Trunk cutting initiates bottom-up cascades in a tri-trophic system: sprouting increases biodiversity of herbivorous and predaceous arthropods on willows

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We examined the effects of trunk cutting on the regrowth responses of two dominant willow species, *Salix eriocarpa* and *S. gilgiana*, and the subsequent effects on the community structure (abundance and species richness) of herbivorous and predaceous arthropods. We studied ten randomly selected pairs of cut and uncut (control) trees of each willow species. Field observations showed that when the trunks were cut, shoots sprouted from the base and developed rapidly. These shoots continued to grow until July, producing lateral shoots and leaves, whereas current-year shoots on uncut trees essentially stopped growing by April. In July, the upper leaves of cut trees were less tough and had a greater water and nitrogen content than leaves of uncut trees. Leaf consumption and abundance and species richness of both herbivorous and predaceous arthropods were significantly greater on cut trees than on uncut trees in both willow species. Overall, trunk cutting resulted in at least a two-fold increase in both relative abundance and species richness within the arthropod community on the willow species. We concluded that the severe physical damage caused by trunk cutting greatly increased the biodiversity of herbivorous and predaceous arthropods through bottom-up cascading effects.

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Many authors have documented that abiotic natural disturbances play a major role in structuring species composition in biological communities (Connell 1978, Sousa 1984, Menge and Sutherland 1987, Molino and Sabatier 2001). These studies suggest that recolonization and species replacement follow disturbances, which open up new sites and are therefore an important factor for increasing species diversity. On the other hand, large-scale destruction caused by abiotic natural disturbances (e.g. floods and fires) and browsing by mammals often stimulates compensatory regrowth of trees and shrubs (Bryant et al. 1991, Whitham et al. 1991, Cooper-Ellis et al. 1999, Bond and Midgley 2001, Del Tredici 2001,

Radho-Toly et al. 2001, Bailey and Whitham 2002, Spiller and Agrawal 2003, Nakamura et al. 2005). This rapid plant growth produces young plant tissues with greater nutritional content (Danell and Huss-Danell 1985, Martinsen et al. 1998, Spiller and Agrawal 2003). Because large-scale destruction provides high quality resources, it often results in increased abundance of insect herbivores (Danell and Huss-Danell 1985, Roini-nen et al. 1994, 1997, Hjältén and Price 1996, Martinsen et al. 1998, Olofsson and Strengbom 2000, Spiller and Agrawal 2003, Nakamura et al. 2005, Ohgushi 2005). In addition, because rapid plant growth can reduce ex-ploitative competition among herbivore species by

increasing resource availability (Price 1992), large-scale destruction may also increase the species diversity of insect herbivores.

Several authors have argued that increased abundance or species diversity at lower trophic levels may result in increased abundance or species diversity at higher trophic levels (Hunter and Price 1992, Siemann 1998). This argument is based on the possibility that rapid plant growth after large-scale destruction has a subsequent indirect effect on abundance and species diversity of predaceous arthropods by altering both species composition and abundance of prey herbivores. Therefore, large-scale destruction may initiate bottom-up cascading effects across several trophic levels, resulting in an increase in abundance and species diversity of the entire arthropod community on a plant. Although Bailey and Whitham (2002) have shown an entire arthropod community response to foliage sprouting following fire, there have been few studies on demonstrating arthropod community responses of herbivores and predators separately.

Woody plants in the family Salicaceae, such as *Populus* and *Salix*, are found in riparian habitats where they are subject to several kinds of large-scale destruction (Nilsson 1987, Craig et al. 1988, Niiyama 1990, Newsholme 1992, Stein et al. 1992, Martinsen et al. 1998, Nakamura et al. 2005). For example, beavers in North America cut down cottonwood trees (*Populus* sp.) and remove nearly all of their aboveground biomass (Martinsen et al. 1998). Floods severely damage the aboveground stems of willows (Craig et al. 1988, Niiyama 1990, Newsholme 1992, Nakamura et al. 2005). Such large-scale destruction stimulates regrowth responses of trees in the Salicaceae, which positively affects herbivorous insects (Stein et al. 1992, Martinsen et al. 1998, Bailey and Whitham 2002, Nakamura et al. 2005).

In mid-March 2003, the River Bureau of the Japanese Ministry of Land, Infrastructure, and Transport removed willow trees from the banks of the Yasu River in Shiga Prefecture (central Japan) for flood control. The trunks were cut 50 cm above ground. In addition to the large-scale destruction mentioned above, artificial cutting also damages the aboveground portions of the trees. We used this opportunity to clarify how severe physical damage initiates willow regrowth responses and influences arthropod community structure.

We studied two dominant willow species, *Salix eriocarpa* (Franch. et Savant) and *S. gilgiana* (Seemen). We tested the hypothesis that trunk cutting indirectly influences the abundance and species richness of the entire arthropod community on the willows because rapid regrowth after cutting initiates bottom-up cascading effects across multi-trophic levels. This hypothesis encompasses four questions in particular: (1) does trunk cutting induce rapid regrowth of the willows? (2) Does

this rapid growth response affect nutritional and/or physical properties of the willows? (3) If so, does the trunk cutting indirectly affect leaf herbivory? (4) And does the trunk cutting indirectly influence the abundance and species richness of herbivorous and predaceous arthropods (and thus the entire arthropod community) on the willows?

Material and methods

Study site

This study was performed in 2003 on the banks of the Yasu River (35°N, 136°E) in Shiga Prefecture, central Japan. At least seven willow species grow naturally at the study site: *Salix chaenomeloides* Kimura, *S. eriocarpa* Franch. et Savantier, *S. gilgiana* Seemen, *S. gracilistyla* Miquel, *S. serissaefolia* Kimura, *S. subfragilis* Andersson, and *S. integra* Thunb. In mid-March 2003, willow trees were patchily cut down by randomly selective logging (Kagata et al. 2005). This cutting was conducted for flood control by the River Bureau of the Japanese Ministry of Land, Infrastructure, and Transport. More than 100 trees, including several willow species, were cut 50 cm above ground. Approximately 20% of the willow trees were cut at the study site. The cut and uncut trees co-occurred in the same area.

Selection of study trees

We chose *S. eriocarpa* and *S. gilgiana* for this study, because they are the dominant willow species in the study area. For the field survey of plant growth and arthropod diversity, we randomly selected ten pairs of cut and uncut (control) trees of each willow species on 15 April 2003. To control for tree size, cut and uncut trees were paired on the basis of similar basal trunk diameter (Wilcoxon signed rank test: *S. eriocarpa*, Z = −1.000, P = 0.317; *S. gilgiana*, Z = −0.250, P = 0.803; Table 1). In mid April, 22 to 46 sprouting shoots grew from cut trees but few grew from uncut trees (*S. eriocarpa*, Z = −2.807, P = 0.005; *S. gilgiana*, Z = −2.805, P = 0.005). Therefore, we chose sprouting shoots on cut trees and current-year shoots on uncut trees for our field observations.

Effects of trunk cutting on willow growth

To determine whether trunk cutting influenced the growth patterns of *S. eriocarpa* and *S. gilgiana*, we conducted a field survey of plant growth monthly from May to July. We randomly selected five sprouting shoots on each cut tree and five current-year shoots on each uncut tree. We counted the numbers of lateral shoots and

Table 1. Characteristics of cut and uncut trees of *S. eriocarpa* and *S. gilgiana* used for this study. Sprouting shoots were counted 50 cm above ground. Different letters show significant difference (P <0.01).

Species	Characteristics	Uncut trees mean ± SE	Cut trees mean ± SE
S. eriocarpa	basal diameter (cm)	14.9 ± 1.3[a]	14.8 ± 1.2[a]
	no. of sprouting shoots	0.0 ± 0.0[a]	22.1 ± 3.0[b]
S. gilgiana	basal diameter (cm)	12.5 ± 1.2[a]	12.4 ± 1.1[a]
	no. of sprouting shoots	1.9 ± 0.5[a]	46.2 ± 8.2[b]

leaves on each shoot and measured total shoot length. To determine the difference in willow growth between cut and uncut trees for each month, the data were analyzed using a Wilcoxon signed rank test. The data were $\log(n+1)$-transformed and analyzed using a repeated-measures analysis of variance (ANOVA) to test the effects of cutting, season, and their interaction. Individual willow trees were used as replicates in the analysis.

Effects of trunk cutting on leaf quality

To examine whether the regrowth response to trunk cutting affected the nutritional and physical properties of the leaves of *S. eriocarpa* and *S. gilgiana*, we measured nitrogen and water content and leaf toughness at the upper reaches of shoots, because many insect herbivores tend to aggregate to these upper leaves. On 1 and 2 July, we randomly selected three sprouting shoots on each cut tree and three current-year shoots on each uncut tree. We sampled one leaf from the upper part of each shoot and immediately brought the samples to the laboratory. To determine the toughness of upper leaves, we used a penetrometer (Aikoh, Inc., Yokohama, Japan) to record the weight necessary to force a rod 2 mm in diameter through the upper leaves. We measured the fresh weight of the leaves and their dry weight after they had been naturally dried in the laboratory for 1 month. Percent water content was calculated as (fresh weight − dry weight)/fresh weight × 100. After grinding the dry leaves, we measured the percent nitrogen content using a CN analyzer (JM 1000CN, J-Science, Kyoto, Japan). A Wilcoxon signed rank test was used to examine the differences in the leaf properties mentioned above. Individual willow trees were used as replicates in the analysis.

Effects of trunk cutting on leaf consumption

To examine whether trunk cutting indirectly influenced leaf consumption on *S. eriocarpa* and *S. gilgiana*, on 24 and 25 July we randomly sampled 100 leaves from each tree. We then visually scored the percent area consumed for each leaf and translated the percentages into ranked indices as follows: 0% =0, 1–20% =1, 21–40% =2, 41–60% =3, 61–80% =4, and 81–100% =5. After observed scores of individual leaves were transferred by 0 =0%, 1 =10%, 2 =30%, 3 =50%, 4 =70%, and 5 =90%, we calculated the mean percentage of leaf consumption for each tree. Individual willow trees were used as replicates in the analysis. These data were analyzed using a Wilcoxon signed rank test.

Effects of trunk cutting on arthropod abundance and species richness

To determine how the regrowth response to trunk cutting affected the community structure of arthropods, we conducted field censuses of arthropod abundance and species richness monthly from May to July. We randomly selected ten sprouting shoots on each cut tree and ten current-year shoots on each uncut tree. We then recorded the number of species and abundance of each species present on each shoot. We sorted all arthropods into species by consulting field guides (Inoue et al. 1982, Hayashi et al. 1984, Ueno et al. 1985, Kurosawa et al. 1985, Morimoto and Hayashi 1986, Hidaka 1998) and a taxonomist (K. Mizota). Morphologically distinct taxa were identified individually.

All census data for species richness were combined and analyzed using a Wilcoxon signed rank test. To prevent common species from swamping the abundance of less common species, we conducted a relative abundance analysis. All census data for abundance were combined. Relative abundance values for each taxa were expressed by $\log(n+1)$-transformed numbers per 10 shoots, which were then standardized so that the number for each taxon had standard deviation of 1 and mean of 1, to make all species weigh equally (Whitham et al. 1994). The standardized values were then summed. These data were analyzed using a Wilcoxon signed rank test. Individual willow trees were used as replicates in the analysis.

To determine the effects of the regrowth response on herbivores and predators separately, the species richness and relative abundance of herbivorous and predaceous arthropods were compared between cut and uncut trees. These data were analyzed using a Wilcoxon signed rank test. Individual willow trees were used as replicates in the analysis.

Results

Change in willow growth patterns

The numbers of lateral shoots and leaves per shoot and the total shoot length all differed significantly between cut and uncut (control) *S. eriocarpa* and *S. gilgiana* (ANOVA: P <0.01; Table 2). After June, the sprouting shoots on cut trees produced more lateral shoots than the current-year shoots on uncut trees (Wilcoxon signed rank test: P <0.01; Fig. 1). Furthermore, the numbers of leaves and the total shoot lengths were significantly greater for cut trees than for uncut trees throughout the study period (P <0.01; Fig. 1). The interaction effect (cutting × season) on the numbers of lateral shoots and leaves and total shoot lengths was also significant (ANOVA: P <0.01; Table 2), suggesting that the differences in shoot growth between cut and uncut trees gradually increased with the approaching summer in both willow species.

Changes in leaf quality

We found significant differences in nutritional and physical properties of upper leaves between cut and uncut trees in both willow species (Table 3). Upper leaves on cut trees contained about 50% more nitrogen and 10% more water and were about 60% less tough than those on uncut trees in both species (Wilcoxon signed rank test; nitrogen: *S. eriocarpa*, Z =2.803, P =0.005, mean of uncut =1.87, mean of cut =2.83; *S. gilgiana*, Z =2.803, P =0.005, mean of uncut =2.59, mean of cut =3.87; water: *S. eriocarpa*, Z =2.803, P =0.005, mean of uncut =0.56, mean of cut =0.68; *S. gilgiana*, Z =2.803, P =0.005, mean of uncut =0.62, mean of cut =0.71; toughness: *S. eriocarpa*, Z =2.803, P =0.005, mean of uncut =2.04, mean of cut =0.92; *S. gilgiana*, Z =2.803, P =0.005, mean of uncut =1.71, mean of cut =0.64).
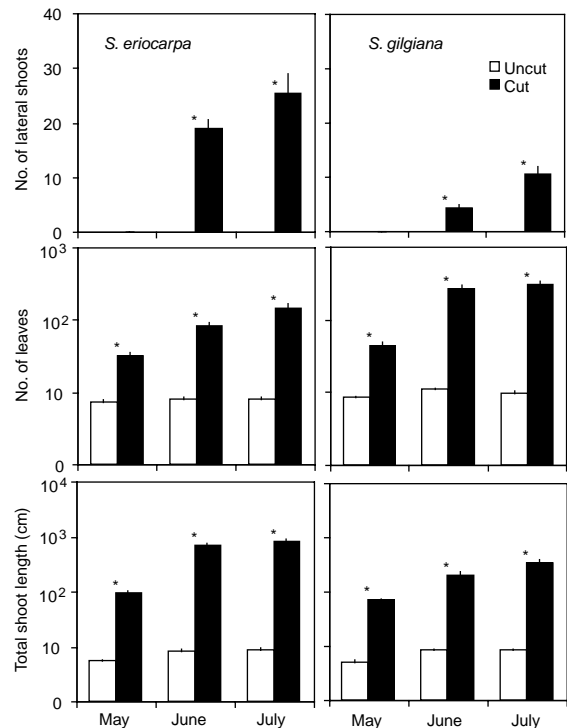

Fig. 1. Numbers of lateral shoots and leaves per shoot and total shoot lengths for *S. eriocarpa* and *S. gilgiana*. Sprouting shoots were measured on cut trees, current-year shoots on uncut trees. Means and SE are presented. Asterisks indicate significant differences (Wilcoxon signed rank test: P <0.01).

Leaf consumption

Leaf consumption differed significantly between cut and uncut trees in both willow species. Percentage of leaf consumption was significantly greater on cut trees than on uncut trees in both willow species (Wilcoxon signed rank test: *S. eriocarpa*, Z =2.803, P =0.005, mean of uncut =10.8, mean of cut =32.7; *S. gilgiana*, Z =2.803, P =0.005, mean of uncut =10.6, mean of cut =33.5; Fig. 2).

Table 2. Repeated-measure ANOVA for the effects of treatment, season, and their interaction on numbers of lateral shoots and leaves, and total shoot length. Asterisks show significant difference (P <0.01).

Species	Characteristics	F values		
		Cutting	Season	C × S
S. eriocarpa	no. of lateral shoots	150.68*	114.13*	114.13*
	no. of leaves	569.22*	20.57*	17.54*
	total shoot length	1002.67*	52.69*	15.66*
S. gilgiana	no. of lateral shoots	2184.22*	354.22*	354.22*
	no. of leaves	966.33*	109.89*	77.84*
	total shoot length	1754.90*	172.13*	80.92*

Table 3. Nitrogen and water content, and toughness of leaves on the upper parts of shoots. Different letters show significant difference (P <0.01).

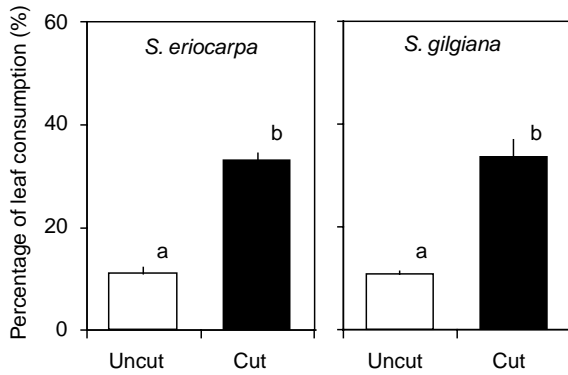| Species	Characteristics	Uncut tree mean ± SE	Cut tree mean ± SE
S. eriocarpa	nitrogen (% dry wt)	1.87 ± 0.09[a]	2.82 + 0.16[b]
	water content (% fresh wt)	0.56 ± 0.01[a]	0.68 ± 0.01[b]
	toughness (N)	2.04 ± 0.04[a]	0.92 ± 0.08[b]
S. gilgiana	nitrogen (% dry wt)	2.59 ± 0.07[a]	3.87 ± 0.15[b]
	water content (% fresh wt)	0.62 ± 0.01[a]	0.71 ± 0.01[b]
	toughness (N)	1.71 ± 0.64[a]	0.64 ± 0.02[b]

Fig. 2. Percentage of leaf consumption for cut and uncut *S. eriocarpa* and *S. gilgiana*. Means and SE are presented. Different letters indicate significant differences (Wilcoxon signed rank test: $P < 0.01$). Most leaves of uncut trees had 1–20% damage, while most leaves of cut trees had 21–40% damage.

Response of entire arthropod communities

We classified the arthropods into 58 taxa from 34 families belonging to seven orders. Fourteen species were not identified (Appendix 1). *Salix eriocarpa* had 53 taxa; 77% were found only on cut trees, 2% only on uncut trees, and 21% on both. *Salix gilgiana* had 35 taxa; 70% were found only on cut trees, 0% only on uncut trees, and 30% on both. Therefore, cut trees had 8.3-fold and 4.1-fold greater species richness than uncut trees in *S. eriocarpa* and *S. gilgiana*, respectively (Wilcoxon signed rank test: *S. eriocarpa*, $Z = 2.805$, $P = 0.005$; *S. gilgiana*, $Z = 2.805$, $P = 0.005$; Fig. 3). Likewise, the relative abundance of arthropods was 2.8-fold and 2.5-fold greater on cut trees than on uncut trees in *S. eriocarpa* and *S. gilgiana*, respectively (*S. eriocarpa*, $Z = 2.803$, $P = 0.005$; *S. gilgiana*, $Z = 2.803$, $P = 0.005$; Fig. 3).

Response of herbivorous and predaceous arthropods

Trunk cutting indirectly influenced not only herbivorous but also predaceous arthropod communities (Fig. 4). Species richness of both herbivores and predators was significantly greater on cut trees than on uncut trees in both willow species (Wilcoxon signed rank test; herbivores: *S. eriocarpa*, $Z = 2.807$, $P = 0.005$; herbivores: *S. gilgiana*, $Z = 2.814$, $P = 0.005$; predators: *S. eriocarpa*, $Z = 2.814$, $P = 0.005$; predators: *S. gilgiana*, $Z = 2.820$, $P = 0.005$). Similarly, relative abundance of both herbivores and predators was significantly greater on cut trees than on uncut trees in both willow species (herbivores: *S. eriocarpa*, $Z = 2.803$, $P = 0.005$; herbivores: *S. gilgiana*, $Z = 2.803$, $P = 0.005$; predators: *S. eriocarpa*, $Z = 2.803$, $P = 0.005$; predators: *S. gilgiana*, $Z = 2.803$, $P = 0.005$).
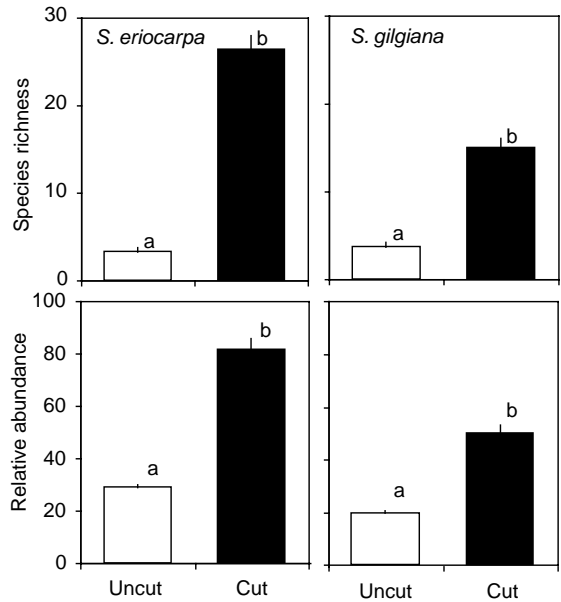

Fig. 3. Species richness and relative abundance per 10 shoots of the entire arthropod community on cut and uncut *S. eriocarpa* and *S. gilgiana*. Means and SE are presented. Different letters indicate significant differences (Wilcoxon signed rank test: $P < 0.01$).

Discussion

This study clearly illustrated that cutting the trunks of *S. eriocarpa* and *S. gilgiana* stimulated the sprouting and development of shoots, which rapidly produced lateral shoots and leaves. Sprouting increased not only plant biomass but also shoot quality, which in turn increased leaf consumption and the relative abundance and species richness of herbivorous and predaceous arthropods on the willows.

Rapid willow growth in response to cutting

The trunk cutting at our study site removed nearly all aboveground biomass and a large proportion of apical buds of the willow trees. This breaking of apical dominance, which physiologically controls the growth of shoots from dormant buds (Cline et al. 1997), may lead to rapid sprouting of shoots from dormant buds on the basal trunks (Mopper et al. 1991, Whitham et al. 1991, Bellingham and Sparrow 2000, Bond and Midgley 2001, Del Tredici 2001). Furthermore, because much of the mass of *Salix* trees is underground (Craig et al. 1988), reallocation of resources from underground storage may also support this aboveground regrowth (Stein et al. 1992, Bailey and Whitham 2002).

Our results agree with the findings of previous studies of plant responses to large-scale destruction (caused by fires, hurricanes, and browsing by mammals;
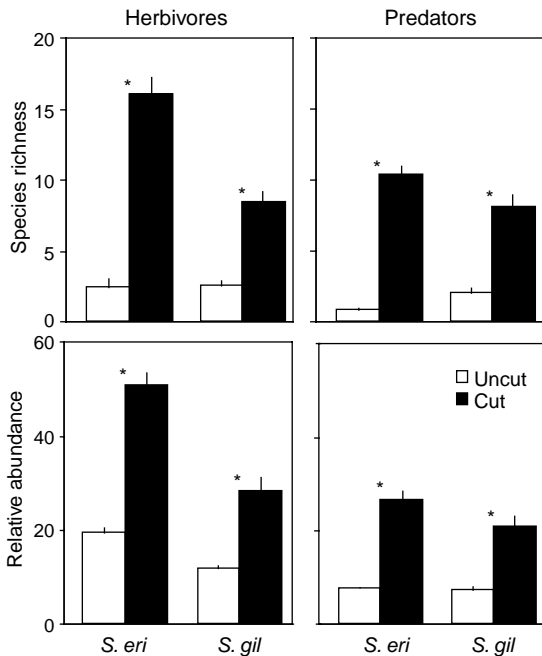
Fig. 4. Species richness and relative abundance per 10 shoots of herbivorous and predaceous arthropods on cut and uncut *S. eriocarpa* and *S. gilgiana*. Means and SE are presented. Asterisks indicate significant differences (Wilcoxon signed rank test: P <0.01).

Bryant et al. 1991, Whitham et al. 1991, Cooper-Ellis et al. 1999, Bond and Midgley 2001, Del Tredici 2001, Bailey and Whitham 2002, Spiller and Agrawal 2003), which indicate that any type of physical and biological destruction that removes a large proportion of apical buds can stimulate rapid plant growth (Del Tredici 2001). In riparian habitats, flooding often badly damages the aboveground tissues of willow trees (Craig et al. 1988, Niiyama 1990, Newsholme 1992, Nakamura et al. 2005). One adaptive response to floods may be rapid regrowth, which is advantageous in the competition for light and space with other plant species (Craig et al. 1986). The regrowth response of willows to herbivory may therefore be a byproduct of their tolerance to severe physical damage by floods (Craig et al. 1986, Price 1991, Roininen et al. 1994, Rosenthal and Kotanen 1994).

Willow susceptibility to herbivory after cutting

Large-scale destruction often induces nutritional and/or physical changes in terrestrial plants (Danell and Huss-Danell 1985, Martinsen et al. 1998, Radho-Toly et al. 2001, Spiller and Agrawal 2003). For example, Danell and Huss-Danell (1985) reported that birch trees produced larger, nitrogen-rich leaves after browsing by moose. In our study, the upper leaves of cut trees in early July were less tough and had greater water and nitrogen

content than those of uncut trees. These nutritional and physical changes were due to newly developed plant tissues produced by the regrowth responses. Sprouting shoots of cut trees continued to grow until July, whereas current-year shoots of uncut trees mostly stopped growing by April. Therefore, reversals in leaf quality between the two treatments throughout the growing season are highly unlikely to occur.

Increased plant quality caused by rapid regrowth can increase the availability of food resources for insect herbivores (Price 1991, Nakamura et al. 2003). In fact, leaf consumption was significantly greater on cut trees than on uncut trees in both willow species. A similar tendency has been detected in other trees and shrubs that experienced large-scale destruction (Danell and Huss-Danell 1985, Stein et al. 1992, Hjältén and Price 1996, Martinsen et al. 1998, Hunter and Forkner 1999, Radho-Toly et al. 2001, Spiller and Agrawal 2003, Nakamura et al. 2005). For example, Spiller and Agrawal (2003) reported that buttonwood mangrove trees (*Conocarpus erectus*) on islands that were exposed to a hurricane suffered great leaf damage. They experimentally showed that the leaves of pruned trees on the island had higher nitrogen content and less toughness than control trees. Therefore, severe physical damage can increase susceptibility to insect herbivory because regrowth responses often improve plant quality and thus increase resource availability.

Bottom-up cascade across three trophic levels

Several authors have demonstrated that insect herbivores increase in abundance owing to foliage sprouting after large-scale destruction (Danell and Huss-Danell 1985, Roininen et al. 1994, 1997, Hjältén and Price 1996, Martinsen et al. 1998, Olofsson and Strengbom 2000, Spiller and Agrawal 2003, Nakamura et al. 2005). However, little evidence supports that sprouting foliage increases the species diversity of insect herbivores (but see Bailey and Whitham 2002). In our study, the trunk cutting increased not only abundance but also species richness of insect herbivores on both willow species. The increased abundance of chewing insects was most likely due to increased leaf biomass and leaf quality caused by regrowth responses. Plant compensation can increase photosynthesis (Whitham et al. 1991) and in turn increase assimilation, which is likely to increase the abundance of sap-feeding insects. Furthermore, we observed several new species of chafers, macrolepidopteran larvae, and aphids on regrwoth foliage of cut trees. Thus, we recorded 15 and nine more chewing species and eight and four more sap-feeding species on cut than on uncut *S. eriocarpa* and *S. gilgiana*, respectively (Appendix 1). The increased number of herbivore species in each feeding guild on cut trees may have been caused by reduced

interspecific competition, because rapid plant growth can reduce competition among herbivorous insects by providing abundant, available resources (Price 1991). On the other hand, stem galls made by a gall midge, *Rhabdophage rigidae*, were not found on cut trees because sprouting of cut trees initiated in mid-April after its oviposition finished in our study site (Nakamura et al. 2003).

Trunk cutting in our study also increased the abundance and species richness of predaceous arthropods. Hunter and Price (1992) proposed that an increase in abundance or species diversity at lower trophic levels can increase abundance or species diversity at higher trophic levels. Our results strongly support this hypothesis, and add to the growing body of evidence that the number of predaceous arthropods tends to track the number of prey insects (Solomon 1949, Hassell 1978). Although untested, complex branching in plants may contribute to increased spider abundance, because lateral branching may increase the number of web attachment points (Uetz 1991, McNett and Rypstra 2000, Langellotto and Denno 2004). Furthermore, the increase in the number of prey herbivore species should extend the range of food items for specialist predators (Hunter and Price 1992). For example, small ladybird larvae *Scymus* sp. 1, and hoverfly larvae *Syrphus* sp. 1 aggregated to colonies of an aphid, *Aphis farinosa* newly emerged on cut trees. Also, larvae of large ladybird *Aiolocaria hexaspilota* and pupae of parasitic wasp *Anthomyiopsis plagioderae* were often found on cut trees because they preyed on leaf beetle larvae *Plagiodera versicolora*, which were abundant on cut trees but rare on uncut trees. Thus, we found three and four more specialist predator species on cut than on uncut *S. eriocarpa* and *S. gilgiana*, respectively (Appendix 1). Since the cut trees had more herbivores, the increase in ant and spider species, which are generalist predators, may have been caused by such an increased abundance of prey herbivores. We found 11 and six more new species of generalist predators on cut than on uncut *S. eriocarpa* and *S. gilgiana*, respectively (Appendix 1). Previous studies have suggested that generalist predators can be an important factor for regulating leaf beetle populations after harvesting willows in willow coppice (Björkman et al. 2000, 2004). However, our study did not detect top-down forces that influenced herbivore abundance probably because insect herbivores may have a potential to recover more rapidly than generalist predators immediately after trunk cutting.

In conclusion, our study clearly illustrates that trunk cutting stimulated rapid sprouting in *S. eriocarpa* and *S. gilgiana*; this sprouting subsequently increased the relative abundance and species richness of the entire arthropod community through bottom-up cascading effects. There have been few studies that show an arthropod community response to plant sprouting following disturbance (but see Bailey and Whitham 2002). Until recently, the intermediate disturbance hypothesis (recolonization and species replacement) has mainly focused on explaining changes in community structure after disturbance (Connell 1978, Sousa 1984, Menge and Sutherland 1987, Molino and Sabatier 2001). In particular, arthropods are thought to recover quickly because of their rapid colonizing ability and high reproductive rate (Spiller et al. 1998). Therefore, to fully understand how disturbance reorganizes arthropod community structure on terrestrial plants, we must focus on plant regrowth responses to severe physical damage caused by disturbance. These responses can considerably alter arthropod community structure through bottom-up cascading effects.

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Appendix 1. Arthropod species found on observational trees of *S. eriocarpa* and *S. gilgiana*

Order	Family	Species	Guild	S. eri C	S. eri U	S. gil C	S. gil U
Araneae		sp.1	GP	Y		Y	
	Thomisidae	*Misumenops tricuspidatus*	GP	Y		Y	
		Thomisus labefactus	GP	Y			
	Agelenidae	*Agelena opulenta*	GP	Y	Y	Y	Y
	Tetragnathidae	*Tetragnatha praedonia*	GP	Y		Y	Y
		Tetragnatha squamata	GP	Y	Y	Y	
	Salticidae	*Mymarachne japonica*	GP	Y			
	Clubionidae	*Chiracanthium lescivum*	GP	Y			
Diptera	Tachinidae	*Anthomyiopsis plagioderae*	SP	Y		Y	
	Cecidomyiidae	*Rhabdophaga rigidae*	GM		Y		
	Syrphidae	*Syrphus.* sp.1	SP			Y	
Hymenoptera	Formicidae	*Formica japonica*	GP	Y		Y	
		Lasius sakagamii	GP	Y	Y	Y	Y
		Pristomyrmex pungens	GP	Y		Y	
	Tenthredinidae	*Phyllocolpa.* sp.1	GM	Y	Y		
		Stauronematus compressicornis	Ch			Y	
Hemiptera	Aphididae	*Aphis farinosa*	SF	Y		Y	
		Chaitophorus saliniger	SF	Y	Y	Y	Y
		Cavariella salicicola	SF	Y			
		Pterocomma pilosum	SF	Y			
		Tuberolachnus salignus	SF	Y			
	Pemphigidae	sp.1	SF	Y	Y	Y	
	Aphrophoridae	*Aphrophora pectoralis*	SF	Y		Y	
	Cicadellidae	sp.1	SF	Y			
	Tingidae	*Metasalis populi*	SF	Y		Y	
	Delphacidae	sp.1	SF	Y			
	Reduviidae	sp.1	GP	Y			
Coleoptera	Chrysomelidae	*Plagiodera versicolora*	Ch	Y	Y	Y	Y
		Crepidodera japonica	Ch	Y			
		Fleutiauxia armata	Ch	Y			
		Smaragdina semiaurantiaca	Ch	Y			
		Cryptocephalus perelegans	Ch	Y		Y	
	Attelabidae	*Pselaphorhynchites japonicus*	Ch	Y	Y	Y	
	Curculionidae	sp.1	Ch	Y		Y	
	Elateridae	*Agrypnus binodulus*	O	Y			
	Cantharidae	*Athemus vitellinus*	O	Y		Y	Y
	Scarabaeidae	*Anomala cuprea*	Ch	Y			
		Rhomborrhina japonica	Ch	Y			
	Coccinellidae	*Aiolocaria hexaspilota*	SP	Y			
		Propylea japonica	GP	Y		Y	
		Harmonia axyridis	GP	Y		Y	Y
		Scymnus sp.1	SP	Y		Y	
Neuroptera	Chrysopidae	sp.1	SP			Y	
Lepidoptera	Hepialidae	*Endoclyta excrescens*	B	Y	Y	Y	
	Gracillariidae	*Phyllonorycter pastorella*	M	Y	Y	Y	Y
		Caloptilia stigmatella	M, SM	Y		Y	Y
		Phyllocnistis sp.1	M			Y	Y
		Phyllocnistis sp.2	M	Y			

Appendix 1 (*Continued*)

Order	Family	Species	Guild	*S. eri*		*S. gil*	
				C	U	C	U
	Geometridae	sp.1	Ch	Y			
	Sphingidae	*Smerinthus planus*	Ch	Y		Y	
	Notodontidae	*Clostera anastomosis*	Ch	Y		Y	
	Lymantriidae	*Lymantria dispar*	Ch	Y		Y	
		Orgyia thyellina	Ch	Y			
		Orgyia recens	Ch	Y		Y	
		Leucoma salicis	Ch	Y			
	Limacodidae	*Latoia consocia*	Ch	Y		Y	
	Tortricidae	sp.1	SM	Y	Y		
	Psychidae	*Eumeta minuscula*	SM				Y

Notes: arthropod species are classified into following ten feeding guilds: chewers (Ch), miners (M), shelter makers (SM), gall makers (GM), borers (B), sap feeders (SF), omnivores (O), generalist predators (GP), and specialist predators (SP). Y indicates that individuals of the species were found on cut (C) or uncut (U) trees.