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Succession after Fire in a Coastal Pine Forest in Norway

Oddvar Skre

Abstract

Biomass and chemical composition in six dominant field and bottom layer species have been recorded for 5 years after a wildfire in a coastal pine forest in Sveio, West Norway, in June 1992. As a follow-up of this study, the percentage coverage of field and bottom layer species and the regeneration of main tree species (*Pinus sylvestris*, *Betula pubescens,* and *Salix* spp.) were recorded in 1997, 2001, and 2008. Preliminary results indicate that the three dominant field layer species, *Calluna vulgaris, Molinia caerulea,* and *Pteridium aquilinum*, had expanded at the expense of other species, in particular *Vaccinium myrtillus, V. vitis-idaea*, *Deschampsia flexuosa,* and pioneer moss species, for example, *Polytrichum* spp. Seedlings of pine and saplings of birch and other deciduous species had established in the burned areas, and the succession of these species was followed and compared with nearby control plots. The strong growth of *Calluna vulgaris* after the fire indicates that periodic controlled burning may be an alternative management method of balancing carbon uptake rates in coastal areas of western Norway.

Keywords: succession, fire, coastal pine, coverage, regeneration

1. Introduction

Forest fires have become more common recently as a result of climatic change resulting in warmer and drier summers. However, their effects are not only negative. The reason is that a forest fire makes nutrients more available, by increasing decomposition rates in the forest floor, removing trees and makes light more accessible for plants in the field and bottom layer [1, 2]. Many plant and insect species are dependent on periodic fires in order to survive, and in Norway, as many as 40 red-listed species are related to forest fires [3]. Forest fires may also remove competition from some species, thereby favoring others [4]. Finally, some species like the heather (*Calluna vulgaris*) and the herb *Geranium bohemicum* have seeds that are activated by fire [5, 6]. Most pine species like the coastal *Pinus sylvestris* growing in Fennoscandia are adapted to fire in the sense that they reproduce by seeds, which germinate more easily after a fire.

In an earlier study [7], biomass and chemical composition in six dominant field and bottom layer species was recorded for 5 years after a wildfire in a coastal pine forest in Sveio, West Norway, in 1992, as compared with a control site outside of the burned area. As a follow-up of this study, the percentage coverage of field and bottom layer species and the regeneration of main tree species (*Pinus sylvestris, Betula pubescens,* and *Salix* spp.) were recorded in 1997, 2001, and 2008. The

present study was carried out as part of an integrated study on the rate of succession after fire in coastal pine and heath vegetation types. Although the total amounts of nutrients in soil may decrease as a result of the fire [8], their availability may be temporarily increased by conversion from organic to inorganic forms [9], leading to increased availability of nutrients during several years due to leaching [10]. According to Moe [11], a number of pine trees in the study site survived the fire and produced the seeds that were able to regenerate due to improved light and soil conditions (cf. [12, 13]). Because of the improved light and nutrient conditions, increased productivity was expected on short term in the burned areas. Experiments with pine [14] have shown that controlled burning may be a more successful method of regeneration of *Pinus sylvestris* than, for example, clear cutting.

The reproduction and establishment of vascular plants after a forest fire may take place in three ways, for example, (1) by the transport and spreading of seeds from surviving mother trees, (2) by germination from a seed bank, and (3) by vegetative reproduction from surviving roots, rhizomes, and stumps. In the present study, the further growth and succession rates of the most common trees and field layer species were followed up by comparing results from 1998, 2001, and 2008 with the results from the initial 5 years of succession after the fire in 1992 [7].

Based on the abovementioned relationships, the objectives of the present study may be formulated as follows:

- How has the growth of the main tree and field layer species changed in terms of percentage cover and biomass?

- Will the total plant biomass and productivity change permanently as a result of the fire?

- What are the implications of the present study for the long-term carbon balance?

2. Materials and methods

The forest fire took place in June 1992 south and west of Hopsfjellet in Sveio, western Norway after an extremely warm and dry period. The burned site covered an area of about 300 ha and is located at 59°30′ N, 5°20′ E (see **Figure 1**). Mean temperatures (1961–1990) vary from 2°C in February to 14°C in August, with annual precipitation about 2000 mm [8]. Different parts of the area burned with different intensities [11], depending on soil depth and humidity. *Calluna* heaths dominated in the dry parts of the burned site, while *Vaccinium myrtillus* was more common on moist sites with deeper soil system. The topography is rather variable, and the thickness of the humus layer varied from <2 cm in the most dry and nutrient-poor areas to >20 cm where peat accumulation had taken place. In some cases, the mineral soil was almost absent, and the dry humus layer was burned off, leaving the underlying rock exposed. The fire intensity reached its maximum in these areas, while areas with high water level in soil were relatively little damaged by surface fire [13]. Six representative plots of 10 by 10 m size were established in 1993, covering the whole range of fire intensities.

Growth estimation. Instead of destructive biomass sampling of field layer species, the growth was estimated by measuring the percentage coverage and the corresponding shoot density in pure stands of the same species in 1997 and 2001. From these two parameters and estimates of biomass per shoot (**Table 3**), the total biomass per area was estimated (cf. [15]). The percentage coverage of regenerating
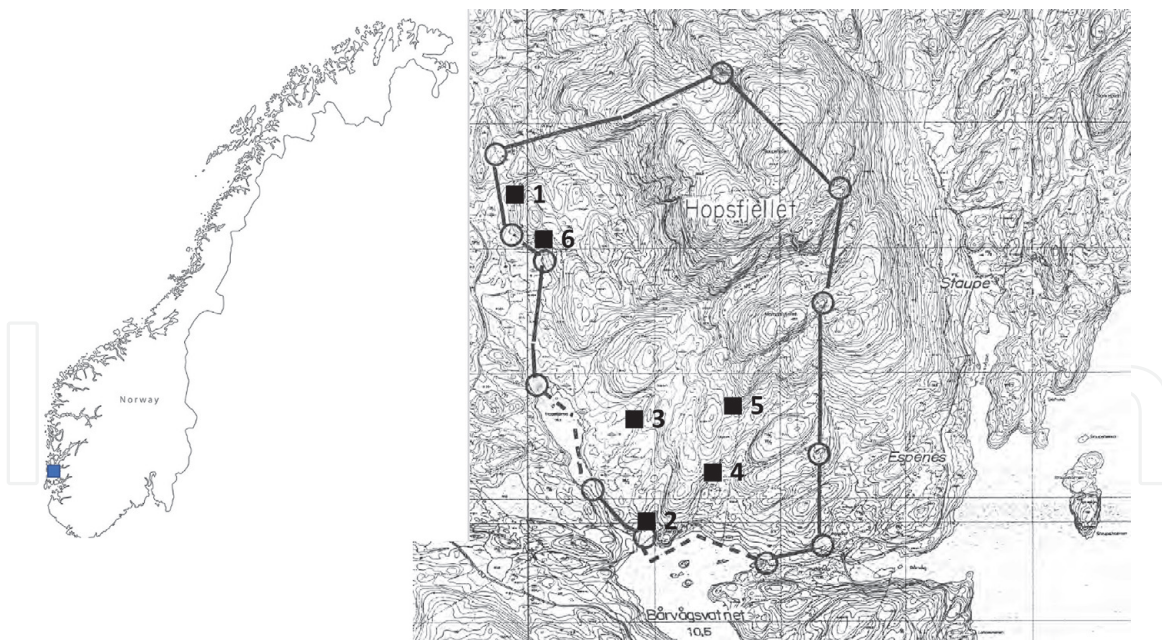
Figure 1.
Map of Norway showing the location of the study area (left). The six study sites are classified on the small-scale (1:15,000) map over the burned study area (right), as follows: low fire intensity (1–2), medium fire intensity (3–4), and high fire intensity (5–6). The control site was located about 500 m outside and west of the burned area.

seedlings of *Pinus sylvestris*, *Betula pubescens*, and *Salix* spp. was recorded in 1995, 2001, and 2008, as well as tree density on 10 by 10 m plots and the stem base diameter (mm), age, and total height (cm). The following field layer species were recorded: *Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Pteridium aquilinum*, *Deschampsia flexuosa*, *Molinia caerulea*, and the mosses *Polytrichum commune* and *P. juniperinum*. The number of shoots per m^2 in pure stands were extrapolated from sampling squares of 10 by 10 cm (*Calluna, Deschampsia, Polytrichum*), 20 by 20 cm (*Vaccinium*), or 1 by 1 m (*Pteridium*). The overall biomass per unit area was then estimated by multiplying the calculated biomass in pure stands with the corresponding percentage cover of each species (cf. [7]). The method was tested out by harvesting random samples of each species by ordinary sampling method using a core with known surface area [15]. In the present study, the results are given as mean values (*n* = 5) from each of the six study sites.

In earlier studies, the biomass per shoot or leaf (*Pteridium*) in most cases was not found to be significantly different from the control plot and was therefore used to estimate the overall biomass of field layer species (cf. [7]). In this study, the shoot density, height, and diameter growth was tested by ordinary statistical methods by using variance analysis [16] in order to find significant differences.

3. Results and discussion

The observations of the sample plots in 1997, 2001, and 2008 confirmed the results from the short-term study [7]. The overall biomass of main field layer species was therefore estimated using the mentioned indirect method [15] where the biomass per shoot was multiplied with the shoot density and the coverage of the same species. The shoot density in pure stands is shown in **Table 1**, where the numbers in the table are referring to the size of the sample plots in cm^2 (10 by 10 cm vs. 20 by 20 cm or 100 by 100 cm). **Table 1** shows a strong increase in shoot density

of *Calluna vulgaris* and a moderate increase in *V. myrtillus* during the period of 1997–2001. In the other species, the shoot density was decreasing, and in *Deschampsia flexuosa* partly missing (see **Table 1**).

Biomass estimates. There was a significant increase from 1993 to 1995 (cf. [7]) in biomass per shoot in green and nongreen *Pteridium*, and in nongreen *Calluna vulgaris* tissue, and a corresponding decrease in green tissue of *Calluna* and *Deschampsia*, and nongreen *V. myrtillus* and *V. vitis-idaea*. During the following period, from 1995 to 2001, however, there were no significant changes in biomass per shoot in any of the investigated species (**Table 2**). The mean values of this parameter were therefore used to estimate the overall biomass of green and non-green tissue in each species in 1995, 1997, and 2001.

The mean estimated biomass in g/m^2 of each of the investigated species was shown in **Figure 2**. From this figure, it may be concluded:

- There was a strong increase in green and nongreen *Calluna* tissue during the period from 1993 to 2001 to a top level that is 3–7 times as high as in the control plots, and the highest level was found in the green tissue.

- In the remaining six investigated species (*Vaccinium myrtillus*, *V. vitis-idaea*, *Pteridium aquilinum*, *Molinia caerulea*, and the moss *Polytrichum* spp.), the biomass in green and nongreen tissue increased from 1993 to 1997 and then decreased – but still at a higher level than in the control plots, except from *Vaccinium vitis-idaea* (see **Figure 2**).

The *Calluna* biomass increased strongly during the whole period, due to a combined effect of increased shoot density and increased coverage. The green biomass in the *Calluna* regrowth after the fire was still very high in 2001, with a shoot/root ratio of 3.7, while the corresponding value was 0.5 at the control plot. The *Calluna vulgaris* has probably been enhanced by a high number of seeds that were present in the soil already before the fire (e.g., [17, 18]) and activated by the fire and better light and nutrient conditions [8]. This result was also confirmed by Måren [19] and Måren and Vandvik [6], who studied the succession after a con-trolled fire in a coastal heathland and found that seed germination in *Calluna* could be stimulated by smoke and ash from the fire. They also found that the seed bank in the soil was acting as a refuge and was not influenced by the management with prescribed burning (cf. [20]).

Coverage of main species. The coverage (%) of the main field layer species in 2001 and 2008 (**Table 3**) was recorded and compared with earlier measurements from 1995 [7]. There was a strong increase in the coverage of *Calluna vulgaris* and in the two *Vaccinium* species (*V. myrtillus* and *V, vitis-idaea*) as well as in the bracken (*Pteridium aquilinum*) during the period from 1995 to 2001 and a moderate increase in the coverage of the grass species *Molinia caerulea*. During the following period from 2001 to 2008, there was a further moderate increase in the coverage of these species, but in *Deschampsia flexuosa* and *Polytrichum* spp., the coverage was decreasing during the whole period. The coverage of *Pinus sylvestris* and *Betula pubescens* seedlings increased during the same period, from 22 to 28%. The total coverage increased strongly from 83 to 152% during the period of 1995–2001, but during the following period up to 2008, there was only a slight increase, from 152 to 157%. Strong variations were found in 2001 between sample plots, from a total of 109% on the nutrient-poor plot 5 to 223% on the mesotrophic plot 4 in accordance with soil conditions [21].

The coverage of *Calluna* was more than 50% already in 2001, and strong com-petition between the well-adapted *Calluna* and more slow-growing plants seemed

Species/plot	1995	2001							2008							Ctr
		1	2	3	4	5	6	Mean	1	2	3	4	5	6	Mean	
Calluna	30	48	64	56	58	48	60	**54**	51	60	71	55	32	78	**58**	20
V. myr	4	4	3	5	0	26	10	**9**	3	13	2	10	30	19	**13**	40
V. v-i	2	11	13	14	6	3	14	**11**	11	10	17	14	7	3	**10**	10
Pteridium	15	46	22	22	19	6	10	**21**	36	30	24	26	1	20	**23**	8
D. flex	6	2	10	2	2	3	3	**4**	0	4	3	0	0	0	**1**	4
Molinia	7	20	12	6	13	11	0	**10**	13	7	3	20	11	9	**11**	12
Polytrichum	19	13	70	16	5	2	13	**20**	12	23	2	5	16	2	**10**	2
Pinus	14	15	5	16	6	5		**12**	18	14	11	8	7	12	**14**	45
Betula	7	14	4	16	4	4		**10**	13	20	9	11	8	11	**14**	20
Total	**83**	**165**	**223**	**130**	**135**	**109**	**119**	**152**	**157**	**186**	**156**	**149**	**98**	**165**	**157**	**161**

Table 1.
Percentage coverage in field layer species, including pine and birch seedlings, at each of the six study sites during 1995–2008 (n = 5) with mean values, as compared with the control site (Ctr).

Species	cm²/ plot	1997							2001						
		1	2	3	4	5	6	Mean	1	2	3	4	5	6	Mean
Calluna	100	97	118	98	84	117	79	**99**	155	143	122	156	168	151	**149**
V. myr	400	142	121	76	135	85	126	**114**	98	166	92	166	107	127	**126**
V. v-i	400	65	43	49	35	54	53	**50**	39	57	40	45	56	39	**46**
Pteridium	10000	12	12	14	14	13	10	**13**	15	12	11	10	10	6	**11**
D. flex	100	84	147	180	182	130	76	**150**	116						
Molinia	100	39	40	36	41	42	34	**39**	31	26	29	26	28		**28**
Polytrichum	100	113	98	70	139	128	73	**120**	72	104	127	112	114	63	**99**

Table 2.
The density in pure stands of the investigated species at each of the six study sites in 1997 and 2001 (n = 5), as related to the size of the sample plots in cm² and the mean density per species.
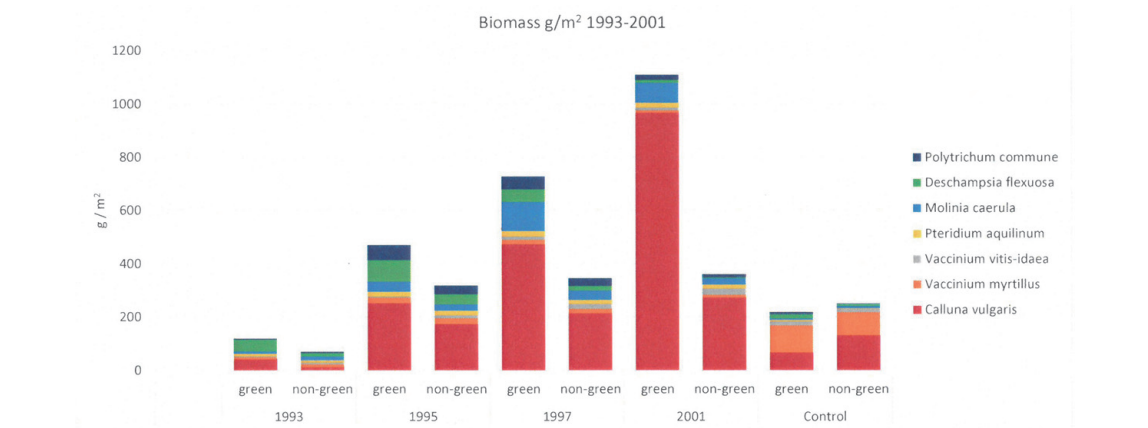

Figure 2.
Mean estimated overall biomass (g/m²) in green and nongreen tissue of the investigated field layer species during the period from 1993 to 2001 as compared with control plants from an unburned area outside the fire.

to have caused a slight decrease in light-dependent species like *Vaccinium myrtillus* and *Deschampsia flexuosa* after an initial rapid period of establishment after the fire. Unlike C*alluna*, the regeneration of the two *Vaccinium* species takes place mainly from surviving rhizomes, and a comparison with the control plots shows that the green biomass had been strongly reduced by the fire (e.g., [22]).

In addition to *Calluna vulgaris*, two other species seemed to have taken advantage of the fire, for example, the bracken *Pteridium aquilinum* and the light-sensitive grass *Deschampsia flexuosa*. Both of these species are reproducing vegetatively, the *Pteridium* by putting out a very deep rhizome network that can survive medium and low intensity fires [23] and producing large leaves that are able to compete successfully on light and nutrients. *Deschampsia* are surviving as resting buds in the upper soil layer [18, 24] that take advantage of improved light and nutrient conditions after the fire [8]. However, the long-term study indicates that increased competition after 2001 may have caused a strong reduction in growth and survival rates of *Deschampsia* (cf. [7]).

The coastal and oligotrophic grass species *Molinia caerulea* also survived the fire because of its deep root system and humid soil conditions. It was not shown in the samplings from the short-term study, but then its coverage increased strongly from 1995 to 2001 and then stayed constant (see **Table 3**). Like *Deschampsia, Pteridium,* and *Calluna*, the *Molinia* tussocks seem to be favored by improved light conditions and are reported to inhibit pine reproduction by removing access to the mineral soil layer [25].

In the two moss species *Polytrichum commune* and *P. juniperinum,* there was also a strong increase in biomass after the fire. The pioneer mosses *Polytrichum juniperinum* and *Ceratodon purpureus* [8] are dominating at the nutrient-poor sites 5 and 6 (see map on **Figure 1**), and in agreement with earlier reports [18] seem to culminate 2–3 years after the fire (**Table 3**).

The present results agree well with the results from a short-term study on the succession in a pine forest in Mykland, southern Norway after a forest fire in 2008 [25]. They found strong *Pinus* regeneration already 4 years after the fire (cf. **Table 4**), and the corresponding mean height of pine seedlings was then 10–50 cm, while the mean height of pine seedlings in the present study 9 years after the fire (2001) was 190 cm. The four most common pioneer species after the fire were the same as in the present study, but in a different order. In the present study, *Calluna vulgaris* was the dominant species with about 30% coverage already 3 years after the fire (**Table 3**), while in the Mykland study, *Molinia caerulea* was the most abundant (5–15%), with *Calluna* only covering 2–4% 4 years after the fire [25]. In both studies, the *Polytrichum* moss species were very common during the first year after the fire.

Long-term successions. Due to a strong increase in the total plant cover during the three first years after the fire, and to a certain degree in the shoot density, there was a strong increase in the overall biomass (cf. **Figure 2**), in particular in *Calluna* and *Molinia caerulea*, but also to a certain degree in *Deschampsia, Polytrichum,* and *Pteridium*. This increase continued in 1997, but then it culminated in all the investigated species except *Calluna*, which was totally dominating in 2001, probably due to the improved light and nutrient conditions. As a result, a gradual increase took place also in the total plant cover in the field layer and reached 90% by 1995 and

	Species	mg/shoot	
		Green	Non-green
Calluna vulgaris		118	40
Vaccinium myrtillus		86	88
Vaccinium vitis-idaea		160	96
Pteridium aquilinum		7290	5500
Desdhampsia flexuosa		90	30
Molinia caerula		270	90
Polytrichum spp.		20	12

Table 3.
Mean biomass in mg per shoot of green and non-green tissue of the investigated species, measured in 2001 (n = 30).

	2001							2008						
Species/plot	1	2	3	4	5	6	**Sum**	1	2	3	4	5	6	**Sum**
Pinus	1.4	5.6	3.6	2.4	1.2	0.8	**2.5**	3.4	6.2	4.6	2.0	2.0	1.6	**3.3**
Betula	0.8	2.4	1.8	3.0	0.6	1.4	**1.7**	2.2	6.4	1.6	4.0	1.6	1.4	**2.9**
Salix	0.2	0.9	1.0	0.6	0.2	0.2	**0.6**	0	0.3	0	0	0	0.2	**0.1**

Table 4.
Mean tree density (n = 5) of Pinus sylvestris, Betula pubescens *and* Salix *spp. on 10 m² study sites at the six investigated study sites, measured in 2001 and 2008.*

150% by 1997 and then stayed constant (**Table 3**). The improved light and nutrient conditions may partly also be a result of the accumulation of dead organic matter after the fire, as reported by Vestmoen [26] and Nygaard and Brean [25], on a much higher scale, and by similar studies in Sweden [27, 28]. The total biomass of the investigated species in 2001 was much higher than the corresponding biomass at the control plot, mainly because of the strong growth of *Calluna*. However, with increasing competition for light, water, and nutrients, a decrease is expected in the production rates of the field layer. **Tables 4** and **5** indicate that in the future there will be more competition also from *Pinus* and *Betula* seedlings that are expected to gradually replace the more light-dependent species in the field layer (see **Figure 3**).

The regrowth and density of trees in 2001 and 2008, that is, 9 and 16 years after the fire, are shown in **Tables 4** and **5**. Seedlings of *Pinus sylvestris* and saplings of surviving *Betula pubescens* seemed to have established at all plots in 2001, and there was a further increase in density, to maximum of 3.3 and 2.9 trees per 10 m² in 2008. In *Salix,* the regrowth was small and insignificant (**Table 4**).

			2001							2008				
Species/plot	1	2	3	4	5	6	Sum	1	2	3	4	5	6	Sum
Diameter (mm)														
Pinus	3.1	1.8	2.8	4.0	3.2	3.4	**3.1**	7.7	3.4	4.1	3.7	5.2	4.2	**4.7**
Betula	2.8	1.6	3.4	3.7	3.1	3.1	**3.1**	5.4	4.3	2.9	4.0	3.5	2.4	**3.8**
Height (m)														
Pinus	2.3	1.7	2.0	2.1	1.4	2.1	**1.9**	4.0	2.5	2.6	2.7	1.8	2.1	**2.6**
Betula	2.7	1.7	2.7	2.8	2.3	2.6	**2.5**	4.0	5.0	2.6	3.2	2.3	1.7	**3.1**
Age (yrs)														
Pinus	9.3	8.8	8.3	9.0	8.9	10.7	**9.2**	13.0	11.0	11.2	11.5	12.3	11.0	**11.7**
Betula	10.0	7.3	9.1	10.3	10.4	10.7	**9.6**	14.2	16.6	9.9	12.2	11.8	12.7	**12.9**

Table 5.
Diameter and height (n = 5) of Pinus sylvestris *and* Betula pubescens *seedlings at the six investigated study sites, with mean values, measured in 2001 and 2008.*

Figure 3.
View of the low-intensity burned site 2 from 2008 with pine regeneration competing with Calluna *and* Pteridium *in the field layer.*

Further information on tree growth and development is shown in **Table 5**. The established seedlings and saplings showed a strong (50%) height and diameter growth during the period from 2001 to 2008 in both species. Finally, it is interesting to note that the recorded age (years) of the two tree species corresponded well with the observed age in 2001 but was considerably lower in 2008, indicating a certain seed regeneration from surviving mother trees also after the fire, in accordance with the results from a similar study by Nygaard and Brean [25].

Carbon-binding capacity. One of the implications of **Figure 2** is that on short term, the CO_2-binding capacity of the forest is severely damaged as a result of the fire, but on longer terms (10–15 years), the reduction in CO_2 uptake is partly compensated by the strong growth in aboveground green *Calluna* tissue. This conclusion is partly supported by results from coastal heathland studies (e.g., [19]) but not by Kjønaas et al. [29] in long-term successional studies on a spruce planta-tion in southeastern Norway as influenced by clear cutting. They found that the CO_2 uptake in understorey biomass and litter during the first 10–15 years after a clear cut was of the same order as the corresponding annual CO_2 output in the living tree biomass during the following succession, up to the mature stage of 130 years. **Table 3** indicates that the percentage coverage of *Calluna* 10–15 years after the fire is of the same order or higher than the combined coverage of the two dominating tree species (*Pinus sylvestris* and *Betula pubescens*) at the control plot. The much higher shoot/root ratio in young *Calluna* relative to old plants at the control plot (3.7 vs. 0.5) also indicates that regularly controlled burning at intervals, for example, 5 or 10 years as described by Måren [19] and Kaland [30], may be as efficient as, for example, spruce plantation in the carbon uptake process as climatic regulators. These results have also been supported by other studies from northern boreal forests, for example, by Ivanova et al. [31], Kukavskaya et al. [32], and Tarasov et al. [33] on succession after fire in Siberian pine forests. Also, other studies emphasize the function of forest fires in the process of recycling nutrients and speeding up regeneration, photosynthesis, and growth, including the CO_2-binding capacity (e.g., [34, 35]; see also [36]).

4. Conclusion

In line with the three objectives of the study, some species may have taken advantage of improved light and nutrient conditions after the fire. This refers particularly to the heather (*Calluna vulgaris*), which seems to be particularly well adapted to fire. In fact, the coastal heaths with pine forests in Norway have been regularly burned for more than 2000 years in order to enhance the growth of green *Calluna* tissue as food for animals [30] and to facilitate seed regeneration in pine [14]. However, the fire also favors other light-dependent species like *Pteridium aquilinum* and *Molinia caerulea*. According to, for example, Måren et al. [37], *Pteridium* is competing with *Calluna* on burned areas of coastal heathlands, but repeated cutting of *Pteridium* will help favoring *Calluna* growth. Furthermore, because seed regeneration of pine is favored by exposed mineral, the fire will increase pine regrowth and juvenilization. On the other hand, plants dependent on vegetative reproduction like *Vaccinium myrtillus* may be permanently suppressed [38].

In some parts of the study site (plots 4 and 5), the humus layer and soil were almost burned off, and the regrowth may have been permanently restricted by lack of nutrients and water (**Figure 4**). In these areas, the succession process may take place over a very long time, after a new soil layer has been formed by mosses and other pioneer plants. But, on the remaining part of the study site, where water and

Figure 4.
View of the high-intensity burned site 5 from 2008 with missing or sparse soil cover and dead fallen pine trees. In the background Hopsfjellet and Mardalsfjellet.

nutrients are not limiting factors, increasing pine and birch growth is expected to shadow out light-dependent plants such as *Deschampsia flexuosa*, *Molinia caerulea*, *Pteridium aquilinum,* and *Calluna vulgaris*, and after a period of time that may take 100 years or more [8], the ecosystem may have reached its climax stage again and be back to the starting point (cf. **Figure 3**).

The study also indicates that periodic burning of old-growth *Calluna* heath (cf. [19]) may be as efficient in the CO_2 uptake process in short terms (10–15 years) as climate regulators as spruce plantations in coastal districts of Norway.

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