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Regeneration of native broadleaved species on clearfelled conifer plantations in upland Britain

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Abstract

In upland areas of Great Britain, large tracts of non-native conifer plantations have been established on poor quality agricultural land. There is now considerable interest in the conversion of some of these plantations to a more natural woodland comprised of native tree species. We studied the tree regeneration and ground flora on 15 upland sites (altitudes ranging from 120 m to 380 m above sea level) that had been clearfelled of conifers. Regeneration of native tree species was successful where a clearcut site was adjacent to mature native trees, which acted as a seed source. Mean regeneration densities of native tree species on clearcut sites were typically greater than 1000 stems/hectare, exceeding minimum recommended planting densities for the establishment of new native woodland. Whilst 10 native woody tree species were recorded, the regeneration was dominated by birch species. Regeneration densities were significantly higher on clearcut sites than on adjacent areas of unplanted moorland, probably due to the lack of a dense ground flora following the clearfelling operations. Our results indicate that where local native seed sources exist, clearfelling upland conifer plantation sites to allow natural regeneration has the potential to be an effective method of establishing native woodland.

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1. Introduction

Timber plantations have been widely established across Northern Hemisphere mid-latitudes (Zerbe, 2002; Yamagawa et al, 2010) with plantation forests now making up 14% of total forest area in western European countries (Forest Europe, 2011) and about 70% of total forest area in Britain (Brockerhoff et al, 2008). These plantation forests usually consist of fast-growing, non-native conifer species located on marginal agricultural land in the uplands (Humphrey et al, 2006). They are typically intensively managed for timber production with substantial site preparation before planting (e.g., ploughing, drainage, use of fertiliser) and harvesting of timber occurring by clearfelling after a short rotation. Whilst plantation forests can provide habitat for a range of species (Humphrey et al, 2000; Quine & Humphrey, 2010; Bremer & Farley, 2010; Coote et al, 2012), semi-natural woodlands typically contain greater biological diversity (Brockerhoff et al, 2008; Bremer & Farley, 2010). Furthermore, plantation forests can result in soil and stream acidification (Carling et al, 2001) as well as potential negative impacts on water resources. Recently, a greater interest in woodlands for their ecological and recreational value means that semi-natural and mixed forests consisting of native species are becoming increasingly valued (Felton et al, 2010). As many plantations are now reaching the end of their rotations, there is considerable potential for establishment of semi-natural woodland on former plantation forest sites (Spiecker et al, 2004; Dedrick et al, 2007).

The restoration of plantation forests to semi-natural woodland can be carried out through a range of methods. The conifer crop can either be clearfelled or the trees can be removed more gradually through multiple thinning operations. There are also a range of methods for establishing native trees including planting, direct seeding or natural regeneration. Natural regeneration is the establishment of trees from seeds produced in situ (Harmer & Kerr, 1995) and is the preferred means of achieving native woodland expansion in Great Britain (Forestry Commission, 1994). Potential advantages of natural regeneration include the preservation of local genotypes and greater structural diversity of the resulting woodland (Peterken, 1996), high seedling density (Holgén & Hånell, 2000) as well as increased cost-effectiveness (Tarp et al, 2000; Jonásová et al, 2006). Natural regeneration has been studied in a range of environments including degraded lowland tropical pasture (Parrotta et al, 1997), tropical mountain forests (Holl et al, 2000), boreal forest (Peltzer et al, 2000; Holgén & Hånell, 2000; Hanssen, 2003; Man et al, 2008, 2009), lowland European forests (Madsen & Larsen, 1997; Emborg , 1998; Olesen & Madsen, 2008; Modrý et al, 2004; Swagrzyk et al, 2001; Harmer & Morgan, 2009; Wagner et al, 2010; Smit et al , 2012) and European mountain forests (Jonásová et al, 2010; Bace et al, 2012). However, the regeneration of native species on clearfelled conifer plantations is still poorly understood (Zerbe, 2002) with Wallace (1998)'s study of birch regeneration in clearfelled spruce plantations the only previous study in upland Britain.

Here we report the first extensive study of natural regeneration of native hardwood species on clearfelled upland conifer plantations in Britain. We addressed the following questions: (i) How well do native tree species regenerate on clearfelled upland conifer plantations? (ii) How does regeneration on clearfelled conifer plantations compare to regeneration on improved farmland and open moorland? (iii) What are the dominant factors controlling regeneration? (iv) How does the ground flora develop in the years following clearfelling and how does this impact tree regeneration?

2. Materials and Methods

2.1. Experimental sites

We surveyed a total of 21 sites at 4 different upland locations: Hardknott forest and Rainsbarrow wood in the Lake District, north-west England and Clashindarroch forest and Bin forest in Aberdeenshire, north-east Scotland. All forests surveyed were managed by the Forestry Commission. The soil type, obtained from Forestry Commission soil maps, was used to predict the natural woodland community that would be expected to develop (Rodwell & Patterson, 1994). Details of the sites selected are given in Table 1 and locations are shown in Figure 1. Hardknott forest was planted on upland moorland between 1940 and 1955 (N. Williams 2008, Forestry Commission, personal communication). There are several broadleaf woodland fragments of *Quercus spp.* (oak spp.), *Betula spp.* (birch), *Sorbus aucuparia* (rowan), *Ilex aquifolium* (holly) and *Salix spp.* (willow). Nearby Rainsbarrow woodland was planted with conifers between 1959 and 1962 and is designated as a Planted Ancient Woodland Site (PAWS) (Thompson et al, 2003). PAWS are sites with a long history of forest cover, with the original semi-natural woodland cleared and replaced by a plantation, a practice that was widespread in the UK before around 1980 (Thompson et al, 2003). Clashindarroch forest was established from 1930 onwards (Forestry Commission, 1964). Prior to afforestation, the land was mostly upland moorland with a dense flora of *Calluna vulgaris* (ling heather) and *Vaccinium myrtillus* (bilberry) with limited areas of *Pteridium aquilinium* (bracken) on the lower elevations (Forestry Commission, 1952). Bin forest was established from 1926 onwards when most of the land was upland moorland with dense ling heather vegetation (Forestry Commission, 1964). Both Clashindarroch and Bin forests retained small fragments of semi-natural woodland consisting largely of birch and rowan as well as *Alnus glutinosa* (common alder) and willow on the wetter ground.

At these 4 locations we surveyed 15 sites that had been afforested with conifers, clearfelled and then left to regenerate naturally. Table 1 details the species of the felled conifer crop, which was generally dominated by *Picea sitchensis* (Sitka spruce), matching the dominant conifer species used across Britain (Forestry Commission, 2012). The harvesting residues, known as brash, were windrowed - that is, gathered into regularly spaced linear mounds or windrows. Date of afforestation ranged from 1926 to 1942 and the date of clearfelling ranged from 1988 to 2009. At the time of our surveys the time since clearfelling varied from 1 to 15 years. Table 1 details the date surveys were carried out. The area of clearfells was estimated using digitized maps and varied between 0.9 to 35.2 ha. We compared the rates of native tree regeneration on these clearfelled sites to nearby areas which had not been previously planted with conifers (control sites). We surveyed 6 control sites. The control sites were typically situated less than 1 km from the study sites. At a number of the sites former agricultural use had resulted in considerable alteration to the vegetation and the physical and chemical properties of the soil. Therefore we broadly classified all sites as either upland moorland (UM), upland improved farmland (IF) or PAWS (P) based on the present land-use of the control sites or the land-use prior to afforestation for the clearfelled sites. Both the control and the clearfelled sites were fenced to exclude stock. *Capreolus capreolus* (roe deer) and *Cervus elaphus* (red deer) were present at the Clashindarroch and Lake District sites. Only roe deer occurred in Bin forest. Deer control was practiced by the Forestry Commission at all sites.

2.2. Sampling methods

Sites were surveyed using 2 × 2 m temporary quadrats placed along equally spaced line transects. The separation S (in m) between transects and between quadrats on transects was computed by the formula (Harmer & Morgan, 2009): $S = 100\sqrt{A/n}$, where A is the site area (ha) and n the number of quadrats (detailed in Table 1). Quadrats on forest track margins were omitted. In total we surveyed 1140 quadrats. Within each quadrat the species, number and height of all regenerating juveniles (defined here as either seedlings with a height $\leq$ 50 cm or saplings with a height $>$50 cm) were noted. The height of saplings was measured with an extensible folding rule. The incidence of leading stems damaged by browsing on trees $<$2m tall was noted. No attempt was made to distinguish the different birch, oak and willow spp. The distance to the nearest seed source (defined as a mature tree) was measured in the field for each tree species (all the sampled plots lay within 250m of a native seed source.) Within each quadrat we recorded the percentage of quadrat area beneath the canopy of each vascular plant species (as 2 or more species can overlap, this can result in a total vegetation cover of more than 100%) as well as the percentage cover of decaying woody

Site label^a	Site Name	Lat. (°N)	Lon. (°W)	Altitude /m	Area /ha	Soil Type^b	NVC Type^c	pH	Former crop spp.^{d}	Land-use^e	Years since clear-fell	No. quadrats [No. transects]	Month / Year of survey
Bin Forest (Aberdeenshire)													
U5	Ordiquhill	57.470	-2.807	160	7.4	1	W11	4.5	SS/NS	UM	5	120[6]	6/10
U6a	Binside B	57.490	-2.831	170	11.1	1	W11	4.5	SS/SP	UM	6	100[6]	7/10
U10	Binside A	57.478	-2.849	190	2.9	7	W7	4.6	SS	UM	10	60[4]	6/10
Clashindarroch Forest (Aberdeenshire)													
U6b	Longbank	57.379	-2.908	380	35.2	4	W18	4.0	SS	UM	10	60[4]	6/10
U15	Hareetnich A	57.379	-2.941	380	4.1	4	W18	4.2	LP	UM	15	60[4]	6/10
F1	Coynachie	57.390	-2.903	200	0.9	1	W11	5.3	SS	IF	1	60[4]	7/10
F2	Raibet B	57.391	-2.865	230	0.4	1	W11	5.4	SS	IF	2	60[4]	6/10
F4	Raibet C	57.392	-2.860	220	2.3	1	W11	5.4	SS	IF	4	60[4]	6/10
Ua	Raibet D	57.390	-2.873	290	—	1	W11	5.4	—	UM	—	60[4]	6/11
Ub	Hareetnich B	57.381	-2.911	300	—	4	W18	4.2	—	UM	—	60[4]	6/11
Fa	Drumfergue A	57.392	-2.863	230	—	1	W11	5.5	—	IF	—	60[4]	6/11
Fb	Drumfergue B	57.430	-2.873	200	—	1	W11	5.5	—	IF	—	60[4]	6/11
Fc	Raibet A	57.392	-2.867	230	—	1	W11	5.3	—	IF	—	60[4]	7/10
Hardknott Forest (Lake District)													
U2L	Hardknott A	54.309	-3.182	325	3.7	1	W11	3.3	SS	UM	2	22[2]	6/08
U3L	Hardknott B	54.373	-3.188	240	1.5	1	W11	3.1	SS	UM	3	38[3]	6/08
U4L	Hardknott C	54.376	-3.193	200	1.7	1	W11	3.3	SS	UM	4	37[2]	6/08
U7L	Hardknott D	54.373	-3.185	250	1.4	1	W11	3.4	SS	UM	7	40[2]	6/08
U9L	Hardknott E	54.300	-3.182	275	1.7	6	W4	3.5	SS	UM	9	35[3]	6/08
U10L	Hardknott F	54.300	-3.185	300	1.7	6	W4	3.5	SS	UM	10	37[4]	6/08
UL	Grassguards	54.370	-3.194	230	—	1	W11	3.5	—	UM	—	18[2]	5/08
Rainsbarrow Forest (Lake District)													
P7L	Rainsbarrow	54.324	-3.250	120	1.7	1	W11	3.4	SS	PAWS	7	38[4]	5/08

a Site label indicates former land use (U: upland moor, F: improved farmland, P: PAWS) & number of years since clearfelling (indicated by number). All Lake District sites are distinguished by a label L. Control sites are distinguished by lower case alphabetical labels.

b Soil types follow the Forestry Commission classification (Pyatt, 1982). 1: Typical brown earth; 4: Ironpan soil; 6: Peaty gley; 7: Surface-water gley.

c National Vegetation Classification: Potential woodland community predicted from soil characteristics (see Rodwell & Patterson (1994))

d Species: HL=Hybrid larch (*Larix x eurolepis*); LP=Lodgepole pine (*Pinus contorta*); NS=Norway spruce (*Picea abies*); SS=Sitka spruce (*Picea sitchensis*); SP=Scots Pine (*Pinus sylvestris*)

e UM: upland moor, IF: improved farmland, PAWS: planted ancient woodland site.

Table 1: Location and environmental characteristics of study sites.

debris (stumps, fallen logs and brash). Soil samples were taken from each quadrat and the pH was measured electrometrically using a soil-water paste. We were interested in the effect of brash on regeneration density so in sites that had been recently clearfelled (U6a, F2 and F4) a transect with equally spaced quadrats was oriented along a windrow and, parallel to this, another transect along the adjacent area(interrow) between the windrows. It was not possible to do this analysis on sites that had been clearfelled more than a few years ago as the vegetation growth and rotting of the brash made it increasingly difficult to discern windrows.

2.3. Statistical analyses

2.3.1. Trees and shrubs

(i) The effect of environmental characteristics (distance to seed source, % vascular plant cover, % woody debris, altitude and soil pH) on the tree regeneration densities were examined using Spearman rank correlation coefficients. The analyses were carried out separately for the dominant species that were identified (birch, alder, rowan, willow and oak).

(ii) To explore the influence of site type, regeneration densities on clearfelled upland moorland (UM) and clearfelled improved farmland (IF) were compared to control areas of unplanted UM and unplanted IF using a nested analysis of variance (ANOVA). To avoid confounding the effects of site type, time since clearfelling and soil type this analysis was conducted on a subset of 4 clearfelled brown earth UM sites that were predicted to develop to NVC type W11 (U2L, U3L, U4L and U5) with similar times since clearfelling to our clearfelled IF sites (also brown earth sites predicted to develop to W11). Our control sites were also all brown earth soils (UL & Ua; Fa, Fb & Fc.)

A lack of Lake District IF sites meant that we were unable to account for the effect of site location as a covariate. The data was transformed using logarithms and the Satterthwaite approximation used due to unequal sample sizes. When the difference was found to be significant the means of the site types were compared by Tukey's honestly significant difference (HSD) test.

(iii) Regeneration densities on Lake District brown earth sites (U2L, U3L, U4L & U7L) were compared with densities on Lake District peaty gley sites (U9L & U10L) using a nested ANOVA. The data was transformed using logarithms and the Satterthwaite approximation used due to unequal sample sizes.

(iv) The Clark-Evans nearest neighbour method (Blackith, 1958) was used to analyse the distribution pattern of regeneration for the animal-dispersed tree species of oak and rowan. This method computes the ratio (R) of the mean distance between nearest neighbours and the expected distance in the case of random distribution d_{ran} ($d_{ran} = 1/2\sqrt{D}$, where the density $D =$ number of stems/area). For R=1 the population is randomly distributed, for R significantly less than 1 the population is clumped and for R significantly greater than 1 the population is evenly dispersed. A t-test was used to determine whether R was significantly different from 1.

(v) A paired t-test (data transformed by square root) was applied to examine differences in regeneration density between the windrows and interrows at sites U6a, F2 and F4. A 2-proportion z-test was used to compare the proportion of regenerating trees that were rowan in windrows and interrows.

(vi) Linear regression analysis was used to examine the change in height of birch with time since clearfelling.

2.3.2. Ground flora

Ground flora characteristics in each quadrat were analysed as: (i) Total number of species, S (ii) % vascular plant cover of each species (iii) Linear regression analysis was used to examine the difference in vascular plant coverage with time since clearfelling.

3. Results

3.1. Tree regeneration

A total of 14 tree and shrub species were found to be regenerating, of which 10 were species native to Great Britain. The non-native species consisted of three conifers (Sitka spruce, *Pinus contorta* (lodgepole pine) and *Larix x marschlinsii* (hybrid larch)) and one broadleaved species (*Alnus incana* (grey alder)). The native species were birch, oak, rowan, willow, common alder, *Fraxinus excelsior* (ash), holly, *Fagus sylvatica* (common beech), *Corylus avellana* (common hazel) and *Juniperus communis* (common juniper). The mean density of regeneration of native species on clearfelled sites varied from 0 stems / ha to >5000 stems / ha (Table 2). While the regeneration density of non-native tree species is shown in Table 2 it is important to note that in a number of study sites regenerating non-native conifers had been felled, making it difficult to draw any conclusions about the frequency of non-native regeneration. The linear regression of time since clearfelling on regeneration density of native species was not found to be significant (r^2=0.26, n.s.). Table 3 shows the density of regeneration for native species and the fraction of clearfelled sites where each species was recorded. Regeneration was dominated by birch and rowan. Whilst the regeneration of holly and oak were recorded infrequently (<20% of sites), relatively high regeneration densities were recorded at specific sites for these species (for example, 723 stems / ha in the case of oak).

The regeneration density of birch and alder was found to be negatively correlated with distance from seed source (see Table 4). In the case of birch, for example, 63% of regeneration occurred within 20 m of a seed source. No significant relationship was found for rowan or oak. No significant relationship between plant cover and regeneration density was seen for any species. However, when the regenerating trees were divided into sapling (taller than 0.5 m) or seedling (shorter than 0.5 m) categories then a significant negative correlation was seen between birch seedling density and vascular plant cover. Birch also showed a significant negative correlation with the percentage of brash (woody debris). No such effects were noted for alder, willow, oak or rowan.

Regeneration density against distance from seed source is plotted in Fig. 2. In general, birch showed a broad shoulder of dense regeneration close to source, followed by a very rapid decline and then a long tail consisting of a slow decline. Linear regression found a logarithmic decline in birch density with increased distance to seed source (see Fig. 2.) No significant correlation between distance from seed source (for distances up to 100 m from the source) and regeneration density was seen for animal-dispersed species (oak and rowan). However, the regeneration of both rowan and oak were still strongly clumped (R=0.23 and 0.28 respectively, both $p<0.0001$.)

We found significantly higher regeneration in interrows (mean (M)=2313, standard deviation (SD)=3463) than in windrows (M=522, SD=1113; t(66)=5.694,

Site label [a]	No. of seedling spp.	Native juveniles / ha [b]	Non-native juveniles/ha [b]	% quadrats without native juveniles	% Browsing damage
Bin Forest (Aberdeenshire)					
U5	2	5121(945)	83(41)	38.3	1
U6a	2	3875(824)	0(0)	53.3	0
U10	8	5210(903)	0(0)	28.3	1
Clashindarroch Forest (Aberdeenshire)					
U6b	0	0(0)	250(114)	100	0
U15	1	2101(487)	708(198)	60	76
F1	1	42(42)	0(0)	98.3	0
F2	1	1042(240)	42(42)	70	4
F4	2	417(101)	0(0)	88.3	0
Ua	1	42(42)	42(42)	98.3	0
Ub	0	0(0)	167(81)	100	0
Fa	0	0(0)	(0)(0)	100	0
Fb	1	42(42)	(0)(0)	98.3	0
Fc	0	0(0)	(0)(0)	100	0
Hardknott Forest (Lake District)					
U2L	0	0(0)	-	100	0
U3L	3	1053(373)	-	76.3	0
U4L	3	5000(1332)	-	48.6	0
U7L	4	3625(881)	-	42.5	0
U9L	3	3857(790)	-	40	0
U10L	5	5270(1104)	-	38	0
UL	1	139(139)	-	94.4	0
Rainsbarrow Forest (Lake District)					
P7L	5	5790(915)	-	29	0

a Site label indicates former land use (U: upland moor, F: improved farmland, P: PAWS) & number of years since clearfelling (indicated by number). All Lake District sites are distinguished by a label L. Control sites are distinguished by lower case alphabetical labels.

b Numbers in parentheses are standard errors.

Table 2: Summary of natural regeneration. Details of sites given in Table 1.

	Median density[a]	Max density	% of sites recorded
Alnus glutinosa	0	1250	7
Betula spp.	1364	4474	87
Corylus avellana	0	263	7
Fagus sylvatica	0	33	7
Fraxinus excelsior	0	277	13
Ilex aquifolium	0	375	20
Juniperus communis	0	144	7
Quercus spp.	0	723	13
Salix spp.	0	1714	40
Sorbus acuparia	200	723	13

a Median values are calculated from the mean values for each site.

Table 3: Regeneration density of native tree species in clearfelled sites.

$p=5\text{x}10^{-5}$). We found no statistically significant difference between the proportion of trees that were rowans in windrows and interrows (z=-0.456, n.s.)

Table 5 shows that the regeneration density of different site types (upland improved farmland or upland moorland). Site type (upland improved farmland or upland moorland) produced a significant variation in total regeneration densities (F(3,8.9)=4.1, p=0.03). 20% of the total observed variation was due to variation between the different site types. The overall regeneration density on clearfelled upland moorland was significantly greater than on unplanted upland moorland (p<0.01). However there was no significant difference between the regeneration density of clearfelled improved farmland and unplanted improved farmland (see Table 5). No significant difference in regeneration densities was found between brown earth and peaty gley soils

	Distance from seed source		% vascular plant cover		% woody debris cover		Altitude		Soil pH	
	r	p	r	p	r	p	r	p	r	p
Betula										
All juveniles	-0.84	***	-0.17	ns	-0.27	*	-0.09	ns	-0.01	ns
Seedlings[a]	—	—	-0.21	*	-0.39	*	—	—	—	—
Alnus										
All juveniles	-0.79	**	0.2	ns	0.1	ns	—	—	—	—
Seedlings[a]	—	—	0.06	ns	-0.15	ns	—	—	—	—
Salix										
All juveniles	0.13	ns	-0.18	ns	0.02	ns	0.26	*	0.07	ns
Seedlings[a]	—	—	-0.07	ns	0.05	ns	—	—	—	—
Sorbus										
All juveniles	-0.2	ns	0.04	ns	0.24	ns	0.04	ns	-0.01	ns
Seedlings[a]	—	—	0.31	ns	0.01	ns	—	—	—	—
Quercus										
All juveniles	-0.09	ns	0.24	ns	—	—	-0.12	ns	-0.19	ns
Seedlings[a]	—	—	0.11	ns	—	—	—	—	—	—

[a] Seedlings defined as height <50 cm. ns: $p>0.05$; * $0.01<p<0.05$; **$0.001<p<0.01$; ***$p<0.001$

Table 4: Spearman rank correlations (r) between natural regeneration densities and environmental characteristics.

	Clearfelled upland moorland	Clearfelled improved farmland	Unplanted upland moorland	Unplanted improved farmland
Total density	3392(505)^{a}	500(103)^{b}	64(45)^{b}	14(14)^{b}
Betula sp.	2834(468)^{a}	458(95)^{b}	0(0)^{b}	14(14)^{b}
Salix sp.	239(84)	0(0)	0(0)	0(0)
Sorbus aucuparia	287(93)	42(42)	64(45)	0(0)

Table 5: Effect of site type on regeneration density. Mean values (standard error) of regeneration density (stems / ha) are shown. For each row, non significant differences between site type are marked by the same letters and significant differences by different letters (Tukeys HSD; $p<0.05$). No mark means there is not a significant difference. Analysis was restricted to sites with similar time since clearfelling and soil type (see Section 2.3.1).

(F(1, 3.95)=1.75, p=n.s.)

Mean birch height increased significantly with time after clearfelling from 19cm tall at 2 years to 101 cm tall 10 years post felling (p=0.03). Fig. 3 contrasts the height distributions of birch trees 4 years post-felling (measured at U4L) and 10 years post-felling (measured at U10L.) Four years post-felling the number of regenerating trees declines exponentially with tree height so that we see large numbers of seedlings and few saplings. Ten years post-felling this has changed to a more Gaussian distribution of heights with fewer seedlings.

3.2. Ground flora

We recorded 70 species of vascular plants across the study locations (detailed in Supplementary Table 1). The most frequent and abundant species was the perennial *Deschampsia flexuousa* (wavy hair-grass), being found on 78% of quadrats surveyed. The similarity of upland clearfelled sites was noteworthy: 5 species (bilberry, *Galium saxatile* (heath bedstraw), ling heather, foxglove and *Potentilla erecta* (tormentil)) occurred in all upland sites and only 2 species occurred at a single site (*Ajuga reptans* (bugle) and *Valeriana dioica* (common valerian), both found at U10.) The predicted woodland type on clearfelled brown earth sites was W11 - upland oak - birch woodland with *Hyacinthoides non-scripta* (bluebell) (see Table 1). However, on UM clearfelled sites desired invader species such as *Oxalis acetosella* (woodsorrel), *Anemone nemorosa* (wood anemone), *Conopodium majus* (pignut) and *Primula vulgaris* (primrose)were not found, while bluebell was seen on only 15 quadrats and *Teucrium scorodonia* (wood sage) on just 2. The solitary PAWS site that was examined had a considerably richer ground flora with wood sorrel, wood sage and bluebell seen on 21%, 29% and 79% of quadrats respectively.

We found that the sites which had been clearfelled 10 years ago had significantly greater vascular plant coverage (111%) compared to sites that had been clearfelled 2 years ago (11.7%, p=0.001.) The % mean woody debris on spruce clearfell sites declined from 51% 2 years after felling to 12.7 and 5.1% at 5 and 10 years post-felling respectively.

4. Discussion and Conclusion

We have explored the regeneration density of native broadleaved species on clearfelled conifer sites in upland Britain. We compared regeneration on clearfelled sites to control sites that had neither been planted with conifers or clearfelled. We restricted our analysis to a subset of sites with similar time since clearfelling and soil type. Mean regeneration density on this subset of clearfelled upland moorland sites (3392 individuals / ha) was significantly greater than on upland moorland (64 individuals / ha) or improved farmland (14 individuals / ha) sites. Availability of data meant that in this analysis we combined sites across regions (Lake District and eastern Scotland) and were unable to account for site location as a covariate.

Regeneration density on all clearfelled upland moorland sites (3515 individuals / ha) was at the lower end of that recorded by Harmer & Morgan (2009) (3000-11000 individuals / ha) in a storm damaged lowland conifer site in south-east England that had been allowed to naturally regenerate. The regeneration density we recorded was lower than conifer regeneration within small windthrows (Jonásová et al, 2010) or clearfells (Modrý et al, 2004; Holgén & Hånell, 2000) where sapling densities as great as 160 000 individuals / ha have been recorded (Modrý et al, 2004; Holgén & Hånell, 2000; Jonásová et al, 2010). The high regeneration density in these studies was likely due to an ample seed source due to the surrounding woodland whereas in our study the seed source was limited to individual mature trees. Nevertheless, the regeneration density on clearfelled upland moorland sites and a clearfelled PAWS site (5790 stems / ha) exceeded the suggested sapling stocking densities for new native woodland in Britain of between 500-2000 stems / ha (Forestry Commission, 2010).

The diversity of regenerating species was usually lower than that of the adjacent seed sources with regeneration dominated by birch on all but one clearfelled site, as has been found previously at storm damaged lowland sites in Britain (Harmer & Morgan, 2009; Harmer et al, 2011) and elsewhere in Europe (Degen et al, 2005). Overall, birch accounted for 56% of regenerating saplings in our study. The density of birch regeneration on clearfelled upland moorland on our study sites is similar to that recorded in a storm damaged lowland conifer site in Britain (Harmer & Morgan, 2009) and to clearfelled upland conifer sites in Scotland (Wallace, 1998). Despite the presence of mature individuals of ash, beech, juniper and hazel adjacent to clearfelled sites only a handful of saplings of these species were noted. Overall we found that pioneer, shade-intolerant species such as birch, rowan and willow regenerated more frequently than shade-tolerant species such as beech and holly (Brzeiziecki & Kienast, 1994).

We explored the role of distance from seed source on regeneration density for distances up to 100 m from the source. The regeneration of the small-seeded and wind-dispersed alder and birch species were found to be strongly dependent on the distance from parent trees. The majority of the saplings were found within 20 m of a parent tree, although for birch there was a long tail, limited in our study to the width of the clearfelled site. The patchy distribution which results from this clumping around seed sources is not necessarily a disadvantage for establishment of natural woodland. Rodwell & Patterson (1994) suggest that 20-50% of woodland sites should be retained as open ground to enhance structural diversity and wildlife value. The fluctuations in sapling density may result in a more natural woodland structure to that produced through planting. The shoulder of the regeneration curve at distances less than 10 m from the woodland edge could be attributable to an edge effect - root competition or light and rain interception from the mature trees counteracting the increased regeneration caused by the rise in seed density as you approach the edge. The seed dispersion curve for a point source (Harper, 1977; Nathan et al, 2001) is similarly shaped to the regeneration curves for solitary trees in having a peak in seed fall density a short distance from the parent tree.

Regeneration of oak and rowan was found to be significantly clumped although not significantly dependent on distance from the seed source. Rowan is primarily dispersed through ingestion by birds, particularly various thrush species (Raspe et al, 2000), while oak relies on hoarding by both birds and mammals but especially *Garrulus glandarius* (jay) and *Apodemus sylvaticus* (wood mouse) (Forget et al, 2005), both of which occur at the study sites. The distribution of regenerating saplings will therefore be partly controlled by the behaviour of the dispersing animal. Previous work in central Europe has demonstrated that the majority of oak regeneration occurs within 100 m of a seed source and declines rapidly at greater distances (Mirschel et al, 2011). However, our findings are in contrast to previous work carried out in lowland sites in the U.K. that found positive relationships between the number of oak seedlings and distance to parent trees but no significant effect for birch seedlings (Harmer et al, 2005), possibly indicating differences between the shelterwood examined by Harmer et al (2005) and the more extensive clearfells that we considered.

The determination of any relationship between vascular plant cover and regeneration density was complicated by the constantly changing nature of ground flora - the current vegetation structure doesn't necessarily reflect that present when the seedlings first started growing. Indeed, the only significant correlation between regeneration density and vascular plant cover was the negative correlation found for birch seedlings (shorter than 0.5m.) The small size of a birch seed means that its food reserve is only sufficient to grow to 2 cm in height (Miles & Kinnaird, 1979), before it must be able to support itself through photosynthesis. This results in birch's difficulty in establishing itself in thick vegetation. Scarification (exposure of mineral soil) can increase seedling density in birch spp. (Kinnaird, 1974; Karlsson, 1996). The ground disturbance and lack of ground vegetation after clear felling provides opportunities for seedlings to become established in bare ground before it is covered with vegetation. In contrast, the lack of regeneration seen on the unplanted upland moorland and unplanted improved farmland sites is likely due to the dense flora coverage (120% and 142% respectively) in combination with the lack of any ground disturbance.

The rate of tree growth was slow, with regenerating trees achieving a median height of 104 cm after 10 years of growth post-felling. These growth rates are markedly poorer than those recorded by Harmer & Morgan (2009) in lowland England or by Worrell et al (2000) in upland NE Scotland. We found that the height distribution of the regenerating trees changed with time since clearfelling (Fig. 3), with large numbers of small trees 4 years post-felling changing to a more even distribution of heights 10 years post-felling. This indicates that the recruitment of new trees is most prolific in the first few years following felling, with fewer seedlings 10 years post-felling indicating a slowdown in this process. This decline is likely to be driven by the increase in herbaceous cover following clearfelling combined with the negative correlation between birch regeneration and herbaceous cover. The weighting of seedling recruitment to the years immediately following clearfelling may also contribute to the observed site to site variability in regenerating tree number since any temporal fluctuations in the ability of trees to regenerate will have substantial effects on the resulting density. Potential factors influencing interannual variability in seed dispersal and seedling germination include temporal variation in seed production (Harper, 1977) and climatic factors such as wind speed or precipitation (Nyland, 1996) and amount of snow cover (Greene & Johnsson, 1997; Forestry Commission, 2004).

We found that the dense layers of brash produced by windrowing significantly reduced the amount of natural regeneration. Windrows could be up to a metre high and several metres wide, producing a physical barrier that prevented seedling establishment and creating regions with little or no regeneration. While we might expect seedlings from larger seeded species like rowan (200000 seeds weigh 1 kg) to have an advantage over seedlings from smaller seeded species such as birch (5.9 million seeds weigh 1 kg) in growing through brash (Leishman & Westoby, 1994) we found no significant difference between the proportion of rowan in windrows and interrows. Furthermore, previous studies have found that where grazing pressure is high, brash (Truscott et al, 2004) and coarse woody debris (Smit et al , 2012) can help protect seedlings from browsing. However, it is difficult to draw any conclusions from our study as only a single site (U15) recorded significant browsing. The low incidence of browsing at our study sites (grazing pressure was controlled) means that grazing is unlikely to limit regeneration (Palmer et al, 1994; Olesen & Madsen, 2008; Yamagawa et al, 2010).

Clearfelled sites undergo substantial ground disturbance resulting in a mean 19% ground flora coverage 2 years post-felling. On upland moorland sites, vegetation after clearfelling was largely comprised of ruderal species such as wavy hair-grass and *Deschampsia cespitosa* (tufted hair-grass) before being joined by species associated with open moorland like ling heather and *Galium saxatile* (heath bedstraw). Colonisation by woodland ground flora species was poor.

Many previous studies have focused on restoration of PAWS to semi-natural woodland with current advice advocating a gradual approach to restoration through thinning (Thompson et al, 2003; Woodland Trust, 2005). In this study we explored the potential conversion of conifer plantations on upland moorland and improved farmland to semi-natural woodland through a process of clearfelling followed by natural regeneration. There has been comparatively little work carried out on this despite the large area of uplands used for conifer plantations in Britain. We found that where remnants of native woodland survive, clearfelling results in conditions favourable for natural regeneration and typically producing regeneration densities of native species equal to or greater than that recommended for planting. Where forest managers aim to develop part of their forest estate as native woodland, we recommend sites be surveyed for native woodland remnants and adjacent conifers clearfelled to allow regeneration of native woodland. Where seed sources of non-native conifer exist these species may also regenerate at high densities (Stokes et al, 2009; Stokes & Kerr, 2013) and further work is needed to explore to what extent this hinders the development of semi-natural woodlands. Gradual thinning of the conifer crop may be less likely to produce ideal conditions for natural regeneration (disturbed soil and little ground vegetation) while extending the supply of non-native conifer seed sources (Stokes et al, 2009), although further work is required to compare these approaches. Taking advantage of the natural regeneration process means that it may be possible to produce semi-natural woodland of a high ecological and landscape value at a substantially reduced cost (Jonásová et al, 2006). However, where extensive thinning of non-native species would be required this would greatly increase costs (Stokes & Kerr, 2013). We found natural regeneration was mostly of shade-intolerant pioneer species and was dominated by birch. The lack of important timber producing species within the regeneration has been raised as a concern in lowland British sites (Harmer & Morgan, 2009) but is less likely to be a issue for upland sites where timber production may be a lower priority. The dominance of birch within natural regeneration follows the expected pattern of natural succession and, given oak seed sources in the area, we might expect oak regeneration to follow in due course (Patterson, 1993). Future work will quantify the rate at which oak seedlings establish and explore whether supplementary planting may be required. Given that recent work (Harmer & Kiewitt, 2007; Harmer et al, 2011) has shown that a gradual conversion of lowland conifer PAWS may not always allow satisfactory regeneration of broadleaved tree seedlings, we feel that clearfelling of conifer plantations followed by natural regeneration as a method of establishing semi-natural woodlands warrants further research and consideration.

5. Acknowledgments

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Figure 1: Map of location of study sites.

Figure 2: The regeneration density as a function of distance from seed sources: (a) clump of mature birch (U10, U5). Linear regression gives birch density =18800-9465($\log_{10}$(seed source distance), r^2=0.76,p<0.001 (b) Solitary mature birch (U10, U6a, U5). Linear regression gives birch density = 6740-3416($\log_{10}$(seed source distance), r^2=0.56, p=0.005. Error bars are the standard error of the mean.

Figure 3: Height distribution of regenerating birch trees, comparing 4 years (open bars) and 10 years (filled bars) post-felling. The y-axis shows the fraction of each site's birch trees that lie within the height range.

Figure

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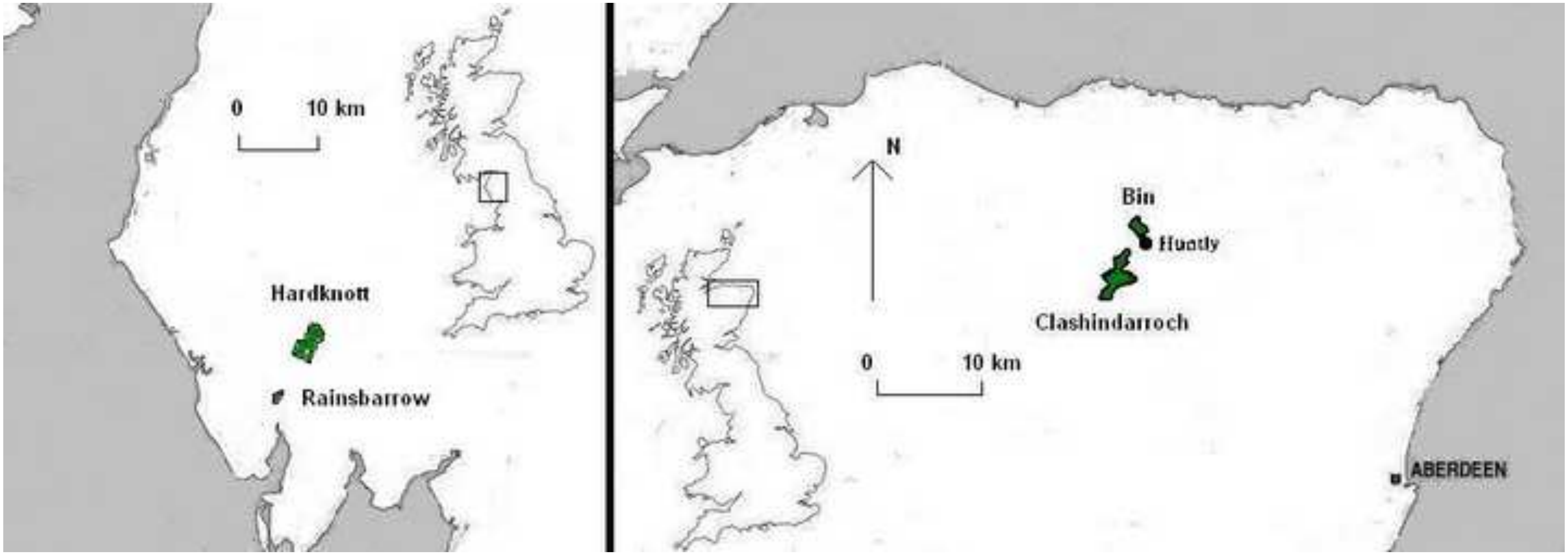

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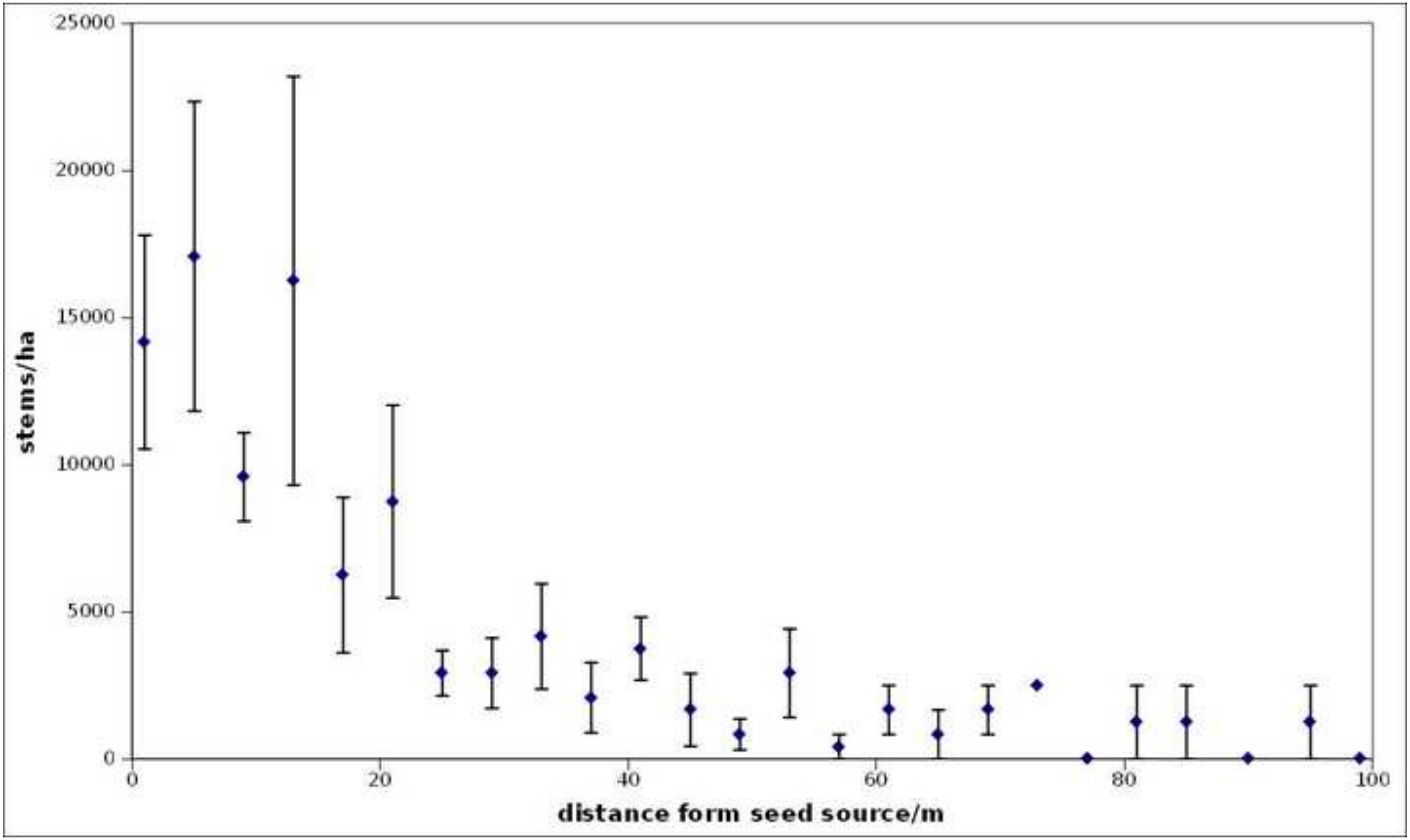

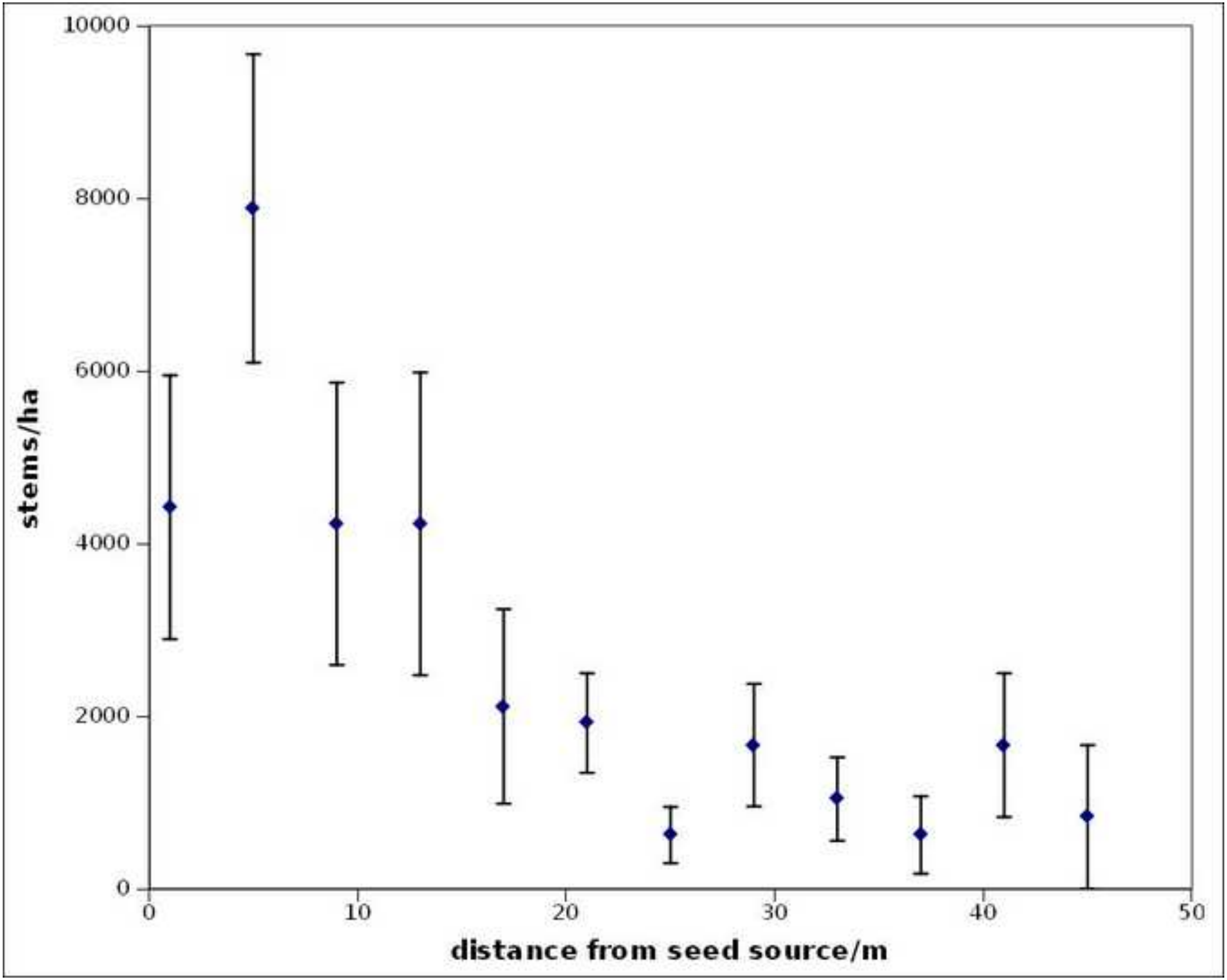
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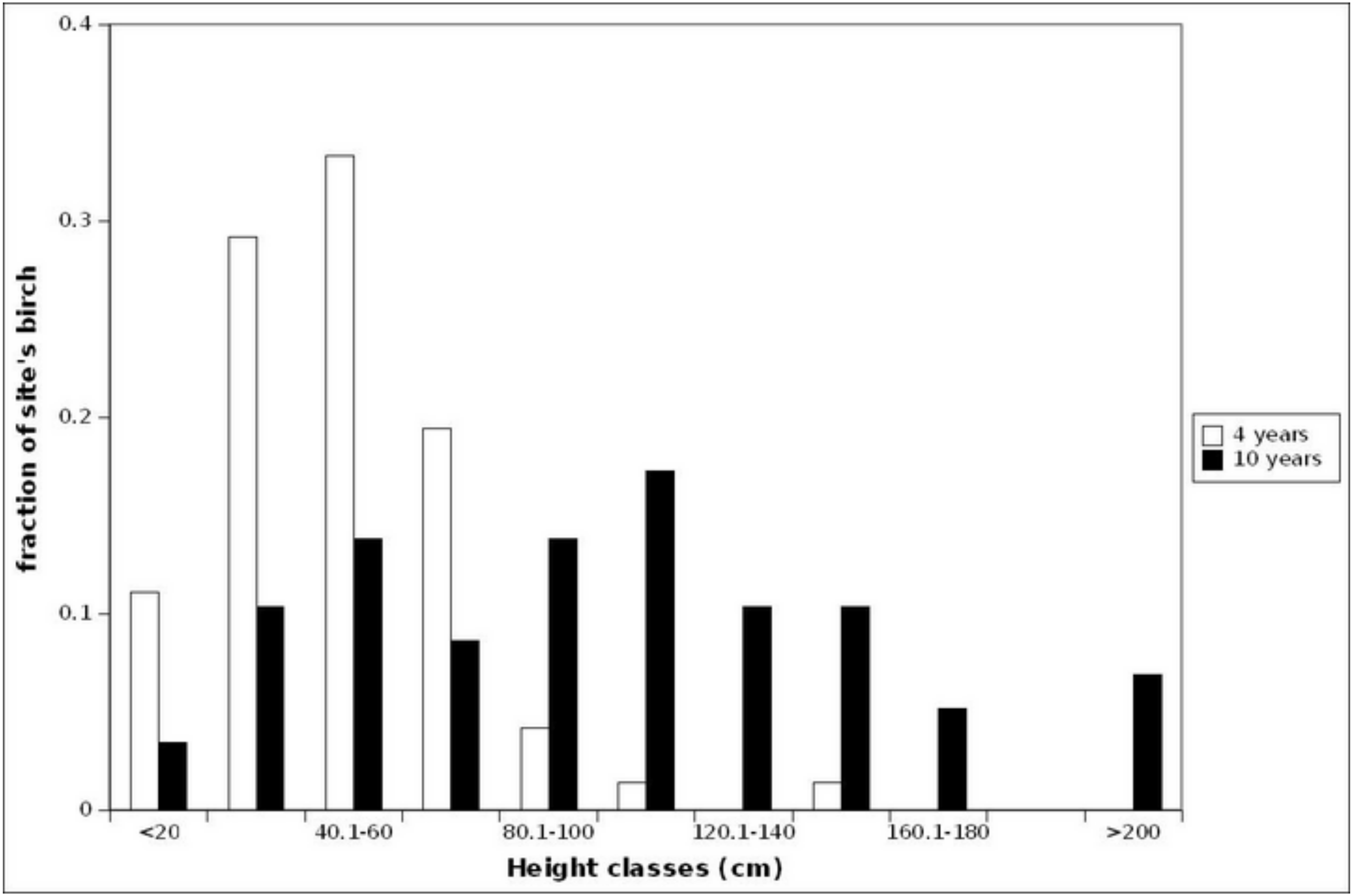

Regeneration of native broadleaved species on clearfelled conifer plantations in upland Britain

Spracklen et al.

Response to Review

We thank both referees for their continued interest in our paper and for their comments which have improved our manuscript. We are happy to note that both referees think that the revised manuscript is much improved.

We have responded to all the reviewer comments and made changes to our manuscript. We list the reviewer comments below in italics and our responses in normal text. To guide the review process we have highlighted the major changes we have made to our manuscipt in red.

Reviewer 1

The authors have taken into account most of my previous comments but I have a few further comments: Table 1 (and 2): The changes made have improved clarity, but the meaning of the lower case letters - a, b, c - in the site label column (e.g. Ua or Fc) need explaining.

Thanks for spotting that this was not clearly explained. To clarify this issue we have added "Control sites are distinguished by lower case alphabetical labels." to footnote a of Table 1 and 2. The footnote now reads "Site label indicates former land use (U: upland moor, F: improved farmland, P: PAWS) & number of years since clearfelling (indicated by number). All Lake District sites are distinguished by a label L. Control sites are distinguished by lower case alphabetical labels."

Line 216: Suggest change 'the linear' to 'a linear'

Changed as suggested.

Table ??: I think that the table on page 17 should be table 6, but there is no table number, title or footnotes which will need to include the definition of 'S' again.

This table was longer than one page and the table number, title etc were pushed off the bottom of the page. We apologise for this. In response to Referee 2 we have moved this table to on-line supplementary data.

Figure 2: None of the figures are labelled in my printed copy but I assume that the first 2 graphs are Fig 2a and Fig2b. Figure 3: I am very confused, the legend implies that this should be a bar chart showing height distribution, but all figures are line graphs showing stem numbers against distance. I do not think that this figure has been included. Figure 4: The answer to question 34 says that fig 4a has been deleted, and that a legend has been changed to "fraction of site's birch". Is the third of the 3 graphs figure 4? My copy had no labels on the axes.

There were some issues with the file conversion which occurred during the on-line production process. We apologise that we did not spot these problems before we submitted. These issues have now been resolved and the figures in the resubmitted version are correct. We apologise for the confusion that this caused.

Reviewer 2

Thank you for the detailed response to the previous reviews. I think the manuscript is now improved and believe that it merits publication subject to the editor's considered view of the statistical analysis that has been presented. I have suggested that he take advice as to whether it is permissible to combine sites across regions in the way you outline in lines 163-176.

We thank the referee for continued discussion about our statistical analysis and the method we have used to combine sites across regions. The method we use is a relatively standard technique used in a range of studies similar to ours. For example, the following studies have all applied a similar statistical analysis and have combined their sites in a similar way (Chamberlain et al., 1999; Bradbury et al., 2000; Humphrey et al., 2002; Drinan et al., 2013). The way we have combined sites is necessary given our available data. The alternative would be to carry out additional sampling at additional sites which we are unfortunately not in a position to do. We acknowledge this limitation in the methods (line 154) : "we were unable to account for the effect of site location as a covariate". We have added the following line to the conclusions to further recognise potential limitations of the method for this aspect of the study (line 280-282): "Availability of data meant that in this analysis we combined sites across regions (Lake District and eastern Scotland) and were unable to account for site location as a covariate."

There are also a few minor points which need tidying up as follows:

1. Line 80 and elsewhere. You introduce the Hardknott and Rainsbarrow sites as being in Cumbria, but elsewhere you use the term Lake District. I suggest that you standardise on one or the other.

Changed all mentions of Cumbria in text to Lake District.

2. Line 109. Replace sitka by Sitka.

Changed as suggested.

3. Notes on Table 1. The old Latin name for hybrid larch is used and this should be replaced.

Changed as suggested.

4. Lines 227-231. These have not been moved to the discussion - see response 22 to Reviewer 2. You might also want to tidy up the tenses in this sentence when you make this change?

Moved to lines 342 and now reads: The determination of any relationship between vascular plant cover and regeneration density was complicated by the constantly changing nature of ground flora - the current vegetation structure doesn't necessarily reflect that present when the seedlings first started growing. Indeed, the only significant correlation between regeneration density and vascular plant cover was the negative correlation found for birch seedlings (shorter than 0.5m.)

5. I could not find a Legend to Table 6?

This was caused by the length of the table pushing the legend of the end of the page. We have moved this table to on-line supplementary data as suggested below.

6. I think some material could be presented as on-line supplementary data. Table 6 and supporting text could be one example.

We thank the referee for this suggestion. We have moved Table 6 to on-line supplementary data. We retain the supporting text and point to the supplementary data where appropriate.

References

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Regeneration of native broadleaved species on clearfelled conifer plantations in upland Britain

Spracklen et al. submitted

Highlights

- We examine native tree regeneration on clearfelled conifer plantations.
- Mean regeneration density exceeded 1000 stems / ha and was dominated by birch.
- Regeneration is increased by the absence of ground flora after clearfelling.
- Proximity to a wind-dispersed seed source increased natural regeneration.
- Brash piles reduced regeneration density.