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Distribution of Woody Biomass on the Outwash Plain of a Retreating Glacier in Southern Iceland: Role of Microhabitat and Substrate

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Abstract: The Skaftafellsjökull is an outlet glacier in southern Iceland that has been retreating since 1890. While multiple studies have examined primary succession on the foreland of this glacier, no study has examined the distribution of woody biomass on the outwash plain. We investigated the distribution of one species, *Betula pubescens*, that grows on the foreland moraines and outwash plain of this glacier. The topography of the outwash plain is heterogeneous, consisting of broad bars of outwash gravel and boulders that are separated by narrow incised channels and broader swales. Vegetation on the outwash plain is primarily a moss–heath community. Birch are sparse on the outwash bar tops, but are more abundant and larger in the channels and swales between the bars. Although the area of the channels on the outwash plain is much less than that of the bar surfaces, the woody biomass of the outwash plain is dominated by the birch within these channels. Consequently, the mean woody biomass of the outwash plain exceeds that of the moraines. We propose that the microhabitat of the outwash plain channels provides a favorable environment for the growth of birch, primarily by providing a fine-grained substrate that promotes successful seeding and growth.

Keywords: outwash plain; biomass; glacial foreland; microhabitat; moraines

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1. Introduction

As highlighted by recent IPCC reports, anthropogenic climate change has impacted the cryosphere profoundly, most particularly at higher latitudes [1]. Changes in the mass balance of glaciers in Arctic and subarctic settings, as well as of alpine glaciers in temperate latitudes, has resulted in a near-global retreat of glacial termini. One of the most significant consequences of this widespread glacial retreat is the cascade of ecological processes on the exposed forelands that constitutes primary succession [2,3]. Irrespective of latitudinal or elevational setting, the retreating ice exposes a geomorphic land area, the glacial foreland, that is subject to a host of abiotic processes, including chemical weathering and pedogenic modifications [4], as well as biotic colonization [5,6] on scales ranging from the microbial to the macroscopic. These complex and intricately linked processes ultimately result in the formation of new ecosystems in terrain previously occupied by ice [7], as primary succession progresses from pioneer, through middle and into mature community stages, each with the potential to accumulate biomass carbon. Consequently, these forelands, many formed following the conclusion of the Little Ice Age, are considered optimal settings for the study of rates and processes of landscape modification through floral colonization and pedogenesis [4].

Research in recent decades has produced an abundance of studies on primary succession in glacial forelands [8–17], despite which there remains considerable disagreement on the specifics of the driving successional mechanisms [5–7,18–21]. Furthermore, the vast majority of glacial foreland studies address successional processes and changes primarily on glacial forelands sensu stricto, i.e., land area formerly covered by ice and now covered by ice-contact glacial sediments (i.e., diamict). But glacial forelands in the broader sense are topographically heterogeneous and include the associated outwash plains. These have received far less attention, in part because the ages of portions of many outwash plains are poorly constrained. Hence, successional processes have been less studied on outwash plains [22], with few comparisons made to the communities formed on the adjacent terrain covered by ice-contact deposits [23].

Curiously, given the importance of carbon sequestration by landscapes of all types in relation to anthropogenic carbon emissions, relatively few studies have addressed quantitatively the biomass accumulated during ecological succession in proglacial settings (the study by Greinwald and colleagues [24] is an exception). More commonly, studies have focused on microbial biomass, due to the importance of the growth of microbial communities for nutrient cycling [25–27], and/or soil carbon (or soil organic matter) accumulation [23,28–32]. One study [33] that made a contribution toward a better understanding of the accumulation of plant biomass on a glacial foreland examined the distribution and temporal dynamics of the woody-stemmed plant species on the foreland moraines, but not the outwash plain, of a retreating glacier in southern Iceland. In addition to investigating the respective roles of these species in colonization and later successional stages, the authors calculated their accumulated biomass carbon. The present study extends this previous work by examining the distribution and calculating the biomass of woody plants on the foreland outwash plain of the Skaftafellsjökull, the location of the earlier study. Other previous studies of this foreland [34,35] found that only one woody species *Betula pubescens* (Downy birch) is common on this outwash plain, but its distribution is highly variable. We examined the distribution of this species on the outwash plain with the objectives of (1) determining the environmental controls on its distribution and (2) evaluating its contribution to the accumulation of biomass carbon of this environment.

2. Methods

2.1. Previous Work

The Skaftafellsjökull, an outlet glacier of the Vatnajökull, started retreating at the conclusion of the Little Ice Age in 1890. Previous studies have documented that vegetative cover and soil development increases dramatically across the foreland with distance from the current location of the glacier, an approximate proxy for time [34,36,37]. As noted in these studies [34,35], the mature successional community on the moraines is a shrub–heath assemblage dominated by low shrubs, including *Empetrum nigrum* (Black crowberry), *Calluna vulgaris* (Scotch heather), *Arctostaphylos uva-ursi* (Bearberry), *Dryas octopetala* (Mountain avens), and *Saxifraga oppositofolia* (Purple saxifrage), in addition to common mosses, primarily *Racomitrium lanuginosum* (Hoary-fringe moss), and the dwarf trees *B. pubescens*, *Salix lanata* (Wooly willow), and *Salix phylicifolia* (Tea-leaved willow). In contrast to the moraines, on which mosses account for <50% of surface cover, the outwash surface, which consists of broad bars separated by narrow channels and swales, is covered by a moss–heath community in which mosses cover 75% to 89% of the bar surfaces, with low shrubs and *B. pubescens* comprising only minor components; *Salix* spp. are nearly absent. Notably, *B. pubescens* is more concentrated in the narrow channels and swales between the bars than on the broad outwash bar surfaces [35]. The authors concluded that the difference in succession trajectory between the moraines and the outwash plain results from the ability of vascular plants to colonize the differing substrates, i.e., glacial diamict vs. outwash gravels, that form the respective landforms.

Building on the earlier work, the temporal and spatial trends of the three woody species that occur on the foreland moraines (*B. pubescens*, *S. lanata,* and *S. phylicifolia*) were studied to investigate their individual responses from early colonization through later successional stages [33]. This study found that the willow species, particularly *S. lanata*, were effective as pioneer species on the foreland. Moreover, the study found that all woody species increased through middle successional stages, but that birch continued to increase in late stages even as willows declined. As a secondary objective, the study gathered data on biomass accumulation by these species on the Skaftafellsjökull foreland moraines and found that the woody biomass on the moraines, which was dominated by birch, increased with time; as noted above, this study did not examine locations on the outwash plain.

2.2. Location

Measurements were carried out on the outwash plain beyond the most distal recessional moraines of the Skaftafellsjökull (Figure 1). The modern climate for this area of the Icelandic south coast is a mean annual temperature of ca. 5 °C, mean July temperature of 10.5 °C, and mean annual precipitation of 1400 mm to 1800 mm [38]. Like most of the other outlet glaciers of the Vatnajökull, the Skaftafellsjökull has been in retreat since the end of the Little Ice Age in 1890 and has retreated ca. 3 km since [39]. This retreat has exposed a foreland area of recessional and push moraines bordered by an outwash plain. The most distal moraine of the Skaftafellsjökull that is clearly identifiable is dated to the position of the ice front in 1890.

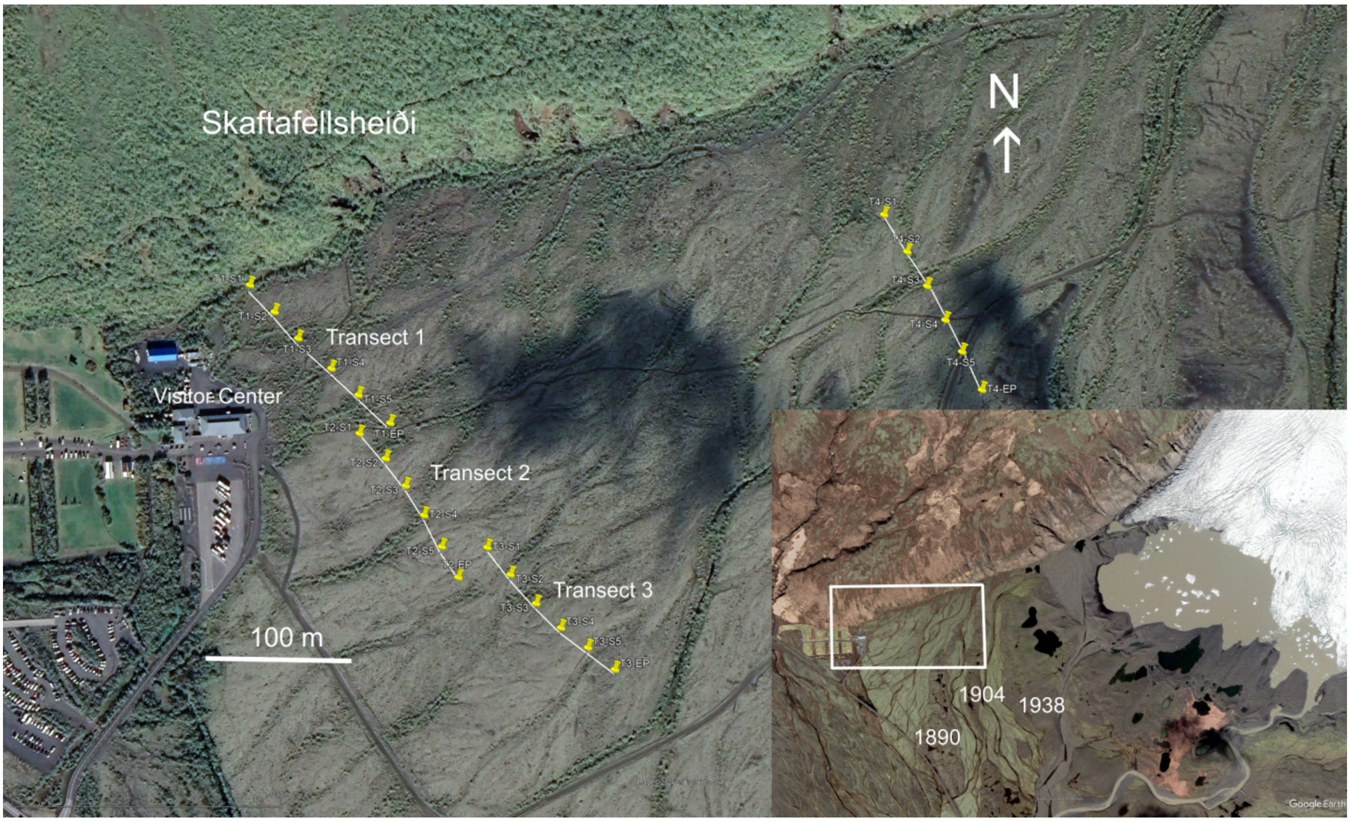

Figure 1. Aerial view of the study area in the Vatnajökull National Park. Skaftafellsheiði is the birch-covered ridge that borders the glacial foreland and outwash plain. Transects oriented with starting point (first pin) to the northwest and end point (sixth pin) to the southeast. Surfaces of the outwash bars are lighter colored, with darker green lines of birch filling the channels and swales. Inset view outlines the study area and illustrates relationship of the outwash plain to the glacial moraines, labeled by year of exposure during glacial retreat, and the Skaftafellsjökull. Darker area in southwest corner of inset map is the margin of the adjacent Skeiðarársandur, the active outwash plain of the Skeiðarárjökull. Imagery adapted from Google Earth®.

The outwash plain surface differs from the moraines in both topography—the outwash bar deposits generally have nearly horizontal surfaces separated by narrow channels and broader swales, in contrast to the slopes of the moraines—and in composition; the moraines consist of very poorly sorted deposits (diamict) with fine-grained material mixed with protruding boulders, while the outwash consists mainly of sorted gravel- to boulder-sized clasts [35]. More specifically, the outwash plain consists of overlapping compound diamond-shaped fluvial bars with a northeast-trending orientation. Their size is variable, ranging in width from thirty to seventy meters, and in length from tens to hundreds of meters. These compound bars are mantled by a dominant hummocky moss and subordinate low heath shrubs. The bars are separated by sinuous swales and narrow channels, varying from 2 m to 12 m in width and from 0.5 to 1.5 m in depth. The age of the outwash channel and bar surfaces generally are not well constrained, other than by the moraines that form the outwash plain boundary, i.e., the possibility of continued reactivation of portions of the outwash plain by floods during glacial retreat over the course of many years removes rigid age constraints. The study area was used for sheep farming, but was largely abandoned for grazing after the Skaftafell National Park (now incorporated within the Vatnajökull National Park) was established in 1967, and formally fenced off in 1987 [37].

2.3. Field Techniques

The distribution of *B. pubescens* was examined by establishing four linear transects crossing the outwash plain bars and channels. Each transect was 150 m in length and 0.5 m wide, subdivided into five contiguous 30 m segments. The coordinates of the transect points were recorded by handheld Global Positioning System devices (manufactured by Garmin Ltd., Olathe, KS, USA) at the transect end points and every 30 m along the transect. The total area studied for each transect covered an area of 75 m^2, or 300 m^2 total for the four transects. The starting point for Transect 1 was 120 m north of the Vatnajökull National Park Visitors Center at the northwestern edge of the outwash plain, near the base of the Skaftafellsheiði ridge. Transects 1 through 3 form a near-continuous linear sequence with the end points of successive transects offset laterally by 20 m. Transect 4 was established approximately 450 m to the northwest of Transect 3. Within the area of each transect, the length of all specimens of *B. pubescence* was recorded and the diameter measured for specimens longer than 0.7 m at 0.5 m height. The location of each specimen was recorded as residing either on an outwash bar or within a channel/swale.

2.4. Data Analysis

The birch specimens all fall into one of two classes based on their location, channel (and/or swale), or outwash bar. By estimating the length of each transit that crossed channels or swales, it was possible to determine the portions of the studied area (300 m^2 total) occupied by outwash plain and channels, allowing comparisons of specimen density and size. The data were analyzed with an independent t-test and a one-way ANOVA test using the statistical software package SigmaStat version 4.0 (manufactured by Systat Software Inc., San Jose, CA, USA) to determine if there was a statistically significant difference between the means of the channel and bar specimens.

The above-ground biomass (AGB) for each specimen was calculated using a species-specific algorithm [40]. For *B. pubescens*, dry weight (in kg)

$$\mathrm{AGB} = 0.0634\ \mathrm{d}^{2.1552}\mathrm{h}^{0.2877} \tag{1}$$

where h = stem height (m) and d = diameter (cm) at 0.5 m height. Root biomass (RB) for each birch specimen was calculated using an empirical equation for *B. pubescens* [41],

$$\log(\mathrm{RB}) = 0.985 \times \log(\mathrm{AGB}) - 0.124. \tag{2}$$

Total biomass was converted to biomass carbon by a conversion factor of 0.498 [42].

3. Results

3.1. Data Summary

The results of the specimen measurements on all four transects are summarized in Table 1. On Transect 1, the transect closest to Skaftafellsheiði (Figure 1), we measured a total of 78 specimens. Of these, 40 occurred on the bars of the outwash plain and had a mean height of 0.74 m. The remaining 38 occurred within the channels between the bars. On Transect 2, located farther out on the outwash plain, we measured a total of 72 birch specimens. Of these, 56 were located on the outwash plain bars and had a mean height of 0.63 m. The remaining 16 specimens were located in channels and had a mean height of 1.12 m. The decrease in the number of birches in this transect reflects the greater distance between channels, i.e., Transect 2 crossed fewer channels and swales than Transect 1. Transect 3 continued in the same direction as Transects 1 and 2 and so was the most distal of the transects from Skaftafellsheiði. Here, we measured a total of forty-six birch specimens, forty-one on the outwash bars, with a mean height of 0.54 m, and five in channels, with a mean height of 1.20 m. Only two segments of this transect (T3-2 and T3-5) crossed channels, as broad outwash bars separate the channels on this area of the outwash plain. Transect 4 was positioned more proximal to the oldest foreland moraines than the other transects (Figure 1), but was oriented parallel to Transects 1 through 3. We measured a total of 40 specimens on this transect, 30 of which were located on the outwash bars, with a mean height of 0.59 m, and 10 in channels, with a mean height of 1.16 m. No birch specimens were encountered on two segments of this transect, T4-4 and T5-5.

Table 1. Data summary of birch distribution and size. *N* = number of specimens in transect segment; h = specimen height (m); d = specimen diameter (in cm) at h = 0.5 m.

Transect	**Outwash Plain**			**Channel/Swale**		
Segment	***N***	**h (m)**	**d (cm)**	***N***	**h (m)**	**d (cm)**
T1-1	11	0.69	0.67	7	1.88	2.59
T1-2	7	0.82	0.64	10	1.28	1.56
T1-3	5	0.65	0.54	6	0.93	1.27
T1-4	10	0.77	0.48	0	0.00	0.00
T1-5	7	0.77	0.63	15	1.28	2.26
T1 mean	8	0.74	0.59	7.6	1.34	1.98
T2-1	16	0.73	0.45	10	1.48	2.00
T2-2	8	0.63	0.46	0	0.00	0.00
T2-3	10	0.55	0.62	3	0.58	0.97
T2-4	8	0.62	0.65	0	0.00	0.00
T2-5	14	0.57	0.38	3	0.94	1.33
T2 mean	11.2	0.63	0.49	3.2	1.21	1.68
T3-1	6	0.64	0.60	0	0.00	0.00
T3-2	19	0.72	0.72	3	1.34	1.60
T3-3	7	0.63	0.43	0	0.00	0.00
T3-4	6	0.43	0.22	0	0.00	0.00
T3-5	3	0.62	1.63	2	1.00	1.80
T3 mean	8.2	0.54	0.65	1	1.20	1.68
T4-1	11	0.59	0.35	4	1.38	1.78
T4-2	4	0.46	0.25	5	1.12	1.24
T4-3	3	0.56	0.40	1	0.44	0.20
T4-4	6	0.72	0.65	0	0.00	0.00
T4-5	6	0.55	0.48	0	0.00	0.00
T4 mean	6	0.59	0.43	2	1.16	1.35

Combined, the four transects cover an area of 300 m^2 (600 m length × 0.5 m width). We measured the total length of the portion of each transect that traversed channels at 85.8 m, or an area of 42.9 m^2. Therefore, the remaining 514.2 m of transect length, or 257.1 m^2 of transect area, represents the tops of the outwash bars. In all four transects, we measured a total of 236 specimens, or a mean of 0.79 specimens m^{-2}. However, the distribution of the individuals is biased toward the channels, with 167 specimens recorded on the outwash bars, for a mean specimen density of 0.65 m^{-2}, and 69 specimens in the channels, for a mean density of 1.61 m^{-2}.

3.2. Biomass Calculation

Using the algorithm described above, we calculated the AGB for each individual measured on the four transects (Table 2). The RB was then calculated from the AGB, to which it was then added. The resulting total biomass was then converted to biomass carbon for the purpose of comparison to other studies [33]. The total biomass (RB + AGB) of the 78 specimens in Transect 1 is 42.14 kg, most of which, 39.36 kg, derives from the 38 specimens in the channels, and just 2.78 kg derives from the 40 specimens on the outwash bars. The biomass in all remaining transects is significantly less than in Transect 1. The 72 specimens measured on Transect 2 yielded a total biomass of 6.08 kg, of which 3.67 kg represents the 16 channel specimens, and the remaining 56 outwash bar specimens contribute 2.41 kg. On Transect 3, we measured 46 specimens with a total biomass of 5.64 kg. The 41 specimens on the outwash bars contain a biomass of 3.32 kg, and the remaining five channel specimens yield a biomass of 2.94 kg. The 40 specimens measured on Transect 4 contain a total biomass of 6.81 kg, with the 30 outwash bar specimens containing 3.87 kg, and the 10 channel specimens yielding 2.94 kg. The total biomass for the four transects combined totals 60.67 kg over an area of 300 m^2, for a mean value 0.202 kg m^{-2}.

Table 2. Biomass calculations for all transect segments, separated by transect segment and specimen location (channel/swale or bar surface). AGB = above-ground biomass; RB = root biomass.

		T1-1	**T1-2**	**T1-3**	**T1-4**	**T1-5**	**Total**	**Total C (kg)**
AGB	channel	7.645	2.585	1.237	0.000	11.290	22.758	
RB + AGB		13.220	4.500	2.170	0.000	19.470	39.360	19.600
AGB	bar surface	0.438	0.394	0.158	0.321	0.265	1.575	
RB + AGB		0.770	0.690	0.280	0.570	0.470	2.780	1.380
AGB	total	8.083	2.979	1.395	0.321	11.555	24.333	
RG + AGB		13.990	5.190	2.450	0.570	19.940	42.140	20.990
		T2-1	**T2-2**	**T2-3**	**T2-4**	**T2-5**	**Total**	
AGB	channel	1.478	0.000	0.224	0.000	0.391	2.092	
RB + AGB		2.580	0.000	0.400	0.000	0.690	3.670	1.830
AGB	bar surface	0.289	0.169	0.384	0.353	0.169	3.035	
RB + AGB		0.510	0.300	0.680	0.620	0.300	2.410	1.200
AGB	total	1.767	0.169	0.608	0.353	0.560	5.127	
RG + AGB		3.090	0.300	1.080	0.620	0.990	6.080	3.030
		T3-1	**T3-2**	**T3-3**	**T3-4**	**T3-5**	**Total**	
AGB	channel	0.000	0.856	0.000	0.000	0.467	1.323	
RB + AGB		0.000	1.500	0.000	0.000	0.820	2.320	1.160
AGB	bar surface	0.035	0.607	0.083	0.012	0.757	1.671	
RB + AGB		0.060	1.070	0.840	0.020	1.330	3.320	1.650
AGB	total	0.035	1.463	0.083	0.012	1.224	2.993	
RG + AGB		0.060	2.570	0.840	0.020	2.150	5.640	2.810
		T4-1	**T4-2**	**T4-3**	**T4-4**	**T4-5**	**Total**	
AGB	channel	1.141	0.533	0.002	0.000	0.000	1.675	
RB + AGB		2.000	0.940	0.000	0.000	0.000	2.940	1.460
AGB	bar surface	1.671	0.011	0.033	0.387	0.105	2.207	
RB + AGB		2.920	0.020	0.060	0.680	0.190	3.870	1.930
AGB	total	2.812	0.544	0.035	0.387	0.105	3.882	
RG + AGB		4.920	0.960	0.060	0.680	0.190	6.810	3.390

4. Discussion

4.1. Comparison of Outwash Plain to Moraines

As described above, previous studies identified differing successional trajectories for the moraines and the outwash plain on the foreland of the Skaftafellsjökull, with a birch–shrub heath constituting the mature community on the former and a moss–heath community dominating the latter [35]. In the most recent study, coverage of the land surface by the different functional groups, including birch and mosses, was measured within m^2 quadrats at five stations along transects on six moraines of varying ages as well as on three transects on the outwash plain in 2022. On the oldest moraine, from 1890, the total vegetation coverage averaged 84.7%, of which mosses covered an average of 39.3%, and birch covered 3.1%; willows were not observed on this moraine (Transect 10 of Table 1 in [35]). In contrast, on the outwash plain distal to the oldest moraine, mean vegetation cover ranged from 81.2% at the transect closest to the moraines to 99.5% on the most distal transect (Transect 9 of Table 1 in [35]); mean moss cover ranged from 74.7% to 89.2%, and birch cover varied from 0.1% to 5.9%, although we note that this study did not differentiate between the channel and bar locations on the outwash plain. These differing successional trajectories have been explained previously as controlled by the differences in landscape substrate [35]. The more heterogeneous texture of the diamict that forms the moraines permits easier penetration of the root systems of vascular plants, with competitive pressures for seeding sites in later stages leading to the decrease in willows and species richness in general [34,35]. In contrast, the consistently coarse substrate of the outwash bars discourages root penetration, but allows coverage by bryophytes.

In another study [33], the size and biomass of birch and willow specimens were measured along transects on a series of moraines ranging in age from 1960 to 1890 (ages based dates of exposure). Notably, mean birch height did not change significantly from the 1960 to 1890 moraines, but woody biomass did increase from 0.005 kg C m^{-2} on the 1960 moraine to 0.029 kg C m^{-2} on the 1890 moraine (Table 3). For this oldest moraine, which borders the outwash plain, the mean specimen density was 1.47 specimens m^{-2}, the mean height was 0.52 m, and the calculated mean woody biomass was 0.005 kg C m^{-2}. By comparison, on the outwash plain in the present study, we measure a mean birch height of 0.63 m on the outwash bars, but 1.27 m in the outwash plain channels and swales. Birch mean biomass on the outwash bars was 0.003 kg C m^{-2}, and 0.56 kg C m^{-2} in the channels, producing a mean for the outwash plain of 0.10 kg C m^{-2}, or 1.0 t C ha^{-1}. Thus, the mean woody biomass carbon accumulation on the outwash plain is approximately three times that on the oldest moraine on the foreland.

Table 3. Summary compiled from data of woody biomass on moraines [33].

	Species	Height cm	Transect Mean g C m^{-2}
1960	*B. pub.*	72	5.26
	Salix spp.		1.89
	combined		7.15
1954	*B. pub.*	54.8	19.86
	Salix spp.		2.26
	combined		22.12
1938	*B. pub.*	54.2	23.49
	Salix spp.		2.25
	combined		25.73
1904	*B. pub.*	46.4	21.13
	Salix spp.		1.35
	combined		22.48
1890	*B. pub.*	51.8	27.91
	Salix spp.		0.63
	combined		28.54

These data demonstrate that the average woody biomass across the outwash plain is strongly weighted by the concentration of birch in the channels. Despite the general appearance that woody biomass is sparse on the outwash plain (Figure 1), it is significantly greater than on the oldest and most vegetated moraines. For additional perspective, the carbon stored in the foreland soils has been measured (in the upper 10 cm) at a maximum of 1.2 kg C m^{-2} on the oldest moraine [34]. Although no studies have examined the soil carbon of the outwash plain, our results indicate that the biomass of a single species makes a small but measureable contribution to carbon storage on this landscape.

4.2. Outwash Bars vs. Channels

Across the outwash plain, it is visually evident that there is a clear difference in the distribution of birch between the outwash bar surfaces and the channels in regard to both the density of birch specimens (number per unit area) and their height, and consequently, the biomasses. From a satellite view, the sinuous channels between the outwash bars are highlighted by the dark leaves of the birch that line the floors of many of the channels (Figure 1). From ground level, it is equally evident that the bar tops are nearly devoid of vegetation other than the nearly continuous moss hummocks, and where birch does occur on the bar surfaces (mean = 0.65 specimens m^{-2}), they are on average shorter than those in the channels (mean = 0.63 m). The channels contain birch arranged in lines and locally in dense thickets (mean = 1.61 specimens m^{-2}) that typically stand higher than the tops of the surrounding outwash bars (mean = 1.27 m; Figure 2). Statistical comparisons of specimen height for the entire dataset by both t-test and one-way ANOVA demonstrate that these differences are significant. The t-test comparison of the heights of all specimens identified as from channels vs. those from bar tops yields a value of t = 9.693 with 228 degrees of freedom, a 95% two-tailed confidence interval for the difference of means of 0.458 to 0.692 with a two-tailed value of $p = 7.949 \times 10^{-19}$, and a one-tailed value of $p = 3.975 \times 10^{-19}$. One-way ANOVA of the same data yields similar results (f = 94.674; $p < 0.001$).

Figure 2. View of the outwash looking west (Skaftafellsheiδi to the right covered by birch) illustrating bar surface covered by hummocky moss and minor low heath shrubs, with most birch occupying the adjacent swale.

This difference is expressed also in the distribution of biomass. The total birch biomass (AGB + RB) measured in the study is 60.67 kg, which, divided by the total measured area of 300 m^2, equates to 0.202 kg m^{-2} (or 0.10 kg C m^{-2}) over the outwash plain. However, the distribution of this biomass is unequal between outwash bar surfaces and channels; 48.29 kg of birch in the channels yields a mean biomass of 1.13 kg m^{-2} (0.56 kg C m^{-2}), while 12.38 kg of birch on the outwash bars produces an average of 0.005 kg m^{-2} (0.03 kg C kg m^{-2}).

The difference in the numbers and sizes of birches in the channels and on the bar tops indicates that the former environment is a microhabitat that is more conducive to seeding and growth than the surrounding outwash bars. In comparing primary succession on the outwash bars to the foreland moraines, it was noted previously [35] that the bar surfaces have a uniformly coarse-grained substrate and it was suggested that this forms a difficult environment for the penetration of the root systems of vascular plants in general. Conversely, the coarse substrate presents no obstacle for the spread of bryophytes, allowing moss to dominate the bar surfaces. We suggest here that following formation of the outwash bars, prior to and during glacial retreat, seasonal melt runoff provided finer-grained sediments to the floors of the channels. This fine-grained substrate would be more conducive to the germination and growth of seeds of *B. pubescens*. As noted by others [33], the nearby ridge Skaftafellsheiði is a likely source of birch seeds to the foreland. Although we did not measure soil moisture in this study, we present the additional possibility that soil moisture is greater in the low areas on the outwash plain, i.e., the channels and swales, and suggest that greater soil moisture may be a factor that promotes the growth of the birch in these locations. The bar tops, conversely, consist of coarse sediments that do not retain appreciable moisture. Soil moisture has been cited as a major control of foreland vegetation patterns in some studies [43,44].

4.3. Transect 1 Anomaly

The data (Table 1) indicate that the distribution of birch within the channels is not uniform across the outwash plain, but is instead subject to a strong locational bias. On Transect 1, which extends southeast from near the base of Skaftafellsheiði and crosses four channels, we measured a total of 38 specimens, the most of any transect in the study. Additionally, the mean height of the channel birch in Transect 1, at 1.38 m, is the highest of all transects in the study. In particular, segment T1-1, proximal to Skaftafellsheiði, contained seven measured specimens with a mean height of 1.88 (ranging from 0.36 m to 3.08 m), but in transect segments T1-2 through T1-5, the mean height of birches in the channels decreases sharply with distance from the Skaftafellsheiδi ridge. Within transects 2 and 3, there is also a general decrease in the mean height of the specimens with increasing distance from Skaftafellsheiði. We note that Transect 4 is not on the same linear trend as Transects 1 through 3, but also displays a trend of decreasing channel specimen size with distance from the ridge. However, these trends of decreasing numbers and heights of birch specimens is not as pronounced on the outwash bar surfaces. There is a distinct negative correlation between the number of birch growing on the moraines and distance from Skaftafellsheiði, although the correlation does not reach the level of statistical significance of $p < 0.05$ [33]. Thus, the trend in the number of birch in the channels may possibly be related to distance from the ridge, as more seeds are available in proximal locations, with dispersal possible via wind, precipitation runoff, or avian vectors. However, the proximity factor alone does not explain the trend in birch height also decreasing with distance from the ridge.

We note here that there are many small landslide scars at the edge of Skaftafellsheiði (visible in Figure 1) that likely serve as ephemeral streams that drain the ridge following precipitation and seasonal snowmelt. We propose that this runoff from the ridge provides moisture to the channels, either directly to the stream beds or by raising the water table of the outwash plain, and promotes the growth of the birch more proximal to the ridge. Thus, the number and size of birch across the outwash plain is biased both by microhabitat (channel floor vs. bar top) and position on the plain (proximity to Skaftafellsheiδi). The relationship between the water table of a glacial foreland and ecological succession is relatively unexplored, although, as described above, soil moisture is considered an important edaphic factor in vegetation development on glacial forelands [43,44].

5. Conclusions

We studied *Betula pubescens* (Downy birch) growing on the outwash plain of the Skaftafellsjökull to identify the factors controlling the distribution and size of this vegetation and to quantify its ability to store biomass carbon. The outwash plain consists of a broad area of relatively flat bars of outwash gravel and boulders that are separated by sinuous narrow channels. The outwash bars are covered mainly by moss hummocks and scattered low heath shrubs, and sparse, small birch as the only woody biomass. In the channels and swales, the birch are more abundant and significantly larger than in the channels. The area of the channels occupies only a small portion of the outwash plain, but the woody biomass of the outwash plain is dominated by the birch within the channels. We propose that the channels and swales constitute a microhabitat that provides a favorable environment for the growth of birch, primarily by providing a fine-grained substrate that promotes seed germination, and additionally provides greater soil moisture. We also note a locational bias to the biomass distribution on the outwash plain. Birch are both more abundant and larger in channels that are in proximity to a ridge that borders the glacial foreland to the northwest. We suggest that rain and seasonal snowmelt runoff from this ridge provides moisture to the channels, primarily to those located more proximal to the ridge. Lastly, we point out that the woody biomass accumulated on the outwash plain is not negligible, and exceeds that of the moraines.

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