

Research Article

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Recovery of heather (*Calluna vulgaris*) flowering in northern Finland

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Abstract: Heather is a slow-growing evergreen shrub, commonly found in moorlands and heaths of high nature conservation value. Heather-dominated areas are used as livestock pasture, and the flowers of heather are harvested also for the natural product industry. Classical studies have focused on the recovery of shoot biomass of heather, while the recovery of flowering after grazing or harvesting has received less attention. In this study, we examined the recovery of heather flowering in one harvesting experiment and two observational areas in northern Finland. The flowers of heather were collected manually by clipping the flowering shoots or stripping the flowers from the shoots or by machine harvesting. We counted the number of short shoots (SS), nonflowering long shoots (NFLS), and flowering long shoots (FLS) after harvesting. We also measured the length of FLS and counted the flowers they produced. Heathers started to recover by producing new short shoots, while the recovery of flowering was slow, and only in one out of the three areas, flowering recovered totally during our study. Our results suggest that the recovery was dependent on the age of heather or individual site characteristics rather than on the harvesting method. Because flowering is one of the most important stages of successful reproduction, which affects the long-term existence of heather-dominated ecosystems, the results of our study can contribute to new guidelines for management practices in heathlands. However, longer-term experiments on the rate of flowering recovery are needed especially if rotational cutting is favored as a management practice in heathlands in the future.

Keywords: clipping, flower, flowering, machine harvesting, stripping

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1 Introduction

Heather (*Calluna vulgaris* (L.) Hull) is a slow-growing evergreen shrub, typically dominant in heathland communities in Northwest Europe but also found throughout Europe and Northern America. Heather is adapted to nutrient-poor, acidic soils in open habitats and is characteristic species in rare *Calluna*-dominated moorlands and heaths of high nature conservation value. Habitats characterized by heather have declined throughout Europe as a result of changes in N-deposition, land use and management, and grazing (Holden et al. 2007; Damgaard 2019).

Rotational prescribed burning has been the most common management tool in heather-dominated ecosystems (Måren et al. 2010; Velle et al. 2012). However, recent studies suggest that burning may have undesirable effects on ecosystem services (Garnett et al. 2000; Ramchunder et al. 2009). Therefore, clipping is considered as an alternative management tool to burning (Cotton and Hale 1994; Sanderson et al. 2019). The studies conducted in heather-dominated ecosystems have focused on the reproduction of heather mostly in terms of the development of new shoot biomass to support sheep grazing or high densities of game, such as red grouse (*Lagopus lagopus scoticus* Latham) and red deer (*Cervus elaphus* L.). In these studies, the biomass of heather is clipped or cut to mimic the consumption by livestock at different levels of grazing. Grazing and clipping studies suggested that heather can tolerate up to 15–60% of the current year's growth removal without a negative effect on the production of new growth in following years (Grant et al. 1982; Palmer 1997; Read et al. 2002). Low and medium levels of grazing may even enhance the production of green biomass of heather by increasing the number of shoot apices (Mohamed and Gimingham 1970; Grant 1971). However, heavy grazing and intense clipping may have damaging effects on the production of new shoots (Mohamed and Gimingham 1970; Hester et al. 1991).

Heather recovers by vegetative means after clipping and grazing, whereas sexual reproduction measured by seedling emergence is enhanced after burning

(Barker et al. 2004). Successful flowering is the first, crucial step in the sexual reproduction pathway and manifests itself in soil seed bank, affecting thereby the genetic diversity and long-term existence of heath ecosystems. Classical studies conducted already about 50 years ago suggest that repeated clipping may reduce the flowering vigor in heathers (Grant and Hunter 1966); later, Grant (1971) suggested enhanced flower production provided that intense grazing is not applied during winter. More recent studies support the findings of slow recovery and low flowering frequencies of heather after clipping (Calvo et al. 2005; Britton and Fisher 2008).

In our study, we compared three flower collecting methods (clipping, machine harvesting, and stripping) on the performance of heather. Clipping and machine harvesting correspond with the mimicked livestock grazing applied in earlier studies conducted in heather-dominated environments. All three methods, clipping, machine harvesting, and stripping, are commonly used when collecting flowering shoots or flowers for the natural product industry. We used the mixed-model analysis to test the effects of collecting methods (clipping, machine harvesting, and stripping) on the recovery of heather over time. We focused on the responses in the production of flowers and floral parts of heather after collecting and estimated the time which heather needed to recover in terms of flowering. Because actual herbivory induces hormonal responses in several plant species (Eichenseer et al. 1999; van Kleunen et al. 2004; Barton 2016), we compared our results with the experiments where artificial grazing was applied by clipping or cutting.

By focusing on the recovery of flowering, this study fills the gap in our knowledge about the long-term effects of clipping and cutting on the rare heather-dominated ecosystems. The results of this study are applicable for planning management practices applied in heathlands and moors or can assist collectors, landowners, and entrepreneurs in the field of natural products to achieve a sustainable level of harvesting.

2 Materials and methods

2.1 Heather flowering

The current year's growth of heather comprises long shoots, in which short shoots are spaced in two zones, separated by a belt of purple lateral flowers in the middle

(Figure 1) (Mohamed and Gimingham 1970). Short shoots produced at the beginning of the growing season locate at the base of the long shoots and are sometimes branched, and those produced later in the growing season after flowering occupy the shoot tips below the apex (Mohamed and Gimingham 1970). The apex of the long shoot may experience new growth in a subsequent year and produce a new, flowering long shoot. However, more often a new cohort of leading flowering long shoots are produced by several end-of-season short shoots located just below the apex, resulting in a system of branching in which each axis is annually replaced by several new axes of growth (Mohamed and Gimingham 1970).

The short shoots usually die and drop off in a couple of years, but some of them may grow and stay as short shoots in forthcoming growing seasons (Mohamed and Gimingham 1970). Moreover, some of the short shoots may produce weaker long shoots referred to as lateral

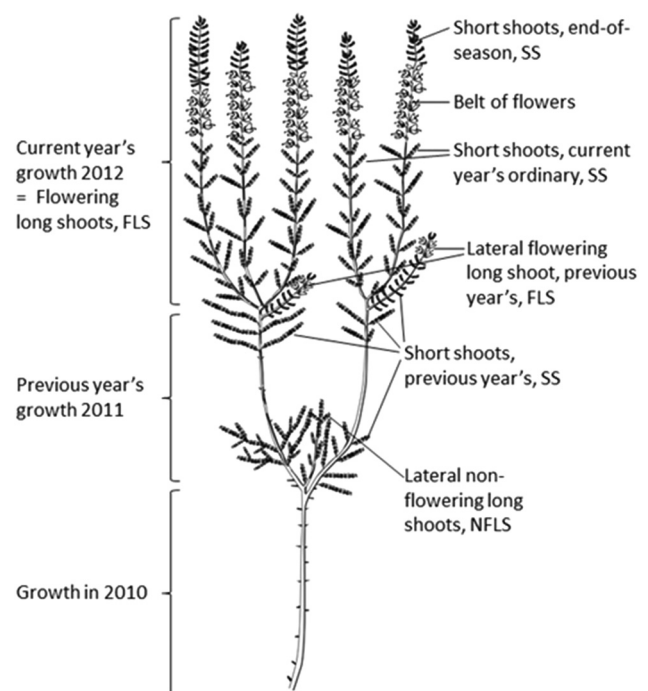


Figure 1: An illustration of annual growth and shoot production in heather (*Calluna vulgaris* (L.) Hull). Abbreviations (SS, FLS, NFLS) refers to the counting and classification of the shoots in the field before the analysis in our study. Short shoots (SS) consist of end-of-season short shoots, current year's ordinary short shoots, and previous year's short shoots. Flowering long shoots (FLS) consists of the current year's flowering shoots and lateral, flowering long shoots that were developed from the previous year's growth. Lateral nonflowering long shoots (NFLS) were identified by light green, soft biomass, and lengthened internodes between the leaves, and they were classified into their group. The figure is modified from Mohamed and Gimingham (1970).

long shoots in the study by Mohamed and Gimingham (1970). Lateral long shoots may produce flowers, but at lower abundances when compared with the leading long, flowering shoots.

2.2 Study sites

The recovery studies were divided into two parts: harvesting experiment (one study site), in which heather vegetation was actively cut, and observational study (two study sites), in which recovery of heather was observed after previously done commercial harvestings.

2.2.1 Description and setup of the experiment

The harvesting experiment was established in a clear-cut area in Petäjävaara (66°18'N; 25°30'E) in northern Finland in July 2010. The area was clear-cut 10 years before the beginning of the experiment. In the clear-cut area, intact heather dominated the field layer and

formed scattered clusters in the vegetation, and bryophytes and lichens constituted the thin ground layer between stones and boulders. The experiment flowchart in Petäjävaara is shown in Figure 2. Altogether, 24 permanent study plots, sized 50 × 50 cm, were established and randomly assigned as controls ($n = 8$) or to one of two harvesting treatments: (1) manual clipping of the flowering long shoots with scissors (clipping, $n = 8$) and (2) mechanical cutting of the flowering long shoots by a harvesting machine (machine harvesting, $n = 8$). The harvesting machine consisted of a hedge trimmer installed to a combustion-engine powered string trimmer, and harvested mass ended up to an aluminum collection tray. Harvested heather shoots were dried at 80°C for 24 h and weighed after drying. The intact aboveground biomass of heather was measured by collecting aboveground vegetation from randomly located, temporary 50 × 50 cm plots ($n = 8$) and treated similarly as harvested biomass.

In each study plot, eight heather individuals were selected randomly and marked permanently with plastic tags. A number of marked heather individual's short shoots (SS hereafter), lateral long shoots that did not bear flowers (referred as nonflowering long shoots,

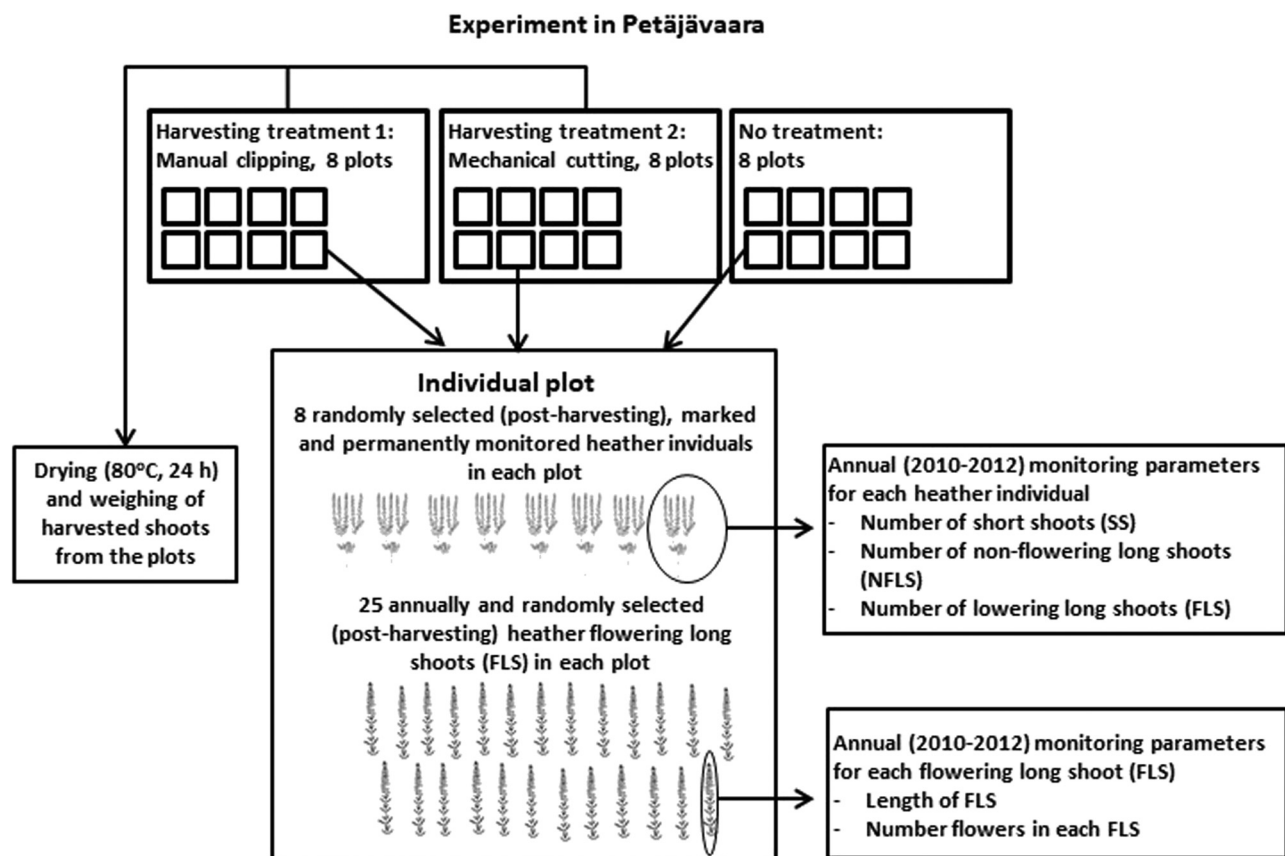


Figure 2: The flowchart of the experiment setup in Petäjävaara.

NFLS), and flowering long shoots (FLS) were counted (Figure 1). In each plot, lengths of 25 randomly selected FLS were measured (mm), and a number of flowers along each FLS were counted every monitoring year. All measurements were conducted in July 2010–2012.

2.2.2 Description and setup of observational study areas

Observational studies were conducted at two sites, Meltaus and Sodankylä, in northern Finland during 2010–2012. Meltaus study site (66°53'N; 25°27'E) was located at dry, Scots pine-dominated forest, where evergreen shrubs such as lingonberry and crowberry are commonly found together with heather in the understory and lichens dominate the ground layer with the low abundance of bryophytes. All flowering long shoots were

commercially harvested manually with scissors in 2009 in this area.

Sodankylä study site (67°25'N; 26°22'E) was located under electricity power lines subjected to frequent cuttings of coniferous trees and tree saplings, leading to an approximately 35 m wide treeless corridor. Heather dominated the understory under the power lines, and dwarf shrubs bilberry and bog whortleberry were commonly found. In the ground layer, bryophytes such as red-stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt.) and *Dicranum* spp. were abundant concomitantly with the lower abundance of lichens. All heather flowers were collected in 2007 by stripping the flowers from long shoots by hand or harvesting the flowering long shoots mechanically by the same machine which was used in the Petäjävaara harvesting experiment.

Recovery monitoring in both harvested areas of observational studies (Meltaus: manual clipping, Sodankylä:

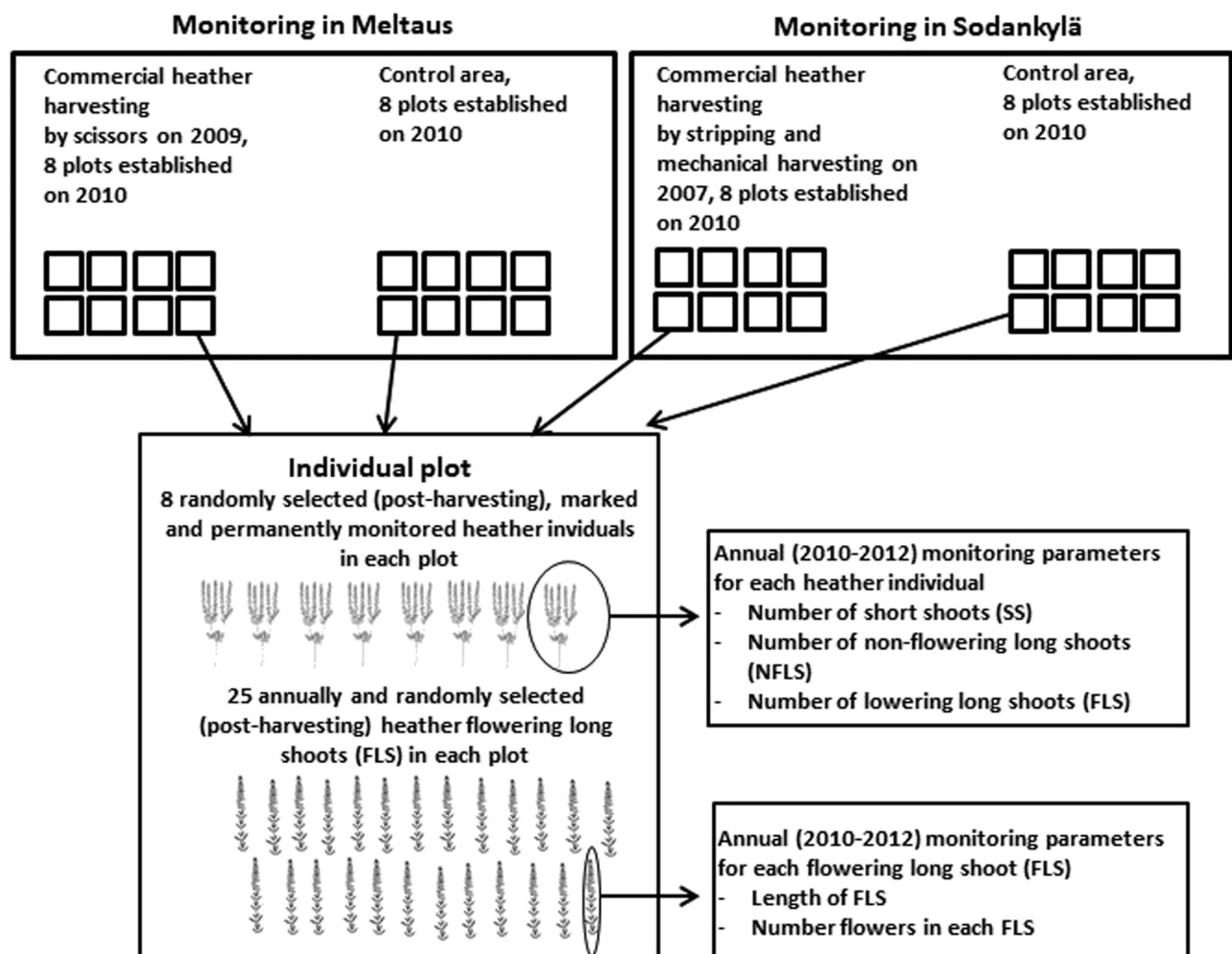


Figure 3: The flowchart of the monitoring procedure in Meltaus and Sodankylä.

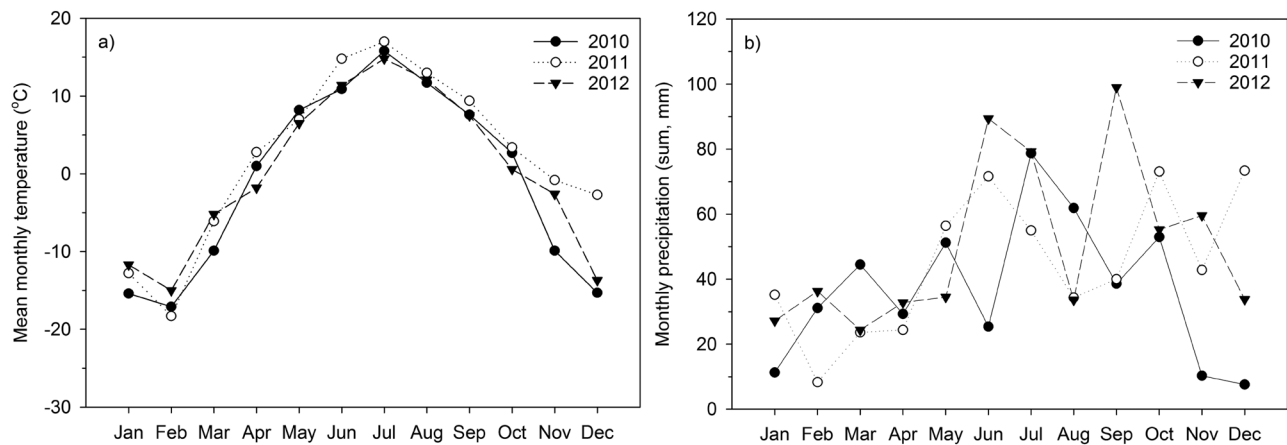


Figure 4: Background information of weather in Rovaniemi during the study period 2010–2012: (a) mean monthly temperature (°C) and (b) sum of monthly precipitation (mm).

manual stripping and machine harvesting) was similar as in harvesting experiment, and unharvested areas in the proximity of harvested areas were used as control areas. The flowchart of the monitoring procedure in Meltaus and Sodankylä is shown in Figure 3. The recovery of heather in both observational study areas was recorded during 2010–2012.

The meteorological background information of the area is shown in Figure 4.

2.3 Statistical analysis

The mean number of SS, FLS, and NFLS of the permanently marked eight individuals in a study plot was determined as well as the average length of 25 randomly selected FLS and the number of flowers they bear.

The relative proportion of shoot (SS, FLS, and NFLS) number in a plot was calculated as the percentage of the number of all shoots in the plot. Mean numbers and relative proportions of shoots, length of FLS, and a number of flowers in FLS were tested with the linear-mixed model analysis for each study site separately. To compare the shoot production and flowering in harvested plots to unharvested controls over time, year was used as a repeated factor and harvesting treatment (control, clipping, stripping, or machine harvesting) as a fixed factor. Thus, the model in the analysis corresponds to the repeated measures ANOVA. However, the linear-mixed model was used to find the best model related to covariance structure. The best final model, based on AIC values, was achieved by using an unstructured covariance structure for repeated effect (year). The results of the repeated measures ANOVA and linear mixed models

were compared to each other, and as the results did not differ at the significance level $p < 0.05$, the results of the linear mixed model are shown.

The results of the mixed-model analysis revealed a significant interaction between year and harvesting method more than in half of the parameters (Supplementary material 1). Therefore, the effect of harvesting methods on the shoot and flowering variables of heather was tested by the one-way ANOVA for each year separately. Tukey's *post hoc* test (significance level $p < 0.05$) was used to find the differences between the harvesting methods in Petäjävaara and Sodankylä.

Data were checked for the normality and homogeneity of variances before testing, and log- and square-root transformations were applied when necessary to fulfill the requirements. All analyses were conducted using SPSS for Windows (IBM Corp. 2017).

Ethical approval: The conducted research is not related to either human or animal use.

3 Results

3.1 Harvesting experiment in Petäjävaara

The intact aboveground biomass of heather at the study site in Petäjävaara was 502 ± 52 (dry weight g m^{-2} , mean \pm SE) at the beginning of the experiment in 2010. Biomass removed by clipping was 72 ± 9 (dry weight g m^{-2} , mean \pm SE) and by machine harvesting was 71 ± 4 (dry weight g m^{-2} , mean \pm SE), which were 14.4% and 14.1% from the intact aboveground biomass, respectively.

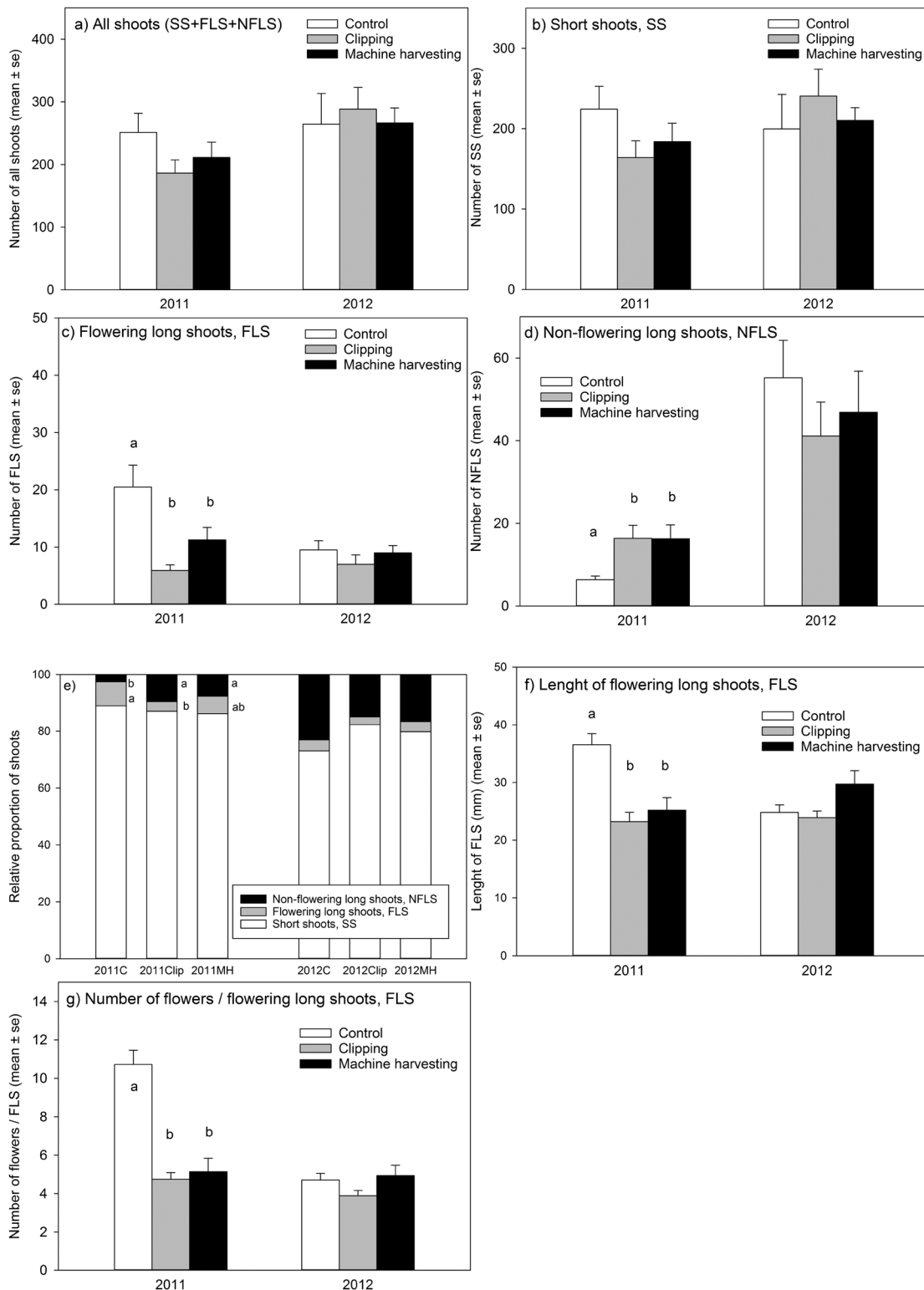


Figure 5: The number of (a) all shoots (SS + FLS + NFLS), (b) short shoots (SS), (c) flowering long shoots (FLS), (d) nonflowering long shoots (NFLS), (e) the relative proportion of SS, FLS, and NFLS from all shoots, (f) the length of FLS, and (g) the number of flowers/FLS in heather (*Calluna vulgaris* (L.) Hull) in the control plots and plots of different harvesting methods (clipping and machine harvesting) in Petäjävaara in 2011 and 2012. Letters above the columns indicate a significant difference between the control and harvesting methods within a year as revealed by the one-way ANOVA and Tukey's *post hoc* test at the significance level $p < 0.05$. Mean values (\pm SE) are shown in all figures except figure (e) in which mean values are shown. $N = 8$.

Heathers started to produce new shoots during the first year after harvesting in 2011. The number of all shoots and SS did not differ between the control and harvested plots (Figure 5a and b, Table 1), suggesting a quite fast recovery of green shoot biomass after harvesting. However, the number of FLS was lower, and the number of NFLS was higher in clipped or machine harvested plots than in the controls 1 year after harvesting in 2011 (Figure 5c and d, Table 1), indicating the lower flowering capacity of harvested heathers.

Both clipping and machine harvesting changed the relative proportions of shoots in the first year after harvest in 2011 (Figure 5e and Table 1). Clipping decreased the relative proportion of FLS, while their share in the machine-harvested plots did not differ from the control or clipping. Moreover, the relative proportion of NFLS was higher in both harvesting treatments than in the controls (Figure 5e and Table 1). Thus, similarly to the results of actual shoot numbers of FLS and NFLS, the results of their relative proportions suggest that harvesting decrease the flowering capacity of heather by increasing the share of nonflowering shoots at the expense of flowering long shoots.

Harvesting affected negatively flowering in the first year after harvesting in 2011: The FLS produced by heathers, which were harvested either by clipping or

cutting by the machine, were shorter and bore fewer flowers than those in the controls in the first year after clipping in 2011 (Figure 5f and g, Table 1).

Two years after the harvesting in 2012, the shoot variables did not differ from each other.

3.2 Observational study in Meltaus, 3 years of recovery after manual clipping

The number of all shoots of heather was lower in clipped plots still in the second year after harvesting in 2011 (Figure 6a and Table 2). Clipped heathers produced fewer FLS than the heathers in the controls throughout the study (Figure 6c and Table 2), and also fewer NFLS in the third year after harvesting (Figure 6d and Table 2).

The actual number of SS was not affected by clipping (Figure 6b and Table 2), suggesting that heathers were recovered in terms of sort shoot production already in the first year after harvesting. Moreover, the relative proportion of SS increased, and accordingly, the relative proportion of FLS decreased by clipping throughout the study (Figure 6e and Table 2). Also, the relative proportion of NFLS was lower in clipped plots than in the controls in 2012 (Figure 6e, Table 2).

Both the length of the FLS and the number of flowers they produced were lower in the clipped heathers than in the controls after 3 years of recovery (Figure 6f and g and Table 2).

When combining the results of actual shoot numbers with the results of their relative proportions and flowering parameters, they all indicate the lower flowering capacity in the clipped heathers than those in the controls still 3 years after harvesting. Moreover, compared to Petäjävaara's experiment, where heathers responded to harvesting by increasing the production of nonflowering long shoots (NFLS), in Meltaus heathers responded by producing new short shoots (SS).

3.3 An observational study in Sodankylä, 5 years of recovery after stripping and machine harvesting

Stripping or machine harvesting did not affect the number of all shoots, SS, or NFLS after 3 years of harvesting or later (2010–2012; Figure 7a, b, and d and Table 3). However, stripping or machine harvesting decreased FLS in the third and fifth years after harvesting in 2010 and 2012

Table 1: Results of one-way ANOVA testing the differences between the control and the harvesting methods (clipping and machine harvesting) on the mean number of shoots, the relative proportion of shoots, and flowering parameters of heather (*Calluna vulgaris* (L.) Hull) in Petäjävaara in 2011 and 2012. $N = 8$ for the control and both treatments. Between groups $df = 2$, and within groups $df = 21$

	2011		2012	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Mean number of shoots				
All shoots (SS + FLS + NFLS)	1.628	0.220	0.131	0.878
Short shoots (SS)	1.619	0.222	0.418	0.664
Flowering long shoots (FLS)	10.843 ^a	0.001	0.784	0.469
Nonflowering long shoots (NFLS)	6.194	0.008	0.611	0.552
Relative proportions				
Short shoots (SS)	0.642	0.536	2.613	0.097
Flowering long shoots (FLS)	4.557	0.023	0.660	0.527
Nonflowering long shoots (NFLS)	12.173	<0.001	2.526	0.104
Flowering parameters				
Length of FLS	13.946	<0.001	3.452	0.051
Number of flowers/FLS	28.916	<0.001	1.843	0.183

^a Log-transformed data were used in the analysis. Significant results ($p < 0.05$) are given in bold.

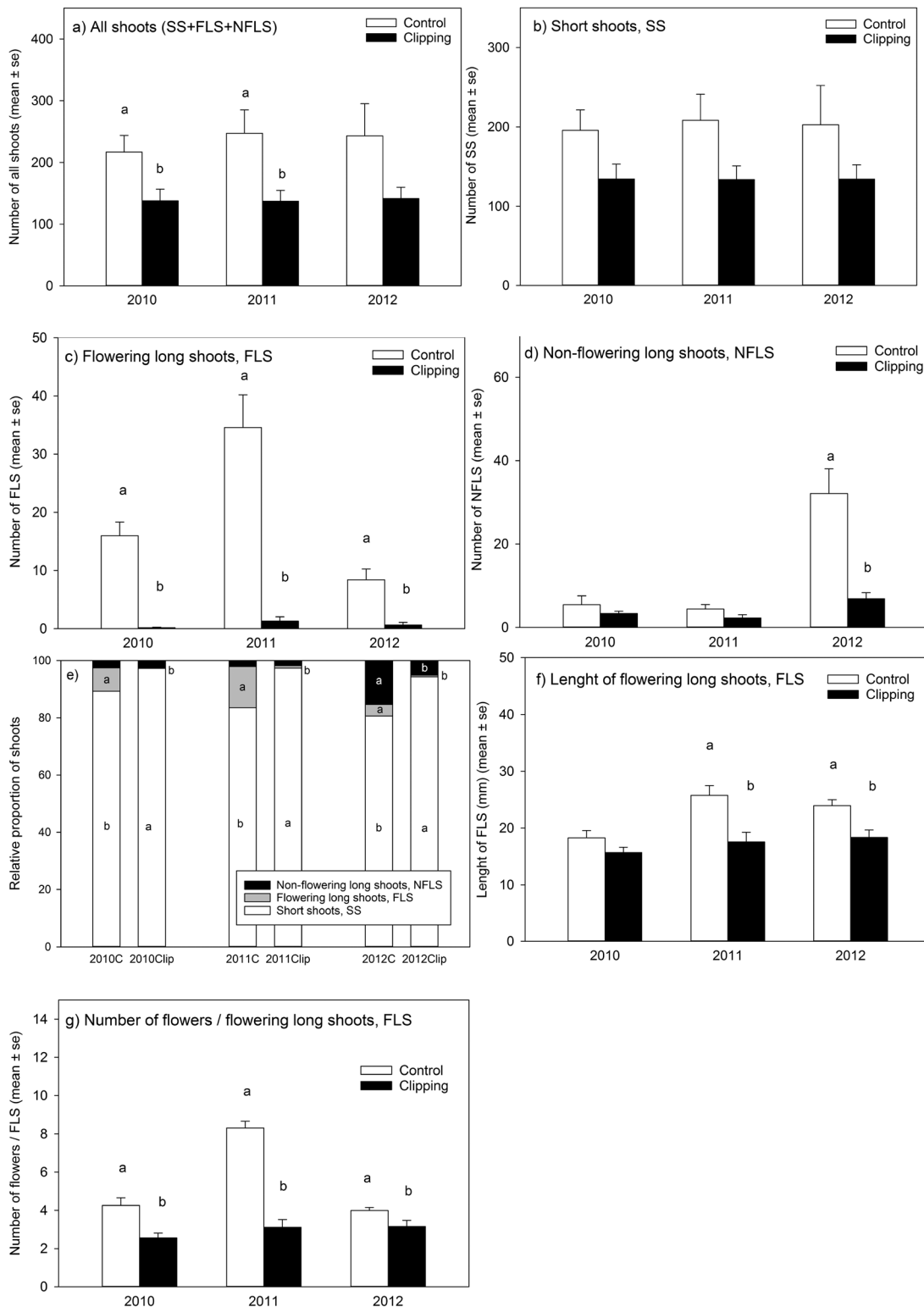


Figure 6: The number of (a) all shoots (SS + FLS + NFLS), (b) short shoots (SS), (c) flowering long shoots (FLS), (d) nonflowering long shoots (NFLS), (e) the relative proportion of SS, FLS, and NFLS from all shoots, (f) the length of FLS, and (g) the number of flowers/FLS in heather (*Calluna vulgaris* (L.) Hull) in the control and harvested plots in Meltaus during 2010–2012. Harvesting was carried out by clipping by hand in 2009. Letters above the columns indicate a significant difference between the control and clipped plots within a year as revealed by the one-way ANOVA at the significance level $p < 0.05$. Mean values (\pm SE) are shown in all figures except figure (e) in which mean values are shown. $N = 8$.

Table 2: Results of one-way ANOVA testing the differences between the controls and harvesting method (manual clipping) in the mean values of shoot number, the relative proportion of shoots and flowering parameters of heather (*Calluna vulgaris* (L.) Hull) in Meltaus in 2010–2012. $N = 8$ for the control and clipping treatment. Between groups $df = 1$ and within groups $df = 14$ in Meltaus

	2010		2011		2012	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Mean number of shoots						
All shoots (SS + FLS + NFLS)	5.773	0.031	5.438	0.035	3.382	0.087
Short shoots (SS)	3.666	0.076	4.065	0.063	1.679	0.216
Flowering long shoots (FLS)	323.226 ^a	<0.001	92.273 ^a	<0.001	28.845 ^a	<0.001
Nonflowering long shoots (NFLS)	0.068 ^a	0.798	2.622	0.128	23.146 ^a	<0.001
Relative proportions						
Short shoots (SS)	33.370 ^a	<0.001	139.201	<0.001	17.896	0.001
Flowering long shoots (FLS)	169.494 ^a	<0.001	142.698	<0.001	18.500 ^a	0.001
Nonflowering long shoots (NFLS)	0.462 ^a	0.508	0.146	0.708	13.735	0.002
Flowering parameters						
Length of FLS	4.213	0.059	11.687	0.004	10.233	0.006
Number of flowers/FLS	40.133	<0.001	93.668	<0.001	4.818	0.046

^a Log-transformed data were used in the analysis. Significant results ($p < 0.05$) are given in bold.

(Figure 7c, Table 3). Also, the relative proportion of FLS decreased by harvesting in 2010, and their relative proportions were lower in the stripped plots than in the controls in 2012 (Figure 7e and Table 3).

The length of FLS in the controls did not differ from those in harvested plots; however, in 2011, stripped heathers produced longer FLS compared to heathers which were harvested by the machine 4 years earlier (Figure 7f and Table 3).

Stripped heathers produced fewer flowers than those in the control plots in the third year after harvesting in 2010 (Figure 7g and Table 3). However, in 2011, the difference in flower number between stripping and control has leveled out, and the lowest number of flowers was found in machine harvested plots.

Taken together, heathers recovered fully by producing new short shoots and nonflowering long shoots in Sodankylä during our observational period. However, harvested heathers produced fewer flowering long shoots than control ones still at the end of this study. Harvesting did not affect the length of the flowering shoots but decreased the number of flowers still in the fourth year of the study.

4 Discussion

The results of this study revealed a quite fast recovery of heather regarding shoot production after harvesting. This is in accordance with earlier studies suggesting that

heather recovers effectively by vegetative means after cutting and light grazing (Mohammed and Gimingham 1970; Grant 1971; Liepert et al. 1993). However, the rates of recovery varied between the study sites and occurred mostly by the production of the new short shoots and nonflowering long shoots, while negative effects on flowering was visible 5 years after the harvesting.

Studies on the regeneration of heather are mostly focused on improving our knowledge about maintaining suitable production of new growth of heather to support grazing and high game densities and to specify rotational cycles of burning to gain the best management practices of the rare *Calluna*-dominated environments (Sanderson et al. 2019). However, these ecological studies provide only a little information about the responses in the flowering capacity of the heather, and the time needed for the recovery of heather in terms of flowering. Generally, damages causing biomass loss, such as clipping and cutting (Grant and Hunter 1966; Calvo et al. 2005; Britton and Fisher 2008), grazing (Welch 1984; Moss et al. 1981; Palmer 1977), and burning (Britton and Fisher 2008) decrease the flowering capacity of heather. This has been suggested to be a consequence of decreasing the number of flower buds when biomass is removed, especially after summer clipping (Grant and Hunter 1966) or due to the slow vegetative recovery of heather after biomass loss (Calvo et al. 2005). Repeated biomass loss may also affect negatively to flowering through the rejuvenation process (Grant and Hunter 1966), as the young, recently produced shoot biomass of heather is associated with lower flowering frequencies (Moss et al. 1981).

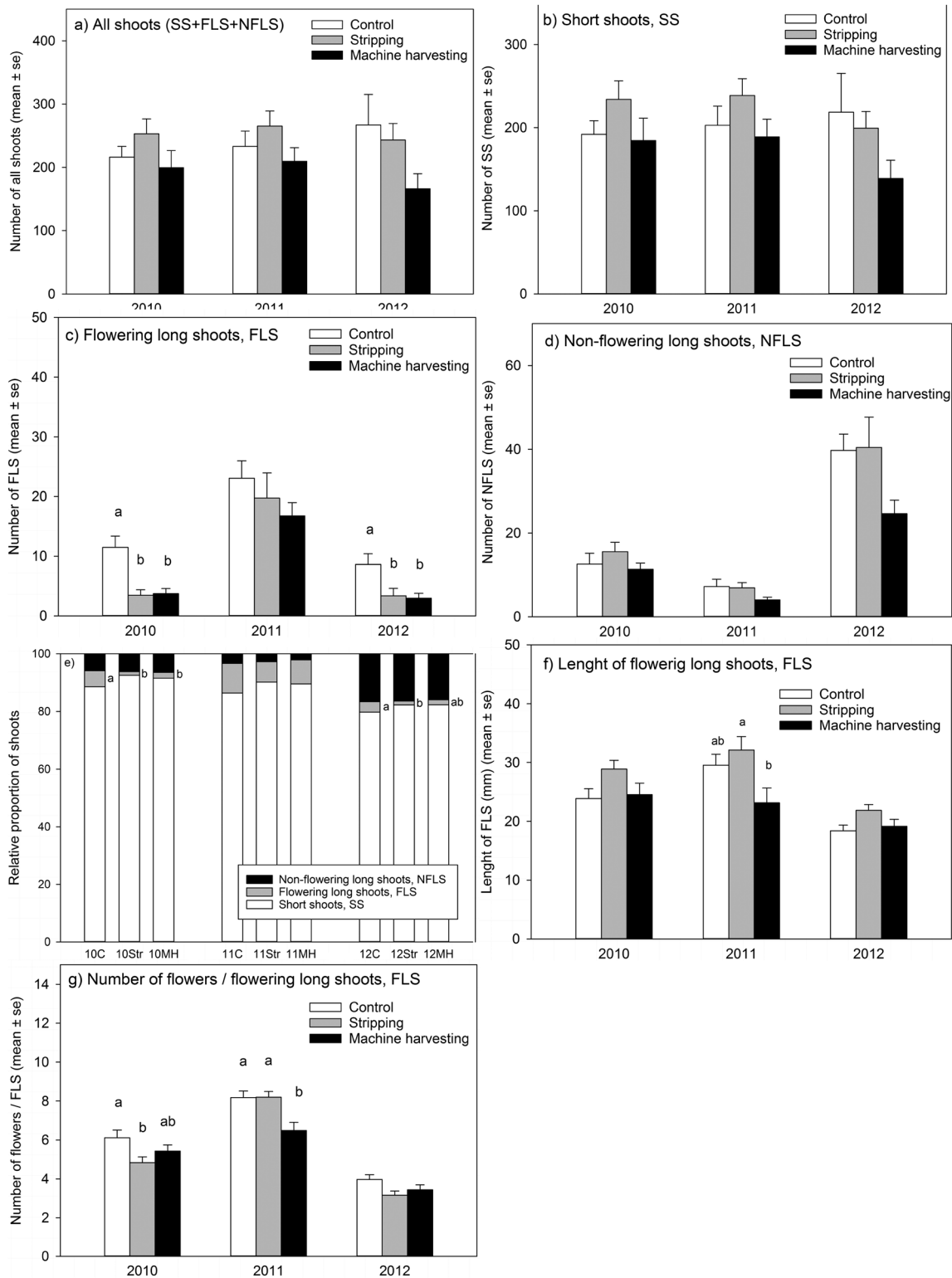


Figure 7: The number of (a) all shoots (SS + FLS + NFLS), (b) short shoots (SS), (c) flowering long shoots (FLS), (d) nonflowering long shoots (NFLS), (e) the relative proportion of SS, FLS, and NFLS from all shoots, (f) the length of FLS, and (g) the number of flowers/FLS in heather (*Calluna vulgaris* (L.) Hull) in the control and harvested plots in Sodankylä during 2010–2012. Harvesting was carried out by stripping and by a machine in 2007. Letters above the columns indicate a significant difference between the control and harvesting methods within a year as revealed by the one-way ANOVA and Tukey's *post hoc* test at the significance level $p < 0.05$. Mean values (\pm SE) are shown in all figures except figure (e) in which mean values are shown. $N = 8$.

Table 3: Results of one-way ANOVA testing the differences between the control and the harvesting methods (stripping and machine harvesting) in the mean number of shoots, the relative proportion of shoots and flowering parameters of heather (*Calluna vulgaris* (L.) Hull) in Sodankylä in 2010–2012. $N = 8$ for the control and both harvesting methods. Between groups $df = 2$ and within groups $df = 21$

	2010		2011		2012	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Mean number of shoots						
All shoots (SS + FLS + NFLS)	1.425	0.262	1.461	0.255	2.329	0.122
Short shoots (SS)	1.438	0.260	1.436	0.260	1.690	0.209
Flowering long shoots (FLS)	12.286	<0.001	0.952	0.402	5.514	0.012
Nonflowering long shoots (NFLS)	1.042	0.370	1.912	0.173	3.078	0.067
Relative proportions						
Short shoots (SS)	2.997	0.072	2.331	0.122	0.497	0.615
Flowering long shoots (FLS)	13.924 ^a	<0.001	2.156	0.141	3.850 ^a	0.038
Nonflowering long shoots (NFLS)	0.104	0.902	0.939	0.407	0.034	0.967
Flowering parameters						
Length of FLS	2.535	0.103	4.294	0.027	3.055	0.068
Number of flowers/FLS	3.609	0.045	7.884	0.003	3.036	0.069

^a Log-transformed data were used in the analysis. Significant results ($p < 0.05$) are given in bold.

Biomass loss breaks apical dominance, induces morphology changes, and increases the number of leading long shoots (Grant and Hunter 1966; Mohamed and Gimingham 1970). New leading long shoots originate after light damage from the uppermost, undamaged short shoots or from the lateral long shoots, or after more severe damage from the cohorts appearing from the lower part of the branches (Mohamed and Gimingham 1970). In our study, we were not able to evaluate the exact severity of the damage caused by harvesting at two monitoring study sites, Meltaus and Sodankylä, but we can assume that all flowering long shoots were collected to gain the maximal amount of flowers similar to the harvesting experiment in Petäjävaara. However, in our study, new leading long shoots were visible only in the Petäjävaara harvesting experiment, where the recovery resulted in the production of new nonflowering long shoots in the first year after harvesting. Furthermore, the recovery regarding flowering occurred in the second year after harvesting in Petäjävaara.

Although we did not investigate the age-structure of the harvested plants in our study sites, age may contribute to the recovery of heather flowering and probably caused between-site differences in the time scale of recovery in our study. For example, in regard to shoot growth and production, young heathers recover more effectively than old plants due to a higher amount of active meristems (Mohamed and Gimingham 1970; Grant et al. 1981; Hobbs and Gimingham 1987). Petäjävaara, where heathers recovered most effectively than in the other study sites in our work, consisted of a clear-cut

opening approximately 10 years old. Given that the threshold age for effective regrowth of green shoot biomass after cutting and burning is defined as less than 15 years (Mohamed and Gimingham 1970; Grant et al. 1981; Hobbs and Gimingham 1987), this may contribute to the fast recovery of flowering in Petäjävaara. Compared to the recovery of flowering in Petäjävaara harvesting study site, clipping affected negatively to the all aspects of flowering still in the third year after harvesting in Meltaus and decreased the amount of flowering long shoots still at the end of the study after 5 years of harvesting in Sodankylä. This reveals that the full recovery of flowering was not achieved during this study either of these two study sites.

The results of our study suggest that the recovery of flowering after removing all flowering long shoots (i.e., current year's growth), which corresponds to about 14% loss of the total aboveground biomass, may take more than 5 years. In their 2-year study, Calvo et al. (2005) found no recovery in terms of flowering after clipping 100% of heather aboveground biomass. Less severe but more frequent biomass loss was applied in the study by Grant and Hunter (1966), who removed annually 80% of the current year's growth of heather and found that clipping reduced both the amount and the length of the flowering shoots during their 7-year study. Even light annual biomass loss may have a long-lasting, negative effect on flowering. For example, the loss of 12% from the annual production of heather reduced the proportion of flowering shoots in the 5-year study by Britton and Fisher (2008).

5 Conclusion

Successful sexual reproduction is crucial but underrepresented in studies focusing on the long-term persistence of heather-dominated ecosystems. In our study, we investigated the very first step of sexual reproduction of heather, i.e., heathers' capacity to produce flowers after removing the flowering heads or flowers. We found that the negative effects of removal lasted at least for 2 years, but the full recovery was not achieved in 5 years at one of our study sites. Therefore, our results suggest that the recovery was dependent on the age of heather or individual site characteristics. The results of our study can contribute to new guidelines for management practices in heathlands and moorlands dominated by heather. However, longer-term experiments and observations on the rate of flowering recovery are needed especially if rotational cutting is favored over rotational burning as the most preferred management practice in heathlands in the future.

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Data availability statement: The datasets analyzed during the current study are available from the corresponding author on reasonable request.

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