Title

Resprouting responses to light environment and cutting season differ across resprouting stages and leaf habit in a heavy-snow Japanese beech forest.

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Abstract

Resprouting is a key mechanism of recovery after aboveground damage and strongly influences forest regeneration and dynamics. This is also true in heavy-snow Japanese beech forests, where canopy-gap formation and snow pressure damage woody species. Understanding how light environment and disturbance season shape resprouting is therefore essential for interpreting life-history strategies and informing forest management. To address this, we tested two hypotheses: (1) the stage-shift hypothesis, which predicts that the relative importance of ecological drivers shifts across resprouting stages, and (2) the leaf habit hypothesis, which predicts that the magnitude of seasonal effects on resprouting differs between evergreen and deciduous species.

We conducted winter and spring cutting experiments on woody species in the understory of a secondary Japanese beech forest and quantified resprout initiation and growth over two years. We tested the effects of stump size, light environment, and cutting season on resprouting responses and whether seasonal effects differed between leaf habits.

Resprout initiation was driven by stump size, whereas light environment and cutting season had little influence. In contrast, first-year growth was enhanced by stump size and winter cutting, while second-year growth was more strongly associated with post-cutting light environment, indicating a shift in resource dependence across resprouting stages. Winter cutting tended to have a stronger positive effect in deciduous than in evergreen species. Overall, the importance of ecological drivers changed across resprouting stages and between leaf habits, highlighting light availability and disturbance season as key determinants of resprout growth for forest management.

Keyword

Resprouting; Light environment; Cutting season; Leaf habit; Forest management

1.Introduction

Resprouting is the ability of plants to recover aboveground parts after disturbance and is generally faster than regeneration from seeds, largely relying on stored belowground reserves (Bellingham and Sparrow, 2000; Del Tredici, 2001). Resprouting therefore plays an important role in forest recovery. Resprouting ability varies among species in relation to life-history strategies (Shibata et al., 2014). However, the factors driving intra- and interspecific variation in resprouting ability remain debated. Improving our understanding of these factors is crucial for predicting forest dynamics and informing forest management (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Weigel and Peng, 2002).

Resprouting ability can be classified into several stages along the resprouting process, and the factors driving intra- and interspecific variation may differ among these stages (Moreira et al., 2012). Resprout initiation (i.e., the probability and number of resprout shoots produced following disturbance) depends largely on the availability of bud tissues on stems, roots, and rhizomes (Clarke et al., 2013; Pausas et al., 2016; Ott et al., 2019). In contrast, early resprout growth (i.e., the amount of resprout biomass produced shortly after disturbance) is primarily driven by stored belowground reserves (Kobe, 1997; Vesk and Westoby, 2004). Thus, stump size, which reflects both bud availability and belowground reserves, is a key determinant of resprout initiation and early resprout growth (Lévesque et al., 2011; Shibata et al., 2014; Matula et al., 2019; Zhang et al., 2021).

Beyond stump size, pre-disturbance light environment and disturbance season can also influence early resprout growth. Individuals growing under higher light availability are expected to exhibit stronger early resprout growth because greater photosynthetic carbon gain prior to disturbance can enhance the accumulation of non-structural carbohydrates, a major source of stored reserves (Gansert and Sprick, 1998; Hoch et al., 2003). In addition, early resprout growth is often higher following winter (dormant-season) disturbance than spring disturbance (Konstantinidis et al., 2005; Pelc et al., 2011; Robertson and Hmielowski, 2014; Vecchio et al., 2025), likely because stored reserves are largely retained to support maintenance respiration during winter dormancy, but are partially depleted in spring to support leaf flush and early growth (Kays and Canham, 1991; Cruz and Moreno, 2001; Barbaroux and Bréda, 2002). As resprouts develop leaves and become increasingly reliant on current photosynthesis, subsequent resprout growth is expected to depend more strongly on newly acquired photosynthate (Bowen and Pate, 1993; Schutz et al., 2009), thereby increasing the importance of the post-disturbance light environment. Taken together, these considerations suggest that the relative importance of ecological drivers shifts across stages of the resprouting process.

Evergreen and deciduous species represent contrasting life-history strategies in seasonal environments and may therefore differ in how disturbance season affects resprouting ability. Seasonal dynamics of carbohydrate storage differ between evergreen and deciduous leaf habits (Kozlowski, 1992; Furze et al., 2019). Deciduous species typically show pronounced seasonal changes associated with winter dormancy and spring leaf flush (Barbaroux and Bréda, 2002), whereas evergreen species often exhibit less seasonal variation (Mooney and Hays, 1973), although exceptions have been reported (Palacio et al., 2018). Consequently, the effect of disturbance season on early resprout growth is expected to be stronger in deciduous than in evergreen species.

Resprouting in woody species has been widely studied in regions experiencing frequent large disturbances, such as wildfires and droughts, where it is recognized as a key persistence strategy (Pausas and Keeley, 2014; Vilagrosa et al., 2014; Zeppel et al., 2015; Pausas et al., 2016). In contrast, resprouting has received less attention in relatively stable forest ecosystems where large disturbances are rare, including forests in snowy environments. Nevertheless, in such ecosystems resprouting can serve as an effective life-history strategy in response to snow damage and gap formation, which constitute the dominant disturbance regime (Kamitani, 1986; Hara, 1987; Homma, 1997). Therefore, examining how light environment and disturbance season influence stage-specific resprouting is essential for evaluating the generality of its ecological drivers across disturbance regimes.

In this study, we investigated how light environment and disturbance season affect resprouting ability in woody species occurring in *Fagus crenata* forests in a heavy-snowfall region where large disturbances such as wildfire are infrequent. We classified the resprouting process into three stages—resprout initiation, first-year resprout growth, and second-year resprout growth—corresponding to the response variables summarized in Table 1. We then examined how the effects of light environment and disturbance season vary among resprouting stages, leaf habits, and species, thereby testing stage-dependent shifts in ecological drivers of resprouting and their implications for life-history strategies of constituent species in stable beech forests. Based on these considerations, we tested the following hypotheses.

Stage-shift hypothesis

The relative importance of ecological drivers shifts across stages of the resprouting process.

H1: Resprout initiation (i.e., the probability of resprouting and the number of resprouts produced) is primarily determined by stump size, reflecting bud availability, and is expected to be less sensitive to light environment and disturbance season.

H2: First-year resprout growth (i.e., total basal area and maximum height after the first growing season) is influenced by stump size, pre-disturbance light environment, and disturbance season, as early growth depends largely on stored belowground reserves accumulated prior to disturbance.

H3: Second-year resprout growth (i.e., total basal area and maximum height after two growing seasons) is influenced more strongly by post-disturbance light environment than by pre-disturbance conditions, as growth at this stage increasingly depends on photosynthesis by newly developed leaves.

Leaf habit hypothesis

The magnitude of seasonal effects on resprouting differs between leaf habits.

H4: The effect of disturbance season on early resprout growth is expected to be stronger in deciduous than in evergreen species, reflecting greater seasonal variation in stored belowground reserves in deciduous species.

2. Materials and Methods

2.1. Study site

The study was conducted in a secondary beech (*Fagus crenata)* forest in Oshirakawa, Uonuma City, Niigata Prefecture, Japan (Fig. 1). This forest has been managed by local communities for timber production through overstory thinning of beech trees and understory vegetation clearing. Based on records from the Sumon Local Meteorological Observatory, the 30-year means (1996–2025) of mean annual temperature and precipitation are 11.4°C and 3,057 mm, respectively. Mean annual cumulative snowfall is 1,124 cm, with snow cover typically persisting from December to May and occasionally until June in years of late melt. Elevation ranges from 530 to 710 m a.s.l. The canopy layer is dominated by *F. crenata* (>90%), with minor contributions from *Acer pictum* subsp. *mayrii*. The shrub layer is well developed and consists primarily of deciduous shrubs, including *Lindera praecox*, *Lindera umbellata* var. *membranacea*, and *Clethra barbinervis*. Evergreen shrubs adapted to heavy snow conditions, such as *Camellia rusticana*, *Daphniphyllum macropodum* subsp. *humile*, and *Aucuba japonica* var. *borealis* are also present (Ino et al., 2003).

2.2. Study design and datasets

To examine how pre- and post-disturbance light environments and disturbance seasons jointly shape stage-specific resprouting, we conducted cutting experiments under contrasting light conditions and seasons. To capture different aspects of this process, we compiled two complementary datasets that differed in taxonomic breadth, light metrics, and monitoring duration.

Dataset 1 focused on stage-dependent shifts in resprouting over two growing seasons. It included eight common woody species occurring in the shrub layer of beech forests (seven deciduous and one evergreen; Table 2). Individuals were sampled from three stands representing contrasting stand-level light environments (Fig. 1c). Of the three stands, the recently thinned stand experienced canopy thinning immediately before the cutting treatment, generating a pronounced shift from pre-disturbance to post-disturbance light conditions. This design allowed us to test whether first-year resprout growth was more strongly influenced by pre-disturbance light availability, whereas second-year resprout growth reflected post-disturbance light environments. Cutting was conducted in winter (December 2023, immediately after complete leaf fall in deciduous species) and in spring (June 2024, immediately after full leaf expansion). Resprouting responses were measured in late September 2024 (one growing season after cutting) and again in late September 2025 (two growing seasons after cutting).

Dataset 2 expanded taxonomic coverage to 16 species (11 deciduous and 5 evergreen; Table 2) to enable explicit tests of leaf habit differences. In addition, post-disturbance light availability was quantified at the individual level, allowing a finer-scale assessment of light-resprouting relationships. Cutting was conducted in November 2024 and June 2025, and resprouting responses were measured in late September 2025 (one growing season after cutting).

Although three canopy-tree species (*F. crenata*, *A. pictum* subsp. *mayrii*, and *Magnolia obovata*) were included, only juvenile individuals occurring in the understory were selected (basal diameter ≤ 6.58 cm, 6.81 cm, and 9.50 cm, respectively), ensuring comparability with shrub-layer species.

2.2.1. Individual measurements and cutting treatment

For each individual, stem size was measured approximately 3 cm above ground using a digital caliper (0.01 mm precision). Two perpendicular diameters were recorded, and basal area (mm^2) was calculated assuming an elliptical cross-section. This value was used as an index of stump size (hereafter, stump basal area). Individuals were labeled and cut at approximately 3 cm above ground using hand saws or pruning shears, leaving a stump. To encompass a broad size range, individuals were stratified into five stem-diameter classes (0–5, 5–10, 10–20, 20–40, and ≥40 mm), with at least one individual per class per species sampled whenever possible. For multi-stemmed individuals, all stems that were visually identifiable as belonging to the same aboveground clump were cut. Subsequent measurements restricted to the largest stem and to resprouting shoots originating from that stem.

2.2.2. Resprouting measurements

Resprouting responses were assessed in late September following each growing season (Dataset 1: 2024 and 2025; Dataset 2: 2025).

For each resprout shoot, two perpendicular diameters at the base were measured with a digital caliper (0.01 mm precision), and shoot basal area (mm^2) was calculated assuming an elliptical cross-section. Total basal area of resprouts per individual, calculated as the sum of all shoots originating from the largest stem, was used as an index of resprout biomass production. Maximum resprout height was defined as the height of the tallest shoot measured from the stump base (1 cm precision). In some species (e.g., *Chengiopanax sciadophylloides*), resprouts occasionally consisted of leaves emerging directly from the stump without shoot elongation. Such resprouts (< 1 cm in length) were included in the number of resprouts but excluded from calculations of total basal area and maximum height. Accordingly, these metrics were calculated only for resprouts ≥ 1 cm in length.

2.2.3. Light environment measurements

In Dataset 1, we quantified stand-level light environments across three stands differing in thinning history, thereby capturing variation in canopy openness (Fig. 1c). The stands comprised: (1) an unthinned stand with a closed canopy and no canopy cutting for at least 30 years; (2) a recently thinned stand, where canopy thinning was conducted in autumn 2023 approximately one month prior to cutting treatment, resulting in an abrupt shift from pre- to post-disturbance light conditions; and (3) a previously thinned stand, where canopy thinning had been conducted during 2019–2021 (i.e., 2–4 years prior to cutting). Thinning in 2019 was carried out in June, whereas thinning in 2020, 2021, and 2023 was conducted from October to November. To quantify the light environment, we measured integrated photosynthetic photon flux density (PPFD; mol m^{-2} day^{-1}) using a light-sensitive photodegradable film (OptLeaf R-3D; Taisei Fine Chemical Co., Ltd., Japan). At each stand, films were installed horizontally 15 cm above the forest floor at 16 points and exposed for 8–11 days in summer (27 July–4 August 2023; 23 July–3 August 2024; 25 August–4 September 2025). Film absorbance was measured before and after exposure using a dedicated reader (D-meter; Taisei Fine Chemical Co., Ltd., Japan), and PPFD was calculated from the degree of fading using the calibration curve provided in the manufacturer's manual. Mean PPFD was calculated for each stand by averaging values across the 16 measurement points.

In Dataset 2, light availability was quantified at the individual level to capture fine-scale variation in canopy structure. Because no additional canopy thinning occurred, the light environment was assumed to remain stable between pre- and post-disturbance periods; therefore, only post-disturbance light availability was assessed. Hemispherical photographs were taken above each individual in early September under leaf-on conditions using a compact digital camera (TG-7; OLYMPUS) equipped with a conversion lens (FCON-T02; OLYMPUS). The camera was mounted on a tripod at 0.5 m above ground and oriented vertically upward. Mean canopy openness was calculated using Canopon2 (developed by Akio Takenaka; Version 2.03). When direct sunlight appeared in images, overexposed areas were masked prior to analysis.

2.3. Data analysis

2.3.1. Testing the stage-shift hypothesis (Dataset 1)

In Dataset 1, we tested the stage-shift hypothesis by examining how the effects of stump size, pre- and post-disturbance light environments, and cutting season varied across resprouting stages. Resprouting responses were analyzed after one and two growing seasons following cutting. We fitted Bayesian generalized linear mixed models (GLMMs) for four response variables after one growing season (probability of resprouting, number of resprouts, total basal area of resprouts, and maximum resprout height) and for two response variables after two growing seasons (total basal area of resprouts and maximum resprout height).

The model structure was:

Resprouting response ~ log10(stump basal area) + pre-cutting PPFD + post-cutting PPFD + cutting season + (1 + log10(stump basal area) + pre-cutting PPFD + post-cutting PPFD + cutting season || species)

Resprouting probability was modeled using a binomial distribution with a logit link. Number of resprouts (count data ≥ 0) was modeled using a Poisson distribution with a log link. Total basal area of resprouts and maximum resprout height were $\log_{10}$-transformed and modeled assuming Gaussian errors with an identity link.

Stump size was represented by $\log_{10}$-transformed stump basal area. Light environment was quantified as stand-level mean integrated photosynthetic photon flux density (PPFD; mol m^{-2} day^{-1}). Pre-disturbance light environment was represented by PPFD measured in 2023, whereas post-disturbance light environment was represented by PPFD measured in 2024 for first-year analyses and by the mean PPFD across 2024–2025 for second-year analyses, reflecting consistent relative differences among stands. All continuous predictors were standardized (z-scored) prior to analysis. Cutting season was treated as a two-level factor (winter vs spring; spring as reference). Species was included as a random effect with uncorrelated random intercepts and slopes to improve convergence and avoid overparameterization.

2.3.2. Testing the leaf habit hypothesis (Dataset 2)

In Dataset 2, we evaluated the effects of stump size, individual-level light environment, cutting season, and leaf habit (deciduous vs evergreen) on resprout initiation and first-year resprout growth. To test whether seasonal effects differed between leaf habits, we included an interaction between cutting season and leaf habit. We fitted Bayesian GLMMs for four response variables: probability of resprouting, number of resprouts, total basal area of resprouts, and maximum resprout height.

The model structure was:

Resprouting response ~ log10(stump basal area) + canopy openness + cutting season × leaf habit + (1 + log10(stump basal area) + canopy openness + cutting season || species)

Log_{10}-transformed stump basal area and canopy openness were standardized (z-scored) prior to analysis. Light environment was represented by canopy openness derived from hemispherical photographs. Cutting season (winter vs spring; spring as reference) and leaf habit (deciduous vs evergreen; evergreen as reference) were treated as two-level factors. Distributional assumptions and link functions followed those used in Dataset 1. Species was included as a random effect with uncorrelated random intercepts and slopes to improve convergence and avoid overparameterization, whereas leaf habit and its interaction with cutting season were included only as fixed effects.

2.3.3. Model fitting

All Bayesian models were fitted in R (version 4.4.1; R Core Team, 2024) using the *brms* package (Bürkner, 2017). Four chains were run with 6,000 iterations each (5,000 warm-up), using adapt_delta = 0.97, and max_treedepth = 15; all other settings were kept at defaults. Convergence was assessed using $\hat{R} \leq 1.01$ (Vuong et al., 2020).

3. Results

3.1. Testing the stage-shift hypothesis (Dataset 1)

Drivers of resprouting responses varied markedly across stages following cutting. At the resprout initiation stage, stump basal area had a significant positive effect on the number of resprouts, but not on the probability of resprouting (Table 3; Fig. 2a, b). In contrast, neither pre- nor post-cutting PPFD nor cutting season had significant effects on either response (Table 3; Fig. 3a, b; Fig. 4a, b).

For first-year resprout growth, stump basal area had significant positive effects on both total basal area of resprouts and maximum resprout height (Table 3; Fig. 2c, d). Neither pre- nor post-cutting PPFD had significant effects on either growth response (Table 3; Fig. 3c, d). In contrast, winter cutting was associated with significantly greater total basal area of resprouts and maximum resprout height than spring cutting (Table 3; Fig. 4c, d).

For second-year resprout growth, stump basal area remained a significant positive predictor of both total basal area of resprouts and maximum resprout height, whereas post-cutting PPFD had a significant positive effect only on total basal area of resprouts (Table 3; Fig. 2e, f; Fig. 3e, f). In contrast, pre-cutting PPFD and cutting season had no significant effects on either response (Table 3; Fig. 2e, f; Fig. 4e, f).

3.2. Testing the leaf habit hypothesis (Dataset 2)

In Dataset 2 (16 species), stump size had a significant positive effect on resprout initiation and first-year resprout growth (Table 4; Fig. 5). Mean canopy openness and winter cutting also had significant positive effects on total basal area of resprouts, indicating greater biomass production in brighter environments and under winter cutting. The interaction between cutting season and leaf habit was not statistically significant for any resprouting response, indicating no clear evidence that seasonal effects differed between deciduous and evergreen species. Nevertheless, response patterns differed between leaf habits. For both the probability of resprouting and the number of resprouts, winter cutting showed positive but non-significant effects in both evergreen and deciduous species (Fig. 5a, b). For total basal area of resprouts, winter cutting had a significant positive effect in both leaf habits, with a tendency toward a larger effect in deciduous species (Fig. 5c). For maximum resprout height, winter cutting had a significant positive effect in deciduous species, whereas the effect in evergreen species was positive but not significant (Fig. 5d). This pattern indicates that the combined effect of the main winter-cutting coefficient and its interaction resulted in a significant response only in deciduous species. Overall, although statistical support for the interaction was lacking, the consistently larger effect sizes and the asymmetric significance patterns suggest that seasonal effects on early resprout growth may be stronger in deciduous than in evergreen species, consistent with the leaf habit hypothesis.

Consistent patterns were also evident when species-specific effects of winter cutting were examined, incorporating the fixed effect of winter cutting, its interaction with leaf habit, and species-level random effects. For total basal area of resprouts, all 11 deciduous species showed significant positive effects of winter cutting. In contrast, one of the five evergreen species showed no significant effect, and the remaining four showed significant positive effects, with a smaller mean effect size than in deciduous species (Fig. 6a). For maximum resprout height, 9 out of 11 deciduous species showed significant positive effects of winter cutting. In contrast, none of the evergreen species showed significant effects, despite consistently positive estimates (Fig. 6b). These species-level patterns further support the interpretation that seasonal effects on early resprout growth tend to be stronger in deciduous than in evergreen species.

4. Discussion

4.1. Drivers of resprout initiation (H1)

H1 predicted that resprout initiation is primarily determined by stump size and less sensitive to light environment and disturbance season. Our results were broadly consistent with this prediction. Stump basal area had a significant positive effect on the number of resprouts, but not on the probability of resprouting (Table 3; Fig. 2a, b), indicating that larger individuals tend to produce more resprout shoots but are not necessarily more likely to resprout. The positive relationship between stump size and resprout number, as reported in previous studies (Hytönen, 2019; Dinh et al., 2019), likely reflects greater availability of bud-bearing tissues and a higher capacity to support multiple resprout shoots, consistent with the role of the bud bank in resprouting dynamics (Klimešová and Klimeš, 2007; Ott et al., 2019).

In contrast, the high overall probabilities of resprouting observed in the studied species (64–100%) suggest that the probability of resprouting is largely governed by species-specific traits rather than variation in stored reserves or stump size. This pattern is consistent with the high resprouting capacity reported for understory shrub species in *Fagus crenata* forests (Hara et al., 2004).

Neither light environment nor cutting season had significant effects on resprout initiation, indicating that external environmental conditions play a limited role at this stage. Overall, these results suggest that resprout initiation is constrained more by intrinsic biological capacity (i.e., bud availability) than by external environmental conditions.

4.2. Drivers of first-year resprout growth (H2)

H2 predicted that first-year resprout growth is influenced by stump size, pre-disturbance light environment, and disturbance season. Our results partially supported this prediction. Stump basal area had significant positive effects on both total basal area of resprouts and maximum resprout height, indicating that larger individuals showed greater first-year resprout growth (Table 3; Fig. 2c, d). This supports the idea that stump size reflects belowground reserve availability and the capacity to sustain early resprout development (Lévesque et al., 2011; Shibata et al., 2014; Matula et al., 2019).

In contrast, pre-cutting light environment had no significant effect on either first-year resprout growth variable. Although higher light availability before disturbance was expected to enhance the accumulation of non-structural carbohydrates (NSC) and thereby promote early resprout growth, our results do not support a strong linkage between pre-disturbance light environment and first-year resprout growth. This is consistent with previous findings showing that NSC levels can be maintained even under low light environments (Weber et al., 2019), suggesting that the relationship between light availability and reserve accumulation may be weaker than commonly assumed.

Winter cutting, by contrast, significantly enhanced both total basal area of resprouts and maximum resprout height (Table 3; Fig. 4c, d), indicating that cutting season strongly influenced early resprout growth, consistent with previous studies (Robertson and Hmielowski, 2014; Vecchio et al., 2025). Because winter at our study site corresponds to a dormant period, stored reserves are likely to be relatively high, whereas in spring they may be partially depleted by leaf flush. This seasonal difference in reserve availability provides a plausible explanation for the observed pattern.

Overall, H2 was partially supported: stump size and disturbance season influenced first-year resprout growth, whereas the predicted effect of pre-disturbance light environment was not detected.

4.3. Drivers of second-year resprout growth and stage-dependent shifts (H3)

H3 predicted that second-year resprout growth would be more strongly influenced by post-disturbance light environment than by pre-disturbance conditions. Our results were broadly consistent with this prediction. After two growing seasons, post-cutting light environment had a significant positive effect on total basal area of resprouts, whereas pre-cutting light environment and winter cutting did not (Table 3; Fig. 3e; Fig. 4e). In contrast, none of these factors significantly affected maximum resprout height.

A comparison across growth stages revealed a clear shift in the relative importance of ecological drivers. After one growing season, winter cutting significantly enhanced total basal area of resprouts, whereas post-cutting light environment had no significant effect (Fig. 3c; Fig. 4c). By the second growing season, this pattern was reversed: the effect of cutting season disappeared, while the effect of post-cutting light environment became significant (Fig. 3e; Fig. 4e).

This stage-dependent shift is consistent with a transition in resource dependence during resprout development. Early resprout growth is likely supported primarily by stored belowground reserves, whereas subsequent growth depends increasingly on photosynthates produced by newly developed leaves (Schutz et al., 2009). The lack of significant effect of post-cutting light environment on maximum resprout height suggests that height growth may be more strongly constrained by structural or developmental factors established during early growth, such as stump size and initial resprout development, rather than by environmental conditions at this stage. This interpretation is consistent with previous findings that early growth strongly predicts subsequent height growth (Swaim et al., 2016). Accordingly, the positive effect of winter cutting on first-year resprout growth may have indirectly influenced subsequent height development, potentially obscuring the direct effect of post-disturbance light environment.

Overall, these results demonstrate a stage-dependent shift in the drivers of resprout growth, from reserve-related factors to light-dependent processes, consistent with the stage-shift hypothesis.

4.4. Leaf-habit hypothesis (H4)

H4 predicted that the effect of disturbance season on early resprout growth is expected to be stronger in deciduous than in evergreen species. Our results provided partial but consistent support for this prediction. Although the interaction between cutting season and leaf habit was not statistically significant, multiple lines of evidence indicated that seasonal effects on early resprout growth tended to be stronger in deciduous than in evergreen species.

At the model level, winter cutting had a significant positive effect on total basal area of resprouts, whereas the interaction term remained non-significant (Table 4). However, comparisons with leaf habits revealed that deciduous species tended to show larger increases in total basal area of resprouts and maximum resprout height under winter cutting than evergreen species (Fig. 5c, d).

This pattern was further reinforced by species-level estimates incorporating both fixed and random effects. For total basal area of resprouts, all deciduous species showed significant positive responses to winter cutting, whereas fewer evergreen species did so and with smaller effect sizes (Fig. 6a). For maximum resprout height, significant positive effects were detected only in deciduous species (Fig. 6b).

The lack of statistical significance in the interaction term may partly reflect limited statistical power, as evergreen species were represented by only five species in our dataset. In *Fagus crenata* forests, the diversity of evergreen woody species is inherently low, making it difficult to increase sample size within this system. Therefore, further tests of this hypothesis in forest ecosystems where deciduous and evergreen species coexist more evenly will be necessary to robustly evaluate the generality of leaf habit-dependent seasonal effects.

In addition, the underlying mechanism assumed in H4—that seasonal variation in belowground stored reserves is greater in deciduous than in evergreen species—remains to be explicitly tested in this study system. Previous studies have reported inconsistent patterns in seasonal dynamics of belowground storage between leaf habits, depending on species, organs and environmental context (Martínez-Vilalta et al., 2016; Palacio et al., 2018). Direct measurements of seasonal changes in stored reserves will therefore be necessary to determine whether deciduous species indeed exhibit greater seasonal variability than evergreen species at this site.

4.5. Implications for forest management

In the study site, overstory thinning is conducted to harvest canopy beech trees and improve light availability at the forest floor, thereby promoting beech regeneration. However, rapid recovery of shrub-layer species via resprouting restores shading at the forest floor, offsetting the intended effects of thinning. As a result, repeated understory cutting is required to maintain favorable light conditions and reduce competition with regenerating beech seedlings, which imposes substantial labor and economic costs (Yildiz et al., 2007; De Lombaerde et al., 2021). These challenges highlight the difficulty of shrub-layer management and underscore the need for more efficient strategies.

Our results indicate that resprout initiation is difficult to control: the probability of resprouting was high across species, and neither light environment nor cutting season had significant effects on resprout initiation (Table 3; Fig. 2). In contrast, resprout growth was significantly affected by both post-disturbance light environment and cutting season, suggesting that management interventions should focus on suppressing resprout growth rather than preventing resprout initiation.

Specifically, reducing overstory thinning intensity may limit light availability at the forest floor and thereby suppress resprout growth, particularly in stands dominated by light-demanding deciduous species. In addition, conducting understory cutting shortly after leaf-out may reduce resprout growth compared with winter or autumn cutting. In contrast, seasonal effects were weaker in evergreen species, suggesting that cutting season may be less critical in stands dominated by evergreen shrubs.

Beyond suppression, these findings also have implications for the utilization of resprouting species. For example, *Lindera umbellata*, which is used for essential oils and medicinal purposes (Maeda et al., 2013, Kusumoto et al., 2022), may achieve higher biomass production through resprouting by optimizing light conditions and cutting season.

Overall, our findings highlight that controlling light availability and optimizing cutting season are key levers for regulating resprout growth. These approaches may contribute not only to more efficient understory management in beech forests but also to the management and utilization of resprouting species in seasonal forest ecosystems more broadly.

5. Conclusions

In this study, resprout initiation and subsequent growth of woody species in a snowy beech forest were governed by different ecological drivers across stages of the resprouting process. Resprout initiation was influenced mainly by stump size, whereas light environment and cutting season had little effect, providing broad support for H1 and indicating that resprout initiation is difficult to control through management interventions.

First-year resprout growth was enhanced by stump size and winter cutting, whereas pre-disturbance light environment showed no clear effect, indicating partial support for H2. In contrast, second-year resprout growth was more strongly associated with post-disturbance light environment than with pre-disturbance conditions, supporting H3 and suggesting a shift in resource dependence from stored reserves to newly acquired photosynthates as resprouts developed.

A tendency was observed for winter cutting to have a stronger positive effect on early resprout growth in deciduous than in evergreen species, although support for H4 was limited and requires further testing under broader species compositions.

Overall, these results indicate that the relative importance of ecological drivers changes across resprout growth stages and differs among leaf habits. From a management perspective, our findings suggest that interventions should focus on regulating resprout growth rather than controlling resprout initiation. In particular, light availability and cutting season are key determinants of resprout growth. This framework may contribute not only to more efficient understory management but also to enhancing biomass production of resprouting species in seasonal forest ecosystems.

. Funding resources

This work was supported by JSPS KAKENHI (23K13981; 26K08884) and the Environment Research and Technology Development Fund (JPMEERF23S12119).

. CRediT authorship contribution statement

Kotaro Masuda: Writing – review & editing, Writing – original draft, Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Visualization. **Rei Shibata:** Writing – review & editing, Writing – original draft, Conceptualization, Methodology, Validation, Investigation, Data curation, Visualization, Supervision, Project administration, Funding acquisition.

. Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT (OpenAI) for English editing to improve the clarity and readability of the manuscript. After using this tool, the authors carefully reviewed and edited the content as needed and take full responsibility for the content of the published article.

. Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

. Acknowledgments

We thank Dr. Michio Oguro for valuable advice on data handling and analysis. We are also grateful to Dr. Masami Tsukahara, Mr. Tatsuki Tanaka, and members of the Niigata Prefectural Forest Research Institute for their assistance with field surveys and collaboration. We further thank the members of the Snow Beech Project for providing access to study sites and permission to conduct fieldwork.

. Data availability

Data are available at Zenodo (DOI: xxxxxxx), and will be made publicly available upon acceptance.

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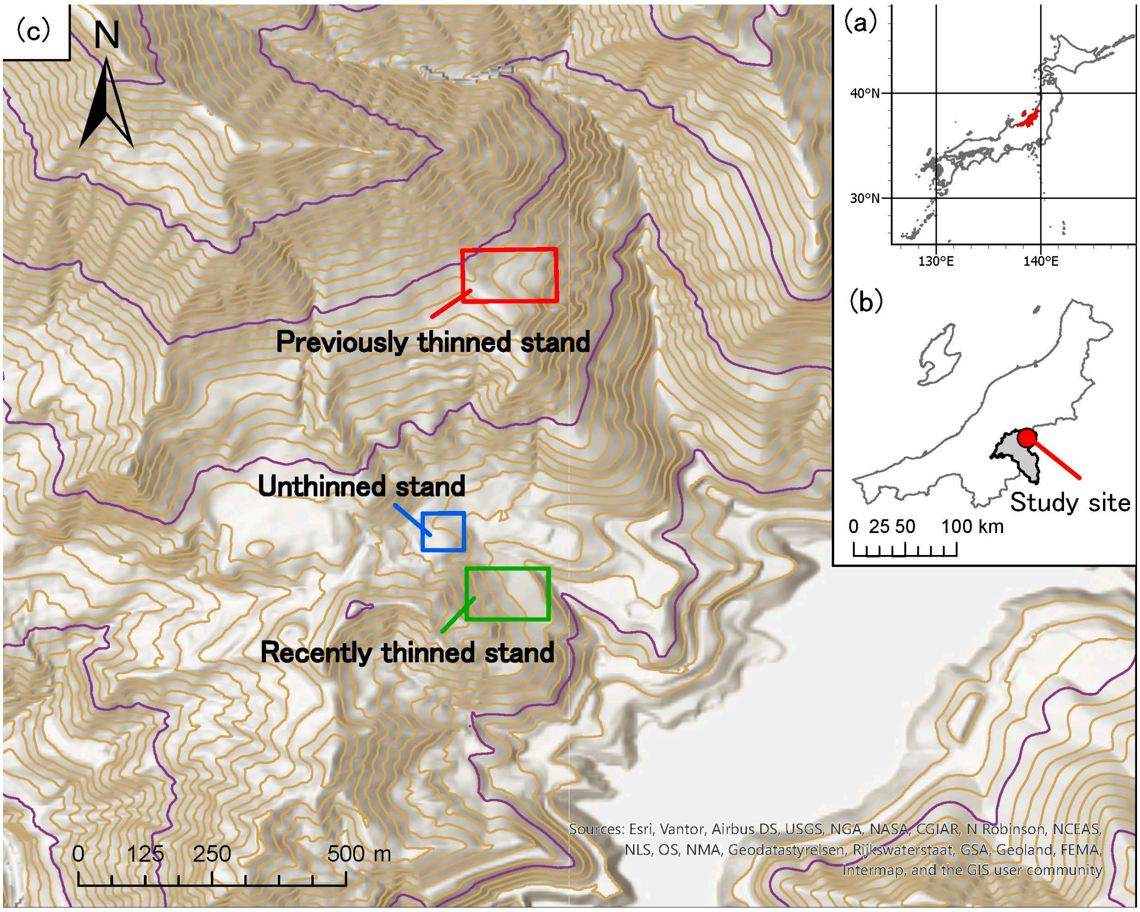
. Figures

Fig. 1: Study location. (a) Niigata Prefecture, Japan, shown in red. (b) Oshirakawa (red circle) in Uonuma City (gray), Niigata Prefecture. (c) Three study stands in Oshirakawa: an unthinned stand (blue), a recently thinned stand (thinned approximately one month prior to cutting; green), and a previously thinned stand (thinned 2–4 years prior to cutting; red).



Sources: Esri, Vantor, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap, and the GIS user community

Fig. 2: Estimated effects of stump basal area (stump BA, $\log_{10}$-transformed), pre-cutting PPFD (pre-PPFD), post-cutting PPFD (post-PPFD), and cutting season (winter cutting vs spring; spring as reference) on resprouting responses in Dataset 1. Bayesian generalized linear mixed model estimates are shown for resprout initiation: (a) probability of resprouting; (b) number of resprouts; first-year resprout growth: (c) total basal area of resprouts; (d) maximum resprout height; second-year resprout growth: (e) total basal area of resprouts; (f) maximum resprout height. Points represent posterior means, and vertical lines represent 95% credible intervals. Filled circles indicate significant effects whose 95% credible intervals do not include zero, whereas open circles indicate non-significant effects. The dashed line indicates zero effect.

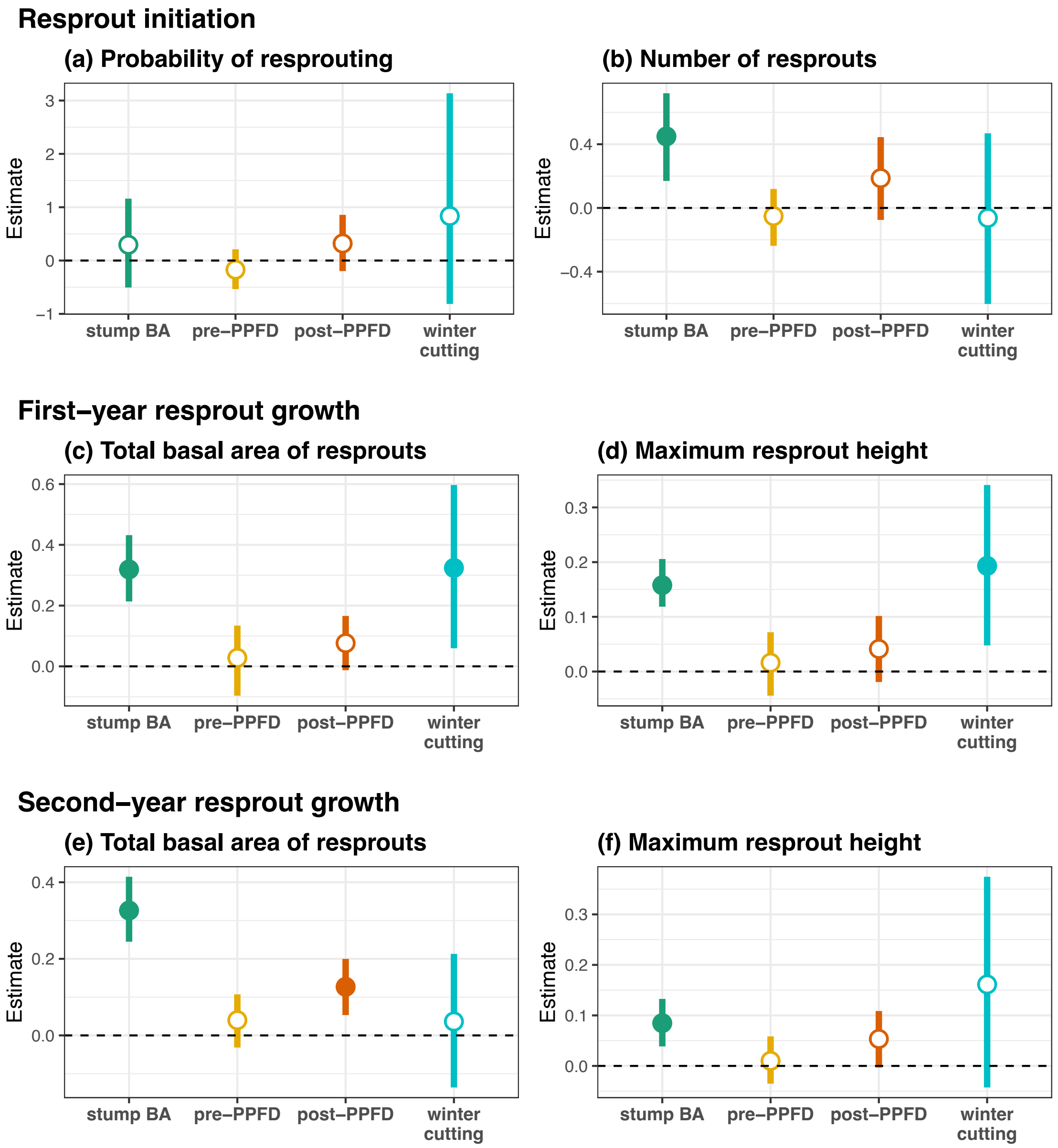

Resprout initiation
(a) Probability of resprouting
(b) Number of resprouts
First–year resprout growth
(c) Total basal area of resprouts
(d) Maximum resprout height
Second–year resprout growth
(e) Total basal area of resprouts
(f) Maximum resprout height
Estimate
3
2
1
0
−1
0.4
0.0
−0.4
0.6
0.2
0.3
0.1
stump BA
pre–PPFD
post–PPFD
winter cutting

Fig. 3: Effects of post-cutting PPFD on the relationships between stump basal area and resprouting responses across growth stages in Dataset 1. Resprout initiation: (a) probability of resprouting; (b) number of resprouts; first-year resprout growth: (c) total basal area of resprouts; (d) maximum resprout height; second-year resprout growth: (e) total basal area of resprouts; (f) maximum resprout height. Points represent observed values for spring-cut individuals. Lines represent posterior mean predictions from Bayesian generalized linear mixed models, and shaded bands represent 95% credible intervals. Predictions were generated with cutting season fixed at spring, and colors denote the lowest and highest observed post-cutting PPFD values. Total basal area of resprouts, maximum resprout height, and stump basal area are shown on a log10 scale. Numerical values in each panel show posterior means and 95% credible intervals for the effect of post-cutting PPFD; asterisks (*) indicate significant effects whose 95% credible intervals do not include zero.

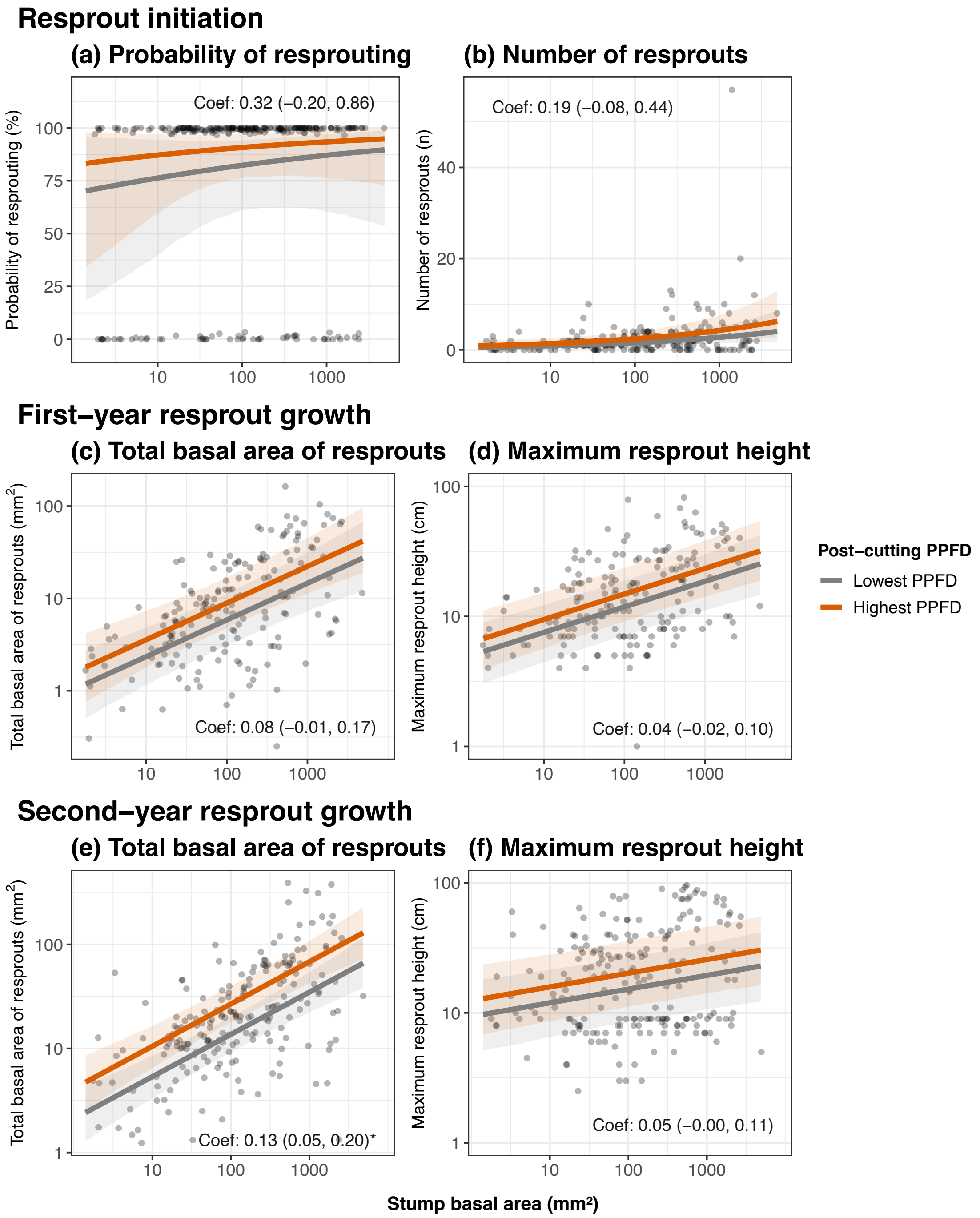

Resprout initiation
(a) Probability of resprouting
Coef: 0.32 (−0.20, 0.86)
Probability of resprouting (%)
100
75
50
25
0
10
100
1000
(b) Number of resprouts
Coef: 0.19 (−0.08, 0.44)
Number of resprouts (n)
40
20
0
10
100
1000
First−year resprout growth
(c) Total basal area of resprouts
Total basal area of resprouts (mm²)
100
10
1
Coef: 0.08 (−0.01, 0.17)
10
100
1000
(d) Maximum resprout height
Maximum resprout height (cm)
100
10
1
Coef: 0.04 (−0.02, 0.10)
10
100
1000
Post−cutting PPFD
Lowest PPFD
Highest PPFD
Second−year resprout growth
(e) Total basal area of resprouts
Total basal area of resprouts (mm²)
100
10
1
Coef: 0.13 (0.05, 0.20)*
10
100
1000
(f) Maximum resprout height
Maximum resprout height (cm)
100
10
1
Coef: 0.05 (−0.00, 0.11)
10
100
1000
Stump basal area (mm²)

Fig. 4: Effects of cutting season on the relationships between stump basal area and resprouting responses across growth stages in Dataset 1. Resprout initiation: (a) probability of resprouting; (b) number of resprouts; first-year resprout growth: (c) total basal area of resprouts; (d) maximum resprout height; second-year resprout growth: (e) total basal area of resprouts; (f) maximum resprout height. Points represent observed values for individuals. Lines represent posterior mean predictions from Bayesian generalized linear mixed models for each cutting season, and shaded bands represent 95% credible intervals. Colors denote cutting season (winter vs spring). Total basal area of resprouts, maximum resprout height, and stump basal area are shown on a log10 scale. Numerical values in each panel show posterior means and 95% credible intervals for the effect of winter cutting (spring as reference); asterisks (*) indicate significant effects whose 95% credible intervals do not include zero.

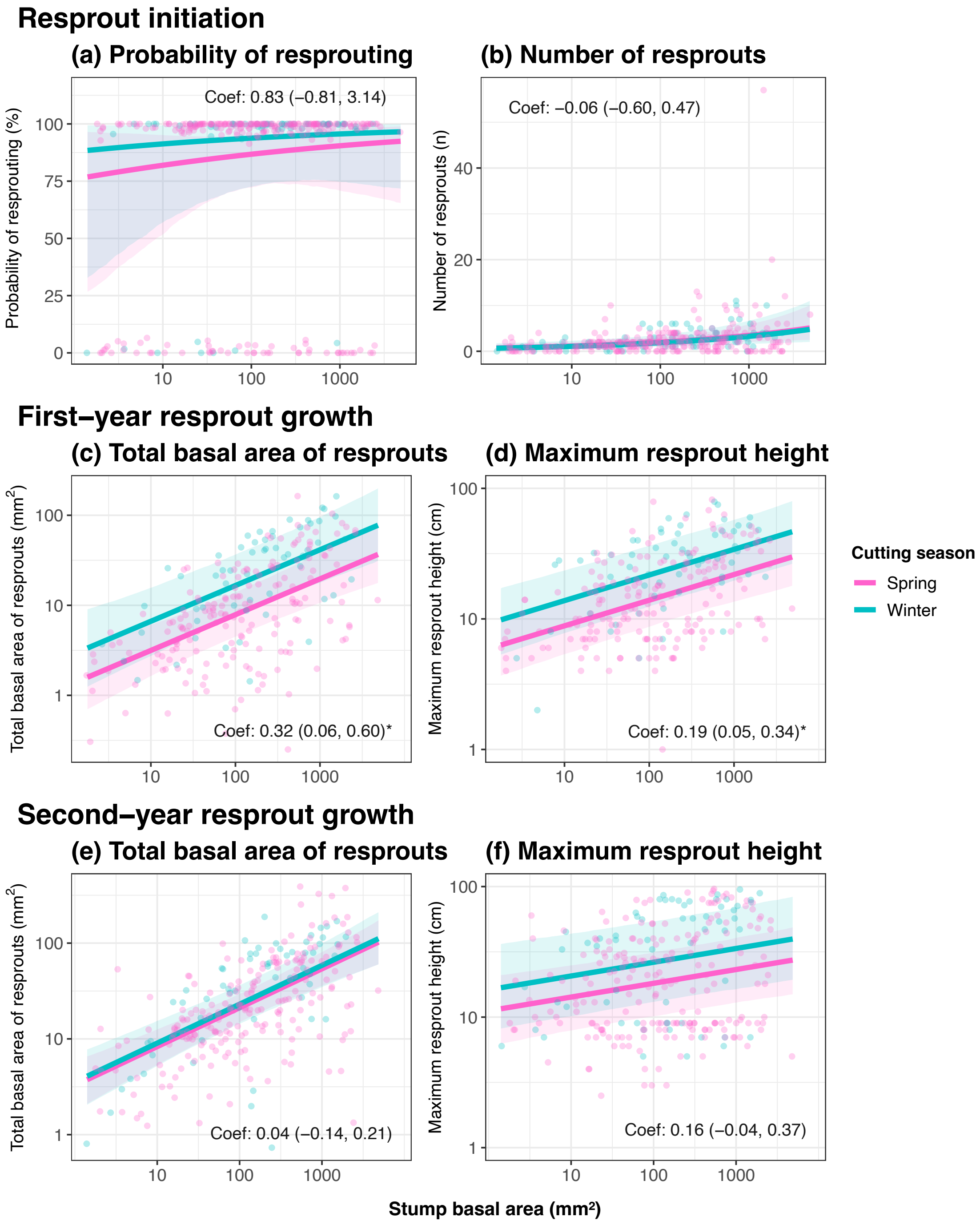
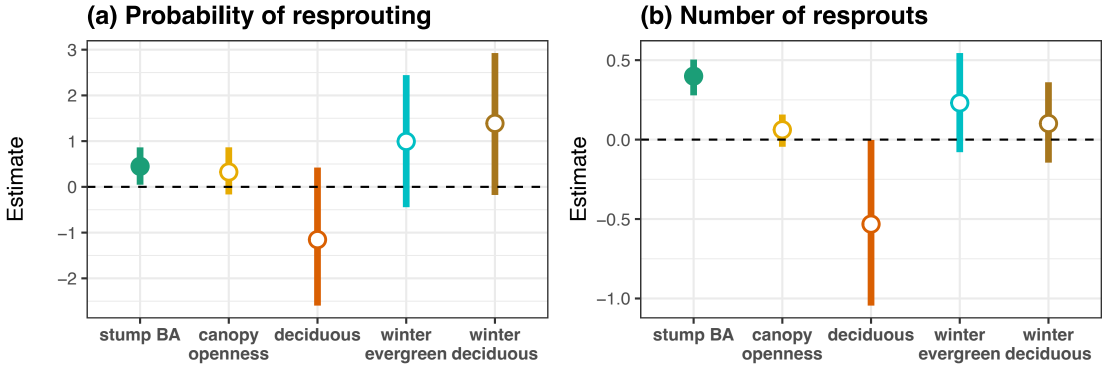

Resprout initiation
(a) Probability of resprouting
Coef: 0.83 (−0.81, 3.14)
Probability of resprouting (%)
100
75
50
25
0
10
100
1000
(b) Number of resprouts
Coef: −0.06 (−0.60, 0.47)
Number of resprouts (n)
40
20
0
10
100
1000
First−year resprout growth
(c) Total basal area of resprouts
Total basal area of resprouts (mm^2)
100
10
1
Coef: 0.32 (0.06, 0.60)*
10
100
1000
(d) Maximum resprout height
Maximum resprout height (cm)
100
10
1
Coef: 0.19 (0.05, 0.34)*
10
100
1000
Cutting season
Spring
Winter
Second−year resprout growth
(e) Total basal area of resprouts
Total basal area of resprouts (mm^2)
100
10
1
Coef: 0.04 (−0.14, 0.21)
10
100
1000
(f) Maximum resprout height
Maximum resprout height (cm)
100
10
1
Coef: 0.16 (−0.04, 0.37)
10
100
1000
Stump basal area (mm^2)

Fig. 5: Estimated effects of stump basal area (stump BA, $\log_{10}$-transformed), canopy openness, leaf habit (deciduous), and winter cutting effects by leaf habit (winter evergreen; winter deciduous) on resprouting responses in Dataset 2. Here, "winter evergreen" and "winter deciduous" represent winter cutting effects in evergreen and deciduous species, respectively. Bayesian generalized linear mixed model estimates are shown for resprout initiation: (a) probability of resprouting; (b) number of resprouts; first-year resprout growth: (c) total basal area of resprouts; (d) maximum resprout height. Points represent posterior means and vertical lines represent 95% credible intervals. Filled circles indicate significant effects whose 95% credible intervals do not include zero, whereas open circles indicate non-significant effects. The dashed line indicates zero effect.

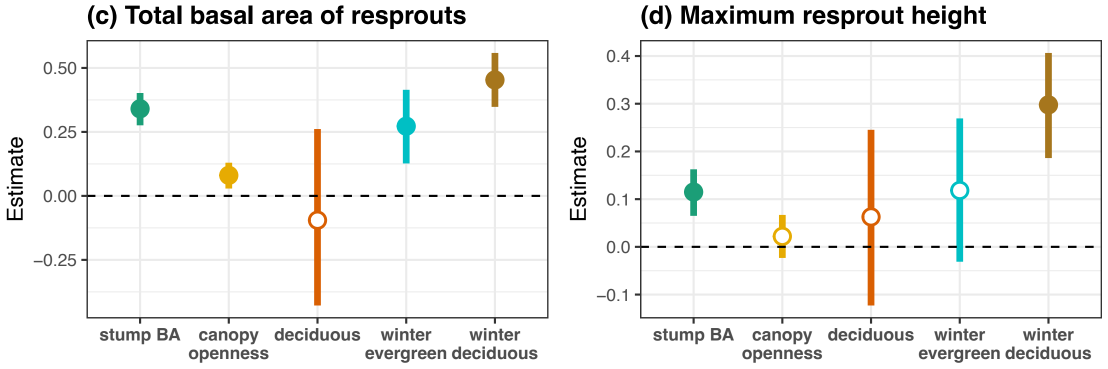
Resprout initiation



(a) Probability of resprouting

(b) Number of resprouts

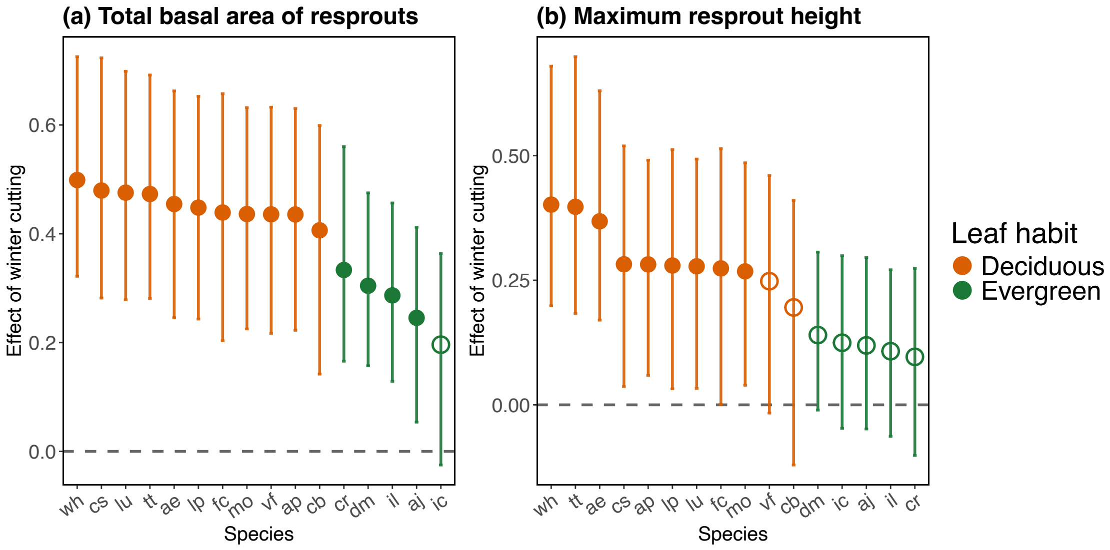
First−year resprout growth



(c) Total basal area of resprouts

(d) Maximum resprout height

Fig. 6: Species-specific effects of winter cutting on first-year resprout growth (Dataset 2). Bayesian generalized linear mixed model estimates are shown for (a) total basal area of resprouts and (b) maximum resprout height. Points represent posterior means, and vertical lines represent 95% credible intervals. Filled circles indicate species with significant effects whose 95% credible intervals do not include zero, whereas open circles indicate species with non-significant effects. The dashed line indicates zero effect. Colors denote leaf habit (deciduous vs evergreen). Abbreviations of species names are shown in Table 2.



Tables

Table 1. Resprouting stages and response variables.

Resprouting stages	Resprouting responses	Unit
Resprout initiation	Probability of resprouting	Proportion (%)
	Number of resprouts	Count (N)
First-year resprout growth	Total basal area of resprouts	mm^2
	Maximum resprout height	cm
Second-year resprout growth	Total basal area of resprouts	mm^2
	Maximum resprout height	cm

Resprouting responses were classified into three stages of resprouting process. Units are shown for each response variable.

Table 2. Species included in the study and their attributes.

Species	Family	Leaf habit	Growth form	N in Dataset 1	N in Dataset 2	Abbreviation
Magnolia obovata	Magnoliaceae	Deciduous	Canopy	–	30	mo
Lindera umbellata var. *membranacea*	Lauraceae	Deciduous	Shrub	39	20	lu
Lindera praecox	Lauraceae	Deciduous	Shrub	42	22	lp
Daphniphyllum macropodum subsp. *humile*	Daphniphyllaceae	Evergreen	Sub-canopy	–	37	dm
Fagus crenata	Fagaceae	Deciduous	Canopy	43	21	fc
Toxicodendron trichocarpum	Anacardiaceae	Deciduous	Sub-canopy	38	24	tt
Acer pictum subsp. *mayrii*	Sapindaceae	Deciduous	Canopy	–	32	ap
Camellia rusticana	Theaceae	Evergreen	Shrub	40	20	cr
Clethra barbinervis	Clethraceae	Deciduous	Sub-canopy	37	21	cb
Aucuba japonica var. *borealis*	Garryaceae	Evergreen	Shrub	–	30	aj
Ilex leucoclada	Aquifoliaceae	Evergreen	Shrub	–	31	il
Ilex crenata var. *radicans*	Aquifoliaceae	Evergreen	Shrub	–	29	ic
Viburnum furcatum	Viburnaceae	Deciduous	Shrub	41	21	vf
Weigela hortensis	Caprifoliaceae	Deciduous	Shrub	–	31	wh
Chengiopanax sciadophylloides	Araliaceae	Deciduous	Sub-canopy	37	23	cs
Aralia elata	Araliaceae	Deciduous	Sub-canopy	–	31	ae

Species included in the two datasets, with family, leaf habit, growth form, sample size in each dataset, and abbreviations used in Fig. 6. Dataset 1 comprised eight species, whereas Dataset 2 comprised 16 species. "–" indicates that the species was not included in the corresponding dataset.

Table 3. Fixed effects (posterior mean [95% credible interval]) from Bayesian generalized linear mixed models for resprouting responses in Dataset 1.

Resprouting stages	Resprout initiation		First-year resprout growth		Second-year resprout growth	
Explanatory variable	Probability of resprouting	Number of resprouts	Total basal area of resprouts	Maximum resprout height	Total basal area of resprouts	Maximum resprout height
Intercept	1.90 [0.97, 2.92]	0.71 [0.27, 1.13]	0.91 [0.66, 1.15]	1.15 [0.95, 1.34]	1.33 [1.18, 1.48]	1.26 [1.01, 1.50]
Stump basal area (log10)	0.30 [-0.51, 1.16]	**0.45** **[0.17, 0.72]**	**0.32** **[0.21, 0.43]**	**0.16** **[0.12, 0.21]**	**0.33** **[0.24, 0.41]**	**0.08** **[0.04, 0.13]**
Pre-cutting PPFD	-0.17 [-0.54, 0.21]	-0.05 [-0.24, 0.12]	0.03 [-0.10, 0.17]	0.02 [-0.04, 0.07]	0.04 [-0.03, 0.11]	0.01 [-0.04, 0.06]
Post-cutting PPFD	0.32 [-0.20, 0.86]	0.19 [-0.08, 0.44]	0.08 [-0.01, 0.17]	0.04 [-0.02, 0.10]	**0.13** **[0.05, 0.20]**	0.05 [-0.00, 0.11]
Cutting season (winter)	0.83 [-0.81, 3.14]	-0.06 [-0.60, 0.47]	**0.32** **[0.06, 0.60]**	**0.19** **[0.05, 0.34]**	0.04 [-0.14, 0.21]	0.16 [-0.04, 0.37]

Models were fitted for resprout initiation (probability of resprouting; number of resprouts), first-year resprout growth (total basal area of resprouts; maximum resprout height), and second-year resprout growth (total basal area of resprouts; maximum resprout height). Explanatory variables included log$_{10}$-transformed stump basal area, pre-cutting PPFD, post-cutting PPFD, and cutting season (winter vs spring; spring as reference). All continuous explanatory variables were standardized. Pre-cutting light environments were represented by integrated PPFD in 2023, whereas post-cutting light environments were represented by PPFD in 2024 for resprout initiation and first-year resprout growth, and the mean PPFD across 2024–2025 for second-year resprout growth. Species was included as a random effect with uncorrelated random intercepts and slopes. Bold values indicate significant effects whose 95% credible intervals did not include zero.

Table 4. Fixed effects (posterior mean [95% credible interval]) from Bayesian generalized linear mixed models for resprouting responses in Dataset 2.

Explanatory variable	Probability of resprouting	Number of resprouts	Total basal area of resprouts	Maximum resprout height
Intercept	2.80 [1.33, 4.14]	1.02 [0.60, 1.44]	1.00 [0.69, 1.28]	0.94 [0.79, 1.10]
Stump basal area (log10)	**0.45 [0.05, 0.86]**	**0.40 [0.28, 0.50]**	**0.34 [0.28, 0.40]**	**0.11 [0.07, 0.16]**
Canopy openness	0.33 [-0.17, 0.86]	0.06 [-0.05, 0.16]	**0.08 [0.03, 0.13]**	0.02 [-0.02, 0.07]
Cutting season (winter)	0.99 [-0.44, 2.44]	0.23 [-0.08, 0.54]	**0.27 [0.13, 0.41]**	0.12 [-0.03, 0.27]
Leaf habit (deciduous)	-1.15 [-2.60, 0.42]	-0.53 [-1.04, -0.00]	-0.10 [-0.43, 0.26]	0.06 [-0.12, 0.25]
Cutting season : Leaf habit	0.40 [-1.15, 1.93]	-0.13 [-0.50, 0.25]	0.18 [0.00, 0.35]	0.18 [-0.02, 0.36]

Models were fitted for resprout initiation (probability of resprouting; number of resprouts) and first-year resprout growth (total basal area of resprouts; maximum resprout height). Explanatory variables included log$_{10}$-transformed stump basal area, canopy openness, cutting season (winter vs spring; spring as reference), leaf habit (deciduous vs evergreen; evergreen as reference), and the interaction (cutting season × leaf habit). Species was included as a random effect with uncorrelated random intercepts and slopes. Bold values indicate significant effects whose 95% credible intervals did not include zero.