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Refoliation of deciduous canopy trees following severe insect defoliation: comparison of *Fagus crenata* and *Quercus crispula*

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Abstract Deciduous trees can survive severe defoliation by herbivores and often refoliate in the same season. Refoliation following severe defoliation represents compensatory regrowth to recover foliage biomass. Although the relationship between defoliation intensity and degree of refoliation at the individual level has been quantified following artificial defoliation for saplings and small trees, no study has examined the relationship for canopy trees and interspecific differences in this relationship. In this study, defoliation by gypsy moths in an outbreak year and subsequent refoliation were visually surveyed for canopy trees of *Fagus crenata* (n = 80) and *Quercus crispula* (n = 113) in central Japan. Defoliation and refoliation estimates were scored in 10% classes as the ratio to foliage present before defoliation. The degree of refoliation and the proportion of refoliated trees were high in severely defoliated trees. For 60 and 100% defoliated trees, respective refoliations were 2 and 66% for *F. crenata*, and 37 and 88% for *Q. crispula*. All of the 90 and 100% defoliated trees refoliated. These results indicate that severely defoliated trees show an increased need for refoliation to maintain metabolism. Beta regression analysis showed that *Q. crispula* possessed higher refoliation capability than *F. crenata*. This is likely associated with the relatively large storage reserves and recurrent growth flush pattern of oak species, which are strong characteristics of oaks and adaptive for response to herbivory and catastrophic disturbances. Interspecific differences in refoliation capability may exert differential effects on forest ecosystem processes, such as influencing the growth of understory species.

Keywords Foliage recovery · Compensatory regrowth · Insect herbivory · Gypsy moth defoliation · Stored reserves · Beta regression

Introduction

Deciduous trees can survive severe defoliation by herbivores and often produce new sets of leaves in the same season (termed "refoliation") (Kulman 1971; Schowalter et al. 1986). Together with changes in chemical constituents and photosynthetic capacity of the leaves (Schultz and Baldwin 1982; Heichel and Turner 1983), refoliation is a defoliation-induced response of trees. In addition, as well as sprouting (Del Tredici 2001), foliage recovery by refoliation represents compensatory regrowth using stored

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reserves (Wargo et al. 1972; van der Heyden and Stock 1996).

Severe defoliation by herbivores and subsequent refoliation affect various aspects of forest ecosystem processes, especially when dominant canopy trees undergo these events. The effects on the individual tree include reduction of radial growth (Embree 1967; Kosola et al. 2001; Rozendaal and Kobe 2014) and incidental reduction of competitiveness against non-host tree species (Muzika and Liebhold 1999). Ephemeral foliage loss, after defoliation but before termination of refoliation, facilitates growth of understory tree species and plant invasions owing to increased light availability, consequently changing species composition (Collins 1961; Jedlicka et al. 2004; Eschtruth and Battles 2014). Changes in seasonal distribution and nutritional composition of litter fall affect nutrient cycles of forests (Grace 1986). Damage-induced chemical and physical changes in the residual and refoliated leaves affect the herbivorous arthropod community (Hunter 1987; Neuvonen et al. 1988). For monitoring of insect defoliation using satellite imagery, refoliation should be taken into account to estimate defoliation extent more accurately (Hurley et al. 2004; de Beurs and Townsend 2008). Therefore, it is important to understand how dominant canopy trees respond to severe defoliation with refoliation in order to manage forest ecosystems effectively. This knowledge also will be useful for evaluation of the concern that future climate change will promote insect outbreaks (Logan et al. 2003).

Defoliation-induced refoliation has been studied in relation to natural defoliation by insects or mammals and artificial defoliation. It is well known that refoliation is greater in response to severe defoliation (Embree 1967; Wargo et al. 1972; Heichel and Turner 1976; Hoogesteger and Karlsson 1992; Rooke and Bergström 2007). Refoliated foliage on an individual tree has been quantified following artificial defoliation of seedlings (e.g., Hilton et al. 1987; Hikosaka et al. 2005), saplings (Heichel and Turner 1976; Rooke and Bergström 2007; Piper and Fajardo 2014), and mature individuals of small tree species (Boege 2005). These studies manipulated defoliation levels and quantified total leaf area or leaf biomass by performing a complete measurement of all leaves. For example, saplings of *Quercus rubra* subjected to 100% defoliation refoliated 28% of the total area of primary leaves (Heichel and Turner 1976). However, the defoliation levels applied in these studies were restricted (e.g., 100, 50, and 0%); therefore, it is unclear how the degree of refoliation changes gradually with defoliation intensity. Moreover, for canopy trees, although the amount of refoliation after spring frost damage (Augspurger 2009, 2011) and foliage recovery in the years subsequent to a defoliation event (Långström et al. 2001; Piper et al. 2015) have been examined, I am not aware of any study that has explored the relationship between defoliation intensity and refoliation in the same season at the individual level or that clarified interspecific differences in this relationship. This knowledge gap may be because, first, artificial defoliation at the individual level is difficult to apply for canopy trees. Second, the period for surveying the intensity of natural defoliation is often ephemeral because severe defoliation is usually followed by refoliation within about one month (Collins 1961; Heichel and Turner 1976; Hoogesteger and Karlsson 1992; Neuvonen et al. 1988; Eschtruth and Battles 2014; Rozendaal and Kobe 2014). Third, herbivore-induced defoliation levels are unpredictable, and thus it is difficult to secure samples at various defoliation levels. Fourth, nondestructive quantification of leaves of canopy trees at the individual level is problematic. The litter trap method, commonly used for measurement of forest leaf biomass, is suitable for measurement at the stand level (e.g., Grace 1986) but not at the individual tree level, as falling leaves tend to scatter over a wider area beyond the litter traps.

Augspurger (2009) documented refoliation of canopy trees following spring frost damage during the shoot development period and revealed that crown fullness after refoliation ranged from 46 to 99% among damaged species. She rated crown fullness visually as the percentage of the normal crown fullness based on nonfrost years. Similarly, quantification of crown defoliation has been estimated visually as a percentage in studies of insect defoliation (Embree 1967; Williams et al. 1991; Gottschalk et al. 1998; Muzika and Liebhold 1999; Långström et al. 2001; Palacio et al. 2012) and monitoring of forest health (Dobbertin and Brang 2001). Therefore, visual survey is considered to be a useful method for estimation of crown foliage amount of canopy trees.

Beech (*Fagus*) and oak (*Quercus*) species are the dominant canopy tree species in many temperate forests. Beech species are considered to be shade tolerant, whereas oak species are shade intolerant (Cho and Boerner 1991; Canham et al. 1994; Valladares et al. 2002; Nakajima and Ishida 2014). Oak regeneration is believed to depend on catastrophic disturbances, such as fire and felling by humans (Abrams 1992; Masaki et al. 1992; Mikan et al. 1994; Namikawa et al. 1997). Consistent with this trait, oak trees store higher quantities of carbohydrates in roots (Sakai et al. 1997) and show high sprouting capability (Del Tredici 2001) compared with other tree species. Because refoliation depends on stored reserves (Wargo et al. 1972; van der Heyden and Stock 1996) as well as sprouting, refoliation capability is predicted to be high in oak species.

Gypsy moth (*Lymantria dispar*) is distributed across the Northern Hemisphere and is well known as a serious defoliator. The larvae of gypsy moths can defoliate multiple tree species (Liebhold et al. 1995; Onodera and Hara 2011), and an outbreak of gypsy moths can result in complete defoliation of a forest canopy. Meanwhile, many studies have observed refoliation following severe defoliation by gypsy moths (Collins 1961; Gottschalk 1993; Kosola et al. 2001; Ohno et al. 2008; Eschtruth and Battles 2014).

The present study was conducted in Toyama Prefecture, central Japan. In cool-temperate forests in this region, *Fagus crenata* and *Quercus crispula* are dominant canopy tree species (Nakajima and Ishida 2014). Both species are deciduous and susceptible to gypsy moth defoliation (Onodera and Hara 2011). One subspecies of Asian gypsy moth, *Lymantria dispar japonica*, is distributed in this region (Arimoto and Iwaizumi 2014). An outbreak of this gypsy moth occurred in 2014, causing complete defoliation of canopy trees (Nakajima 2015a). In this study, defoliation by gypsy moths and subsequent refoliation were visually surveyed for canopy trees of *F. crenata* and *Q. crispula*. The aim was to examine the relationship between defoliation intensity and foliage recovery by refoliation and to clarify differences in this relationship between *F. crenata* and *Q. crispula*.

Materials and methods

Study sites

In 2014, an outbreak of gypsy moths occurred in the southwestern region of Toyama Prefecture, central Japan (Nakajima 2015a). The study sites were located within the outbreak region, which covered approximately 30 km from east to west and 20 km from north to south. The survey was conducted at four sites for *F. crenata* and five sites for *Q. crispula* (Table 1). The sites for *Q. crispula* were classified as severely defoliated in a previous paper (Nakajima 2015a). Elevation above sea level of the study sites ranged from 570 to 980 m. The sites had been established previously by the Toyama Prefectural Government to monitor seed production. The monitoring protocol involves at least 20 trees per site, with the same trees being monitored every year unless the tree declined or died. In the present study, the same trees were surveyed ($n = 80$ trees for *F. crenata*; $n = 113$ trees for *Q. crispula*). These trees were canopy trees located along the roads and at least approximately 20 cm in diameter at breast height. Therefore, visibility of the crowns was high, and defoliation and subsequent refoliation could be visually estimated easily.

Data collection

In this region, hatching of gypsy moth from overwintering eggs begins around the middle of April and pupation starts in late June. Defoliation proceeds rapidly just before pupation because a large portion of the defoliation is caused by the last instar larvae (Furuno 1964). Refoliation induced by severe defoliation is completed within about one month of peak defoliation (Collins 1961; Eschtruth and Battles 2014). Thus, the survey of defoliation intensity was conducted in July 2014 just after peak defoliation and the survey of foliage recovery by refoliation was conducted in mid to late August 2014 after termination of refoliation.

As described in a previous paper (Nakajima 2015a), defoliation intensity caused by gypsy moths was visually scored as the percentage loss of crown foliage in 10% classes (Williams et al. 1991; Gottschalk et al. 1998; Muzika and Liebhold 1999; Långström et al. 2001). Here, residual foliage, defined as crown foliage remaining after defoliation, was calculated as

$$F_0 = 100 - D \tag{1}$$

where F_0 is the residual foliage (%) and D is the defoliation (%).

In mid- to late-August, crown fullness after refoliation, comparable to canopy fullness described by Augspurger (2009), was visually scored as the

Table 1 Study site characteristics and defoliation intensity of the study trees

Species	Site	Latitude	Longitude	Altitude (m)	Number of trees	Defoliation (%)		
						Mean ± SD	Min.	Max.
F. crenata	a	36°22′N	136°49′E	980	20	79 ± 25	30	100
	b	36°27′N	136°54′E	700	20	50 ± 39	0	100
	c	36°25′N	137°00′E	730	20	84 ± 23	10	100
	d	36°26′N	137°05′E	710	20	57 ± 30	10	100
Q. crispula	A	36°31′N	136°49′E	570	22	73 ± 31	20	100
	B	36°22′N	136°51′E	600	23	73 ± 26	20	100
	C	36°27′N	136°54′E	700	22	67 ± 29	20	100
	D	36°25′N	137°00′E	720	22	72 ± 27	30	100
	E	36°26′N	137°05′E	630	24	88 ± 18	30	100

proportion of crown foliage after refoliation to crown foliage before defoliation, in 10% classes. The amount of refoliation was estimated as

$$R = F_1 - F_0 \tag{2}$$

where R is the refoliation (%) and F_1 is the crown fullness after refoliation (%). As defoliation and crown fullness were scored in 10% classes, refoliation below 10% was not considered in this study. In a portion of the study sites, crown fullness was checked again in September, but additional refoliation was not observed.

Photographs of sample trees in 2012 with little defoliation were used as a reference. Defoliation and crown fullness were rated by the author alone, who is skilled in rating crown foliage biomass visually in a forest monitoring program (Nakajima et al. 2011). Other than gypsy moths, no outbreak of other insect defoliators was observed in the study year.

Statistical analysis

Under the assumption that refoliation does not exceed defoliation, which is predicted based on the results of previous studies (Heichel and Turner 1976; Rooke and Bergström 2007; Piper and Fajardo 2014) and is also applicable to the data in the present study, refoliation can range from 0 to 100% when defoliation is 100%, but, for example when defoliation is 50%, refoliation can range only from 0 to 50%. Thus, refoliation potential has an upper limit, which is defoliation dependent. To model the degree of refoliation regardless of this defoliation-dependent upper limit, the foliage recovery rate, which represents the degree of foliation recovery after defoliation, was calculated as

$$r = R/D \tag{3}$$

where r is foliage recovery rate. Foliage recovery rates ranged from 0 to 1 and were modeled using beta regression with a logit link function (Cribari-Neto and Zeileis 2010), which is useful for modeling continuous variates that assume values in the standard unit interval (0, 1), such as proportions (Ferrari and Cribari-Neto 2004). One tree of *F. crenata* was not defoliated (0% defoliation), so this tree was excluded from the analysis of foliage recovery rate because the rate could not be defined. Consequently, the numbers of sample trees were 79 for *F. crenata* and 113 for *Q. crispula*. As a preliminary step, to examine the variation in the relationship between defoliation and recovery rate among study sites, the models for foliage recovery rates with and without sites as an explanatory variable were compared using a likelihood ratio test for each species. Defoliation was included as an explanatory variable for both models. No significant differences were observed for both *F. crenata* ($P = 0.15$) and *Q. crispula* ($P = 0.21$); i.e., inclusion of sites did not improve the models. Therefore, variation among study sites was not considered in this study, and data pooled across the sites were used for analysis of foliage recovery rate. To evaluate the relationship between defoliation and foliage recovery rate and its difference between the two species, a model with defoliation and species as explanatory variables was developed. The response variable (foliage recovery rate) was slightly compressed with a commonly used transformation method to avoid values of zero and one (Smithson and Verkuilen 2006; Cribari-Neto and Zeileis 2010):

$$r' = [r(N-1) + 0.5]/N \tag{4}$$

where r' is transformed foliage recovery rate and N is the sample size. Pseudo-R^2, which is the squared correlation between the linear predictor and link-transformed response, was calculated (Ferrari and Cribari-Neto 2004). The model was developed using R 3.1.2 (R Core Team 2014) with the betareg package (Cribari-Neto and Zeileis 2010).

Results

Completely defoliated trees (100% defoliation) were present at all sites. The minimum percentage defoliation at each site ranged from 0 to 30% for *F. crenata* and from 20 to 30% for *Q. crispula* (Table 1). For all sample trees across all sites, defoliation was 67 ± 33% (mean ± SD) for *F. crenata* and 75 ± 27% for *Q. crispula*.

The proportion of refoliated trees and degree of refoliation tended to be high in severely defoliated trees and in *Q. crispula* (Fig. 1). All trees refoliated in defoliation classes greater than or equal to 90% for *F. crenata* and 60% for *Q. crispula*. Few trees (less than 20%) refoliated at defoliation classes less than or equal to 60% for *F. crenata* and 30% for *Q. crispula*. For 100% defoliated trees, refoliation was 66 ± 25% for *F. crenata* and 88 ± 15% for *Q. crispula*. For 60% defoliated trees, refoliation was 2 ± 4% for *F. crenata* and 37 ± 8% for *Q. crispula*. In other words, crown fullness after refoliation for 60% defoliated trees was 42 ± 4% for *F. crenata* and 77 ± 8% for *Q. crispula*. The beta regression analysis (pseudo-$R^2 = 0.74$) showed that defoliation positively affected foliage recovery rate and higher recovery rates were observed in *Q. crispula* compared with those of *F. crenata* (Fig. 2, Table 2).

Discussion

In this study, refoliation of canopy trees was observed following gypsy moth defoliation and an increase in foliage recovery by refoliation with defoliation intensity was clearly shown at relatively high (10% interval) resolution (Figs. 1, 2). Previous studies conducted on small tree species and saplings of canopy tree species also revealed the dependence of refoliation on defoliation intensity (Wargo et al. 1972; Heichel and Turner 1976; Hoogesteger and Karlsson 1992; Rooke and Bergström 2007). Such defoliation-dependent refoliation suggests that more severely defoliated trees would have an increased need for refoliation (i.e., additional photosynthetic activity) to maintain metabolism. The finding that refoliation occurred in all trees experiencing 90 and 100% defoliation (Fig. 1) suggests that refoliation is indispensable for severely or completely defoliated trees.

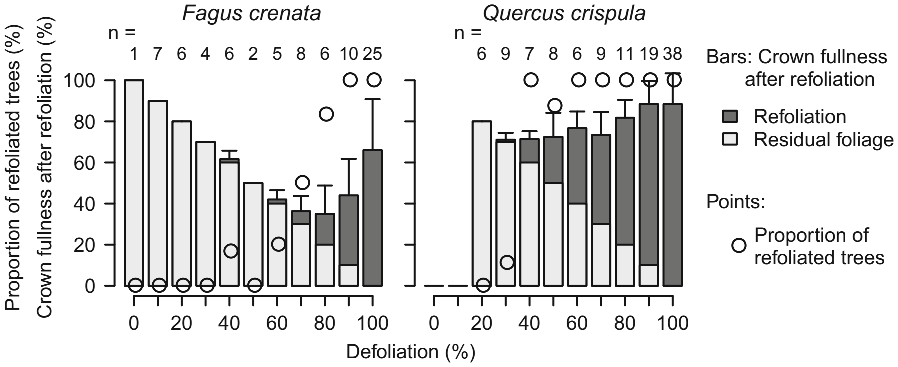

Fig. 1 Relationship between defoliation intensity and crown fullness after refoliation (bars; error bars denote the SD) and between defoliation intensity and proportion of refoliated trees (points). 'Refoliated trees' refer to trees that showed ≥ 10% refoliation. The number of trees in each defoliation class is specified at the top of the figure

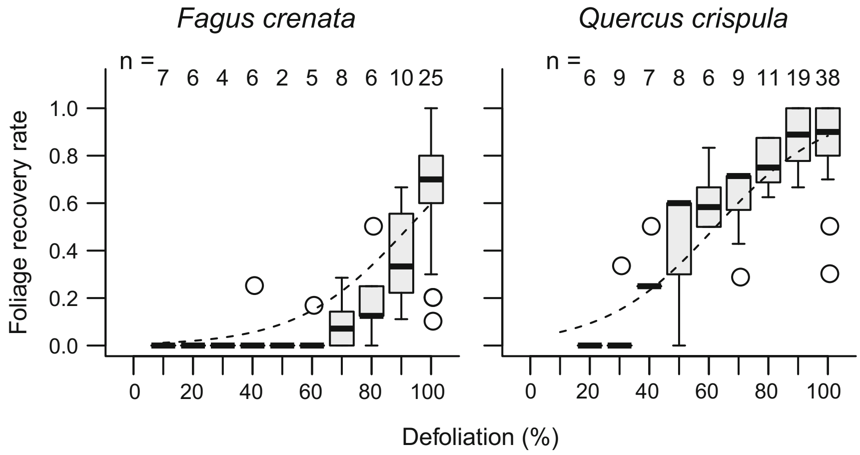

Fig. 2 Relationship between defoliation intensity and foliage recovery rate. Open circles indicate outliers. The dashed line represents expected foliage recovery rate obtained from beta regression analysis (Table 2). The number of trees in each defoliation class is specified at the top of the figure

Table 2 Beta regression model for foliage recovery rate

Explanatory variable	Estimate	SE	*P* value
(Intercept)	−4.978	0.253	< 0.001
Defoliation	0.054	0.003	< 0.001
Q. crispula (*F. crenata* as reference)	1.630	0.153	< 0.001

The key result of this study was demonstration of the high refoliation capability of *Q. crispula* compared with that of *F. crenata* (Figs. 1, 2; Table 2). Refoliation following severe defoliation represents compensatory regrowth to recover foliage biomass and is dependent on stored reserves (Wargo et al. 1972; van der Heyden and Stock 1996). Recovery of photosynthetic organs using stored reserves is an adaptation to cope with abrupt disturbances such as fire, breakage by wind, frost and herbivory, which suddenly remove photosynthetic organs (Iwasa and Kubo 1997). If there is a high probability of substantial loss of photosynthetic organs as a result of disturbance, a plant is likely to store greater amounts of reserves to support regrowth (Chapin et al. 1990). Oak species allocate more carbon to roots compared with other tree species including beech (Sakai et al. 1997; Welander and Ottosson 1998; Takahashi and Goto 2012). Consequently, oak species show high sprouting capability, even trees of large size and old age (Del Tredici 2001). Shibata et al. (2014) studied the sprouting capability of multiple tree species in logged secondary forests ranging in age from 50 to 80 years old, and revealed that *Q. crispula* retained their sprouting capability at a relatively large size and few *Q. crispula* stumps failed to show sprouting. The high sprouting capability of oaks is considered to be adaptive to catastrophic disturbances (Abrams 1992; Takahashi and Goto 2012). For example, oak species dominate European and Asian coppice forests, where felling by humans has occurred repeatedly (Debussche et al. 2001; Nakajima and Ishida 2014). In North America, domination of oak species in presettlement forests is considered to be associated with fire disturbances (Abrams 1992). Therefore, the high refoliation capability of *Q. crispula* revealed in the present study may be partly owing to a relatively large storage reserve as an adaptation to recover from a catastrophic disturbance.

Although leaves of mature trees of both *F. crenata* and *Q. crispula* emerge rapidly immediately after spring budbreak and thereafter no additional leaves usually appear (Kikuzawa 1983), seedlings of both species exhibit a recurrent growth flush pattern (termed lammas growth) if conditions are favorable (Hashizume 1979; Mizumachi et al. 2004). This recurrent growth pattern is widely recognized among oak species (Borchert 1975; Reich et al. 1980; West 1985; Hanson et al. 1986; Hilton et al. 1987; Chaar et al. 1997) but is seldom reported for beech species

(Rozenbergar and Diaci 2014). The occurrence of recurrent growth flushes declines with increasing size of oak trees (Borchert 1975; Reich et al. 1980), but is occasionally observed in mature oaks (West 1985; Buck-Sorlin and Bell 2000). The number of growth flushes of oak seedlings is decreased by environmental stresses, such as shading, frost damage and below-ground resource limitation (Chaar et al. 1997), but in contrast, increases with defoliation (Hilton et al. 1987; Mizumachi et al. 2004). Therefore, growth flushes other than the first flush can act as compensation for lost foliage as well as rapid growth in favorable conditions. Additional flushes of growth occur from June to August in oak seedlings and sprouting stems (Reich et al. 1980; Seiwa and Kikuzawa 1991). Such phenological seasonality implies that mature oaks, which usually produce a single growth flush in spring (Kikuzawa 1983), can compensate for gypsy moth defoliation with the second flush because refoliation after gypsy moth defoliation occurred mainly in July. Hilton et al. (1987) observed that additional growth flushes of oak trees were more noticeable after insect attack. Trees monitored in the present study also refoliated by this flush pattern (pers. obs.). Therefore, growth plasticity achieved with a recurrent growth flush pattern, which is a strong characteristic of oaks and is adaptive for response to herbivory, is likely associated with the high refoliation capability of *Q. crispula*.

The degree of refoliation may be affected by species-specific photosynthetic performance. Species with high photosynthetic efficiency would generate the same amount of photosynthate from fewer leaves and tolerate a reduced degree of refoliation. However, the photosynthetic performance of *F. crenata* and *Q. crispula* is considered to be relatively similar because Koike (1988), who examined the photosynthetic performance of 30 deciduous broad-leaved species in Japan, categorized *F. crenata* and *Q. crispula* in the same group. Nevertheless, Heichel and Turner (1983) artificially defoliated saplings of canopy tree species and demonstrated the high photosynthetic efficiency of refoliated foliage and residual primary foliage compared with that of the primary foliage of undefoliated trees. Such increased photosynthetic efficiency may be associated with reduction in the degree of refoliation.

The extent of refoliation is also affected by the seasonal timing of defoliation (Miquelle 1983; Gregory and Wargo 1986). Refoliation decreases with later defoliation and Miquelle (1983) observed no refoliation in trees defoliated after August. Gypsy moth defoliation and subsequent refoliation occurred mainly in June and July, during the rainy and moist season in the present study region. Kamata (2002) pointed out that low water stress in Japan's moist climate assists trees to withstand defoliation by insects. Therefore, the earlier seasonal timing of defoliation and the moist climate are favorable for refoliation of the study trees.

Reproduction may be associated with resource allocation to refoliation (Boege 2005). Both study species, but especially *F. crenata*, exhibit masting behavior (Saitoh et al. 2008; Nakajima 2015b), and thus allocation to reproduction in the mast year is extremely high. However, for *Q. crispula*, the study year was a regionally synchronous low-crop year regardless of defoliation severity (Nakajima 2015a). For *F. crenata*, the study year was a regionally synchronous no-crop year owing to the almost complete lack of flowering (Nakajima unpublished data). Therefore, resource allocation to current-year reproduction was low or nonexistent in the study trees, and thus the influence on refoliation would be negligible.

Some studies have reported that severe defoliation by insects reduced the foliage biomass in the following years (Långström et al. 2001; Piper et al. 2015). However, for the trees in this study, mean crown fullness in July 2015 (the year following the gypsy moth outbreak) was $> 90\%$ at all sites (Nakajima unpublished data). Therefore, the effect of severe defoliation on the foliage biomass in the following year was undetectable using this method. Nevertheless, other aspects of performance, for example, diameter growth and carbon storage, may be affected for several years after a severe defoliation event (Kaitaniemi et al. 1999; Fajvan et al. 2008; Piper et al. 2015).

Eschtruth and Battles (2014) measured understory light availability in eight hardwood forests (dominated by oak, maple, and birch) that had experienced severe defoliation due to gypsy moth. The mean total transmitted radiation was 14% before the defoliation event, increased to 55% in the peak defoliation period, and then decreased to pre-defoliation levels as refoliation progressed. Similar results were reported by Collins (1961). Therefore, understory light availability is closely related to the defoliation and subsequent refoliation of canopy trees. The observed difference in crown fullness after refoliation between *F. crenata* and *Q. crispula* (Fig. 1) suggests that understory plants in *F. crenata* forests had higher light availability than those in *Q. crenata* forests until autumn leaf fall in the year of the defoliation event.

Differences in refoliation capability among species may exert different effects on forest ecosystem processes. In forests dominated by species that are severely defoliated with relatively low refoliation capability, such as *F. crenata*, growth of understory tree species and plant invasions (Collins 1961; Jedlicka et al. 2004; Eschtruth and Battles 2014) would be greatly promoted owing to increased light availability. The foraging behavior of herbivores would be affected by the difference in amount of refoliated leaves (Price 1991). These direct effects on plants and herbivores may cause cascading impacts at higher trophic levels (Bell and Whitmore 1997; Nakamura et al. 2006).

In conclusion, this study demonstrated that canopy trees of *Q. crispula* show higher refoliation capability than those of *F. crenata* under natural conditions. This capability is inferred to be associated with the disturbance tolerance and growth plasticity of oak species, which are characterized by large storage reserves and a recurrent growth flush pattern. Additional studies are needed to clarify the relationship between refoliation performance of canopy trees and ecophysiological aspects, such as stored reserves of carbohydrates and mineral nutrients, internal resource allocation, and photosynthetic efficiency.

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Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

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