *P. hispida* were subjected to heavier feeding on leaves and stems than on bark. Feeding and debarking damage were recorded in equal quantities on *A. argutum*. The dieback of damaged trees of excessively browsed species increased until the fourth survey (likelihood ratio test, $P < 0.01$; Fig. 9.3, Table 9.3). However, the mortality of damaged trees varied among species. For example, the mortality rates of

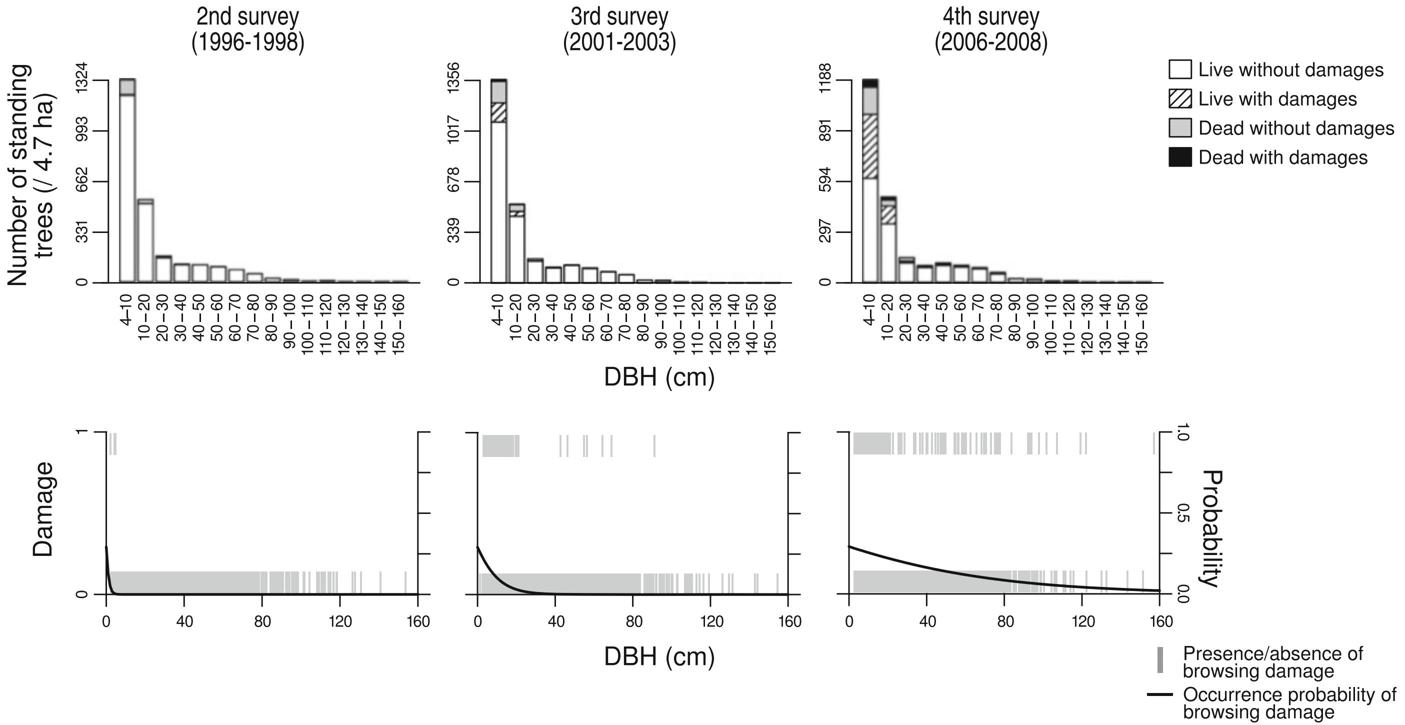

Fig. 9.2 Temporal changes in tree-size preference by sika deer and DBH distributions of all trees in the survey area of the Ooyamazawa riparian forest from the second through fourth surveys (upper three panels). The lower three panels indicate the relationship between DBH and the presence/absence of browsing damage, and estimated probabilities derived using generalized linear mixed models

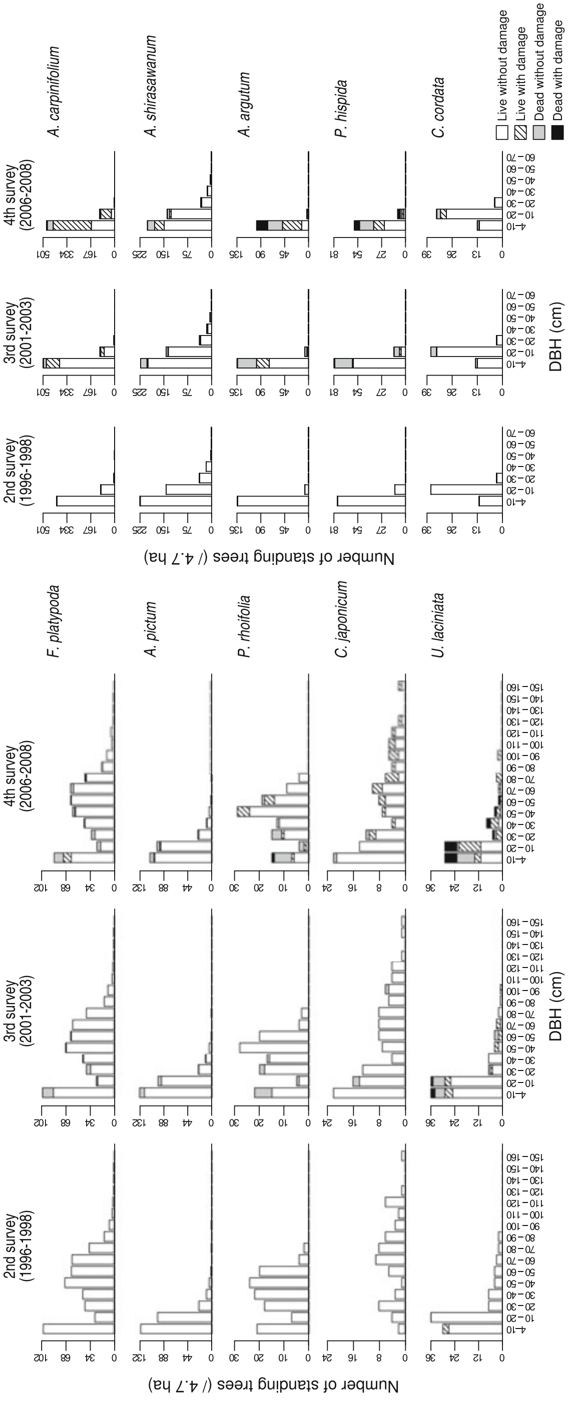

Fig. 9.3 Temporal changes in browsing damage by sika deer and DBH distributions (number of standing trees in 4.71 ha) of the main 10 tree species in the Ooyamazawa riparian forest from the second through fourth surveys. Browsing damage included feeding damage to leaves and stems, bark stripping, and fraying damage to bark

Fig. 9.4 Feeding on leaves and stems of *P. hispida* (left) and debarking of *A. carpinifolium* (right) by sika deer

U. laciniata, *A. argutum*, and *P. hispida* were high, whereas that of *A. carpinifolium* was relatively low (Table 9.3).

These results suggest that *A. argutum*, *U. laciniata*, *P. hispida*, and *A. carpinifolium* were preferentially browsed by deer compared with *F. platypoda*, *A. pictum*, and *A. shirasawanum* (Table 9.3). The diet of deer is determined by the physical ease of feeding, and the nutritional and lignin contents of plants (Gill 1992a; Jiang et al. 2005; Kojima et al. 2006). The major damage to *A. argutum*, *A. carpinifolium*, and *P. hispida* may have been caused by the relatively small size of these three species in the forest (Table 9.1). In general, DBH and tree height variation differ among species in natural forests. These three species have relatively low tree heights and small maximum DBHs, in addition to producing many sprouts without scarring caused by disturbances. Smaller trees have more leaves and stems at lower heights, accessible to deer. In addition, bark becomes thicker, harder, rougher, and more suberizing with increasing tree diameter. Therefore, these three species may be physically easy to feed on by deer. By contrast, *F. platypoda* and *A. pictum* have greater tree heights and trunk diameters. The forest-floor vegetation, which includes the seedlings and saplings of these two species, has almost disappeared due to heavy browsing pressure of deer, except for poisonous herbs such as *Veratrum album* subsp. *oxysepalum* (Turcz.) Hultén *Aconitum tonense* Nakai ex H.Hara, and *Scopolia japonica* Maxim. Thus, the lower preference for these species by deer, despite their palatability, may be caused by the presence of fewer leaves and stems at lower heights, in addition to thicker bark relative to other species. These results suggest that deer browsing activity especially reduces tree-species diversity of certain functional types, such as shrub species (i.e., species with relatively low tree heights and small maximum DBHs). On the other hand, *U. laciniata* was subject to the most damage among the four preferred species. The greater preference for this species has also been confirmed in previous studies (Imagawa and Tanaka 1996;

Kaji et al. 2010). This species may be targeted preferentially due to the low lignin content in its bark (Imagawa and Tanaka 1996; Kojima et al. 2006) and the physical ease of strip-peeling (Imagawa and Tanaka 1996).

9.6 Resistance of Trees to Deer Browsing

Heavy browsing, especially bark-stripping by large herbivorous mammals, induces the dieback of damaged trees (Gill 1992b; Akashi and Nakashizuka 1999). The increase in dieback of damaged trees among the four preferred species in our study (*A. argutum*, *U. laciniata*, *P. hispida*, and *A. carpinifolium*) during 2006–2008 suggests that deer browsing caused serious damage to tree species in this old-growth riparian forest (Fig. 9.3, Table 9.3). However, the mortality rates differed among the four species. *Acer argutum* and *U. laciniate*, which had high mortality rates, were subjected to more debarking than feeding damage. Conversely, *A. carpinifolium* had a lower mortality rate than did *A. argutum* and *U. laciniata*, even though 79 trees of *A. carpinifolium* were affected by debarking damage and 264 trees showed damage caused by feeding on stems and leaves (Table 9.3). These results indicate that these four species have different levels of resistance to deer browsing, with the highest being shown by *A. carpinifolium*. Similar findings were obtained in several previous studies based on simulated experiments of browsing and debarking (Noel 1970; Bergström and Danell 1987; Delvaux et al. 2010). The high resistance of *A. carpinifolium* is considered to be due to its high rates of adventitious bud production and regrowth of bark, including the cambium layer and phloem, after browsing and debarking.

9.7 Effective Management of Ooyamazawa

Previous studies have suggested that browsing by sika deer adversely affects the regeneration of tree species in natural forests (Takatsuki and Gorai 1994; Akashi and Nakashizuka 1999; Suda et al. 2001; Yokoyama et al. 2001). Our study reveals an increase in serious damage to tree species in an old-growth riparian forest due to 18 years of heavy browsing activity by deer. Riparian forests have important and unique ecosystem functions (Malanson 1993; Richards et al. 2002; Ward et al. 2002); however, the areas of these forests in mountain landscapes are smaller than those of other forests on mountain slopes, such as *Fagus crenata* forest. Therefore, deer browsing appears to negatively impact not only riparian forests, but also mountain forest ecosystems. If the deer population density is maintained at the current level or increases further, modification of the forest structure and composition will be induced by the failure of preferred species to regenerate and the dieback of trees with small diameters. To maintain the ecosystems of riparian forests, immediate preventive management is required before browsing damage by deer expands.

Deer-exclusion fences are an effective means of forest management and have been used widely throughout Japan. However, these fences can protect only limited areas of forest, as installation and maintenance costs are very high. The control of the deer population through hunting or culling is an alternative method, and the number of sika deer harvested has increased rapidly over the last few decades (Takatsuki 2009). However, population control by hunting and culling is expected to be insufficient because the number of hunters is gradually declining in Japan (Takatsuki 2009). Hence, temporal and immediate activities, such as the selective conservation of tree-seed sources, are needed until a viable management program becomes operational.

In the Ooyamazawa riparian forest, extensive browsing damage and increased tree mortality were found for *U. laciniata*, *A. argutum*, and *P. hispida*. Therefore, in other riparian forests of similar species composition and size structure, mature trees of these three species with small diameters (i.e., shrub species) should be primarily protected and managed through the use of metallic-mesh trunk protectors.

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