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Variation in aboveground biomass carbon accumulation in Scots pine seed orchards progeny

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Abstract Increasing growth and biomass accumulation in forest stands may positively contribute to carbon (C) sequestration and climate change mitigation. Tree improvement programs develop planting material with enhanced growth and biomass accumulation. Scots pine is commonly planted in Europe, and provides a potential for increased C accumulation in forest biomass when using improved seed origins. Our objective was to investigate variation in standing aboveground C accumulation among the progeny of Scots pine seed orchards in climatically variable environments, where we also compared the amount of accumulated C between the tested populations and commercial stands. The aboveground biomass of trees in two series of replicated common garden trials was estimated with eight allometric equations, converted into C, and expressed per unit area. For each trial site we selected reference stands matching the age, stand composition and forest site type, where the same measurements and calculations were done on sample plots. We specifically expected to find the progeny that would express better growth and greater accumulation of C in their biomass when compared to the reference stands.

Significant and large variation was found among the examined seed sources and trial sites. On average, aboveground C accumulation varied among sites from 31.0 to 60.4 Mg ha^{-1} (age 22) and from 25.5 to 34.0 Mg ha^{-1} (age 17). Differences between populations at individual sites ranged from 41% to 55% (age 22), and from 29% to 54% (age 17). However, only a few of the investigated progeny had C accumulation significantly greater than the reference stands, and some had a lower C accumulation, depending on the study site.

This study for the first time quantifies the amount of and variation in aboveground C accumulation among the progeny of Scots pine clonal and seedling seed orchards in Poland. It also contributes to the knowledge of the patterns of within-species variation in growth and biomass accumulation. Variation we found is promising for the potential to enhance C sequestration in forest stands through tree improvement. However, the lower C accumulation or non-significant differences between research trials and reference stands, indicate that the level of growth enhancement from phenotypic selection practiced so far in Polish forestry is limited. For increased C sequestration in planted forests, selection would need to be intensified.

Keywords: allometry, *Pinus sylvestris*, populations, progeny, productivity, sequestration, tree breeding

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Introduction

Forests contain large amounts of carbon (C) and constitute a large share of the terrestrial C pool (Dixon et al. 1994, Malhi et al. 2002), making them important contributors to the C cycle and climate change mitigation (Canadell & Raupach 2008, Sedjo & Sohngen 2012). Although the most potential for C sequestration is associated with the undisturbed old-growth forests (Ķeniņa et al. 2018, Kenina et al. 2019), especially in the soil compartment (Dixon et al. 1994), the biomass production in forest plantations should be included in consideration of forest C sequestration.

Forest plantations often use planting material developed through the cycles of selection and breeding in tree improvement programs, resulting in enhanced growth and biomass accumulation. Subsequently, C sequestration in forest standing biomass could be increased when improved seed origins were used compared to the unimproved ones. The enhancement of stand productivity for C sequestration is appreciated from the perspective of proper silvicultural actions or species choice (Payn et al. 2015, Sedjo & Sohngen 2012), yet, the potential for enhanced or faster biomass growth and accumulation through the use of genetically improved planting material is rarely considered as a measure for forest C sequestration.

Scots pine (*Pinus sylvestris* L.), with its vast natural and planting range, is an ecologically and commercially important tree species, especially in central, northern and eastern Europe. It is the main coniferous tree species in Poland, with pine forests covering 58% of total forest area and containing 61% of timber volume (GUS 2017). The biomass and C accumulation in Scots pine stands have been frequently examined (Armolaitis et al. 2013, Jagodziński et al. 2019, Jagodziński et al. 2018, Jagodziński et al. 2014, Kenina et al. 2019, Węgiel & Polowy 2020), although less often in the context of genetic variation (Chmura et al. 2021, Chmura et al. 2013, Oleksyn et al. 1999). However, large genetic variation among populations of Scots pine in growth traits, adaptability, climatic sensitivity and wood productivity was reported based on the results from provenance tests (e.g. Barzdajn et al. 2016, Kowalczyk & Wojda 2019, Matisons et al. 2018, Matisons et al. 2019). Thus, given a large extent of planted pine forests and a substantial variation exhibited for growth and productivity among seed sources within the species, Scots pine has a great potential to be a species of choice for increased C sequestration through genetic tree improvement. However, this option requires the capability for biomass growth and C accumulation to be quantified for improved and unimproved material.

The objective of this study was to investigate variation among the progeny of Scots pine clonal and seedling seed orchards in the accumulation of carbon in standing aboveground biomass after the transfer into non local environments in the common garden study. The progeny of Scots pine clonal and seedling seed orchards used in this study represent the first generation of selective tree breeding for this species in Poland. We compared the amount of C the tested populations accumulated in their aboveground biomass with that of commercial stands in the same environments. We expected to find significant variation among examined seed sources, and specifically hoped to find the progeny that would express better growth and greater accumulation of C in their biomass when compared to the reference stands, and thus could be recommended for further breeding for increasing C sequestration in the standing forest biomass.

Materials and Methods

Common garden experiments and reference stands

The two experimental series with Scots pine were planted with one-year-old seedlings consisting of the open-pollinated progeny of clonal (Pine85 series, established in 1999) and seedling seed orchards (Pine96 series, established in 2004, Table 1) (Chmura et al. 2003, Rożkowski et al. 2007). Because the seeds were collected without keeping a record of individual trees within seed orchards, the progeny will further be referred to as populations (Fig. 1, Table S1). Two of the populations in the Pine85 series represent the progeny of seedling seed orchards, and three populations are common to both series, but collected in different years (Table S1).

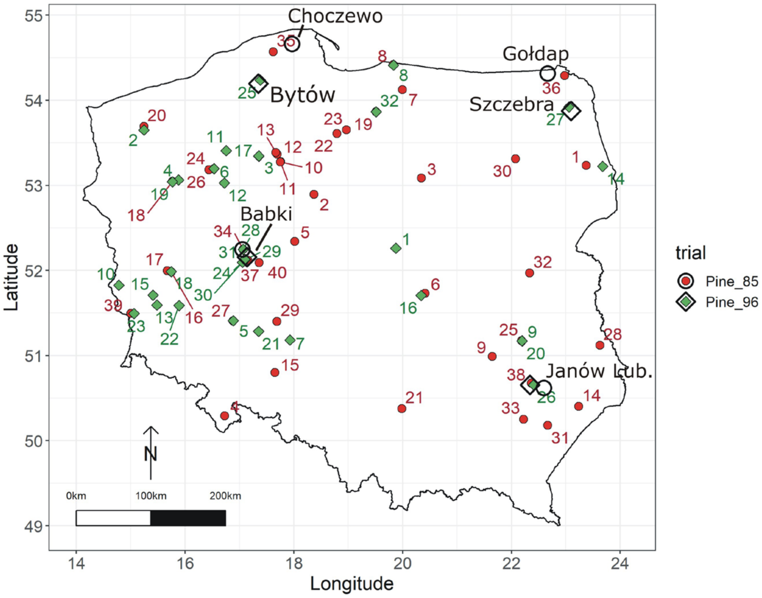

Figure 1 The origin of tested populations (closed symbols) and the locations of trial sites (open symbols) in two experimental series with progeny of Scots pine clonal (Pine 85) and seedling (Pine 96) seed orchards.

Both series were established in a multi-site 100-tree plot design (5 rows × 20 trees) with blocks (between 3 and 5 blocks depending on the site). The size of individual population plots within a block also varied depending on the site due to differences in planting spacing among the sites (Table 1).

For each trial site we selected from 3 to 4 corresponding reference stands matching the age, stand composition and forest site type (according to the forest typology used in the Polish State Forests), and located as close as possible to the trial site (Table 1). In total we sampled 33 plots in 14 reference stands for the Pine85 series, and 36 plots in 14 reference stands for the Pine96 series (Table 1).

Masurements and estimation of aboveground carbon

In 2019 we measured diameters at 1.3 m above the ground (DBH) of all live trees in all trial sites. Tree heights were measured for 33% to 99% of trees in the Pine85 series and for 33% to 51% of trees in the Pine96 series. For the remaining trees the heights were imputed with a site-specific Naslund's curve in the 'lmfor' R package (Mehtatalo 2019). The same measurements were taken at 0.02 ha circular plots (radius of 7.98 m) in the reference stands. Stand characteristics at the trial sites and in the reference stands are presented in Table 2.

When tree biomass data from destructive sampling are not available, it is necessary to use allometric equations to estimate stand biomass. However, the allometric equations developed in other forest sites are mostly site-specific and their generality may be questioned. We specifically addressed this issue by estimating the range of values of aboveground stand biomass C possible to obtain with the available equations for estimating tree biomass. To estimate the aboveground biomass of individual trees we used a series of eight published allometric equations for Scots pine (Bronisz & Zasada 2016, Chmura et al.

2013, Cienciala et al. 2006, Jagodziński 2011, Zasada et al. 2008) (Fig. S1, table S2). The choice of equations was based on the range of tree diameters, heights and age. However, from equations reported for pine by Jagodziński (2011) we used both age-specific equations for the poor and fertile sites, and a common equation for all age classes. Wherever possible a single equation for aboveground biomass was used (Cienciala et al. 2006), otherwise the aboveground biomass was estimated as a sum of individual components.

The aboveground carbon (C) content of individual trees was calculated assuming the fractions of aboveground biomass components as 76% for stem, 16% for branches and 8% for foliage biomass (Chmura et al. 2013, Jagodziński 2011). The carbon content for those components was taken based on the literature data as 48.79%, 49.98%, and 49.40%, respectively (Herrero de Aza et al. 2011, Jagodziński 2011, Janssens et al. 1999, Laiho & Laine 1997, Tolunay 2009, Wutzler et al. 2011). With a set of allometric equations used for modeling the aboveground biomass we obtained a range of variation in aboveground C for individual trees (Figure S1). Thus, the mean of aboveground C from different models was calculated for each tree, together with the estimates of the minimum and maximum C content (as the values from the models giving the lowest and highest estimates); then the values were summed at the plot level and expressed per unit area (per hectare). The same calculations were done for the reference stands.

Table 1 Information on the common garden trial sites analyzed in the study.

Series name	Site (Forest District)	Latitude N	Longitude E	altitude a.s.l (m)	MAT# (ºC)	MAP# (mm)	Age at measure-ment	Number of reference stands (plots)	Spacing and the size of a population plot within a block (ha)
Pine 85	Babki	52.24766	17.05630	90	8.7	507	22	3 (8)	1.5×0.5m (0.0075)
	Choczewo	54.65947	17.97033	121	7.3	666	22	4 (8)	1.4×0.5m (0.0070)
	Gołdap	54.31162	22.66486	203	6.4	627	22	4 (9)	1.5×0.5m (0.0075)
	Janów Lubelski	50.61863	22.59690	221	7.7	558	22	3 (8)	1.5×0.5m (0.0075)
Pine 96	Babki	52.15770	17.13755	85	8.7	503	17	3 (8)	1.45×0.6m (0.0087)
	Bytów	54.19406	17.34732	134	7.1	623	17	3 (8)	1.6×0.7m (0.0112)
	Janów Lubelski	50.65575	22.34110	207	7.8	546	17	4 (9)	1.5×0.6m (0.0090)
	Szczebra	53.87440	23.09595	141	6.8	578	17	4 (11)	1.5×0.7m (0.0105)

Note: # MAT- mean annual temperature, MAP – mean annual precipitation sum; long term average data (1970-2000) from the WorldClim https://worldclim.org/

Table 2 Mean values (and s.e. in the parentheses) of tree diameters (DBH) and height (H), and stand basal area (BA), aboveground biomass (AG) and density (N) in Scots pine experimental sites and their reference stands.

Experimental sites											
Pine 85	**DBH (cm)**		**H (m)**		**BA (m^2 ha^{-1})**		**AG[#] (Mg ha^{-1})**		**N (trees ha^{-1})**	
Babki	10.9	(0.04)	12.3	(0.01)	30.8	(0.4)	112.9	(1.6)	3153	(57)
Choczewo	15.2	(0.08)	13.3	(0.02)	30.9	(0.5)	123.2	(2.1)	1616	(24)
Gołdap	13.7	(0.07)	12.4	(0.02)	24.6	(0.4)	94.6	(1.8)	1583	(30)
Janów Lub	8.6	(0.03)	8.8	(0.02)	19.1	(0.3)	63.2	(0.9)	3091	(42)
mean	11.3	(0.03)	11.3	(0.02)	26.4	(0.3)	98.5	(1.2)	2361	(34)
Pine 96	**DBH (cm)**		**H (m)**		**BA (m^2 ha^{-1})**		**AG[#] (Mg ha^{-1})**		**N (trees ha^{-1})**	
Babki	6.6	(0.04)	6.8	(0.02)	22.5	(0.3)	69.4	(1.0)	5744	(112)
Bytów	7.6	(0.03)	7.7	(0.01)	16.4	(0.3)	51.9	(0.9)	3328	(55)
Janów Lub	8.1	(0.04)	7.7	(0.02)	20.2	(0.4)	65.1	(1.3)	3609	(71)
Szczebra	8.4	(0.03)	8.1	(0.01)	17.1	(0.2)	55.1	(0.8)	2900	(44)
Janów Lub	9.1	(0.11)	10.7	(0.06)	25.6	(0.6)	89.2	(2.7)	3669	(167)
mean	10.8	(0.09)	11.4	(0.04)	27.6	(0.9)	102.1	(4.3)	2714	(167)
Overall mean	9.2	(0.02)	9.1	(0.01)	23.4	(0.2)	83.0	(0.9)	2909	(35)
Reference stands										
Pine 85	**DBH (cm)**		**H (m)**		**BA (m^2 ha^{-1})**		**AG[#] (Mg ha^{-1})**		**N (trees ha^{-1})**	
Babki	9.9	(0.12)	11.0	(0.08)	27.5	(1.5)	97.8	(6.0)	3313	(259)
Choczewo	14.4	(0.27)	12.9	(0.08)	34.3	(1.1)	137.0	(6.1)	1894	(250)
Gołdap	11.8	(0.14)	11.6	(0.06)	23.5	(1.2)	86.2	(4.5)	2061	(128)
Janów Lub	9.1	(0.11)	10.7	(0.06)	25.6	(0.6)	89.2	(2.7)	3669	(167)
mean	10.8	(0.09)	11.4	(0.04)	27.6	(0.9)	102.1	(4.3)	2714	(167)
Pine 96	**DBH (cm)**		**H (m)**		**BA (m^2 ha^{-1})**		**AG[#] (Mg ha^{-1})**		**N (trees ha^{-1})**	
Babki	9.1	(0.11)	9.0	(0.05)	21.4	(1.1)	71.7	(3.9)	3038	(233)
Bytów	7.2	(0.08)	7.7	(0.04)	21.4	(0.4)	67.1	(1.8)	4856	(458)
Janów Lub	7.1	(0.09)	7.3	(0.06)	19.9	(1.3)	62.6	(4.7)	4461	(385)
Szczebra	9.2	(0.10)	8.7	(0.07)	19.9	(1.0)	66.3	(4.0)	2810	(111)
Janów Lub	8.0	(0.05)	8.0	(0.03)	20.6	(0.5)	66.8	(1.9)	3754	(213)
mean	9.1	(0.05)	9.4	(0.03)	24.0	(0.7)	83.9	(3.1)	3249	(149)
Overall mean	9.2	(0.02)	9.1	(0.01)	23.4	(0.2)	83.0	(0.9)	2909	(35)

Note: [#] a mean from the allometric equations used to estimate aboveground biomass

Statistical analysis

All the common garden experiments were laid-out in the randomized complete block design with multiple-tree plots. The analysis was run for the plot-level aboveground C per hectare. The mixed model analysis was used to test for significance of the effects with population as a fixed effect and the site, block within site, and population×site interaction as random effects. The full model was as follows:

$$Y_{ijk} = \mu + S_i + B_{j(i)} + P_k + PS_{ik} + e_{ijk}$$

where Y_{ijk} is plot level value, μ is overall mean, S_i is a random site effect, $B_{j(i)}$ is a random effect of block nested within a site, P_k is a fixed population effect, PS_{ik} is a random effect of population × site interaction, e_{ijk} is a random error. The analysis was first performed across the experimental sites in each series according to the above model. Separate analyses were also done for each site, testing for the effects of population and block.

The full model was fitted first and then it was reduced to the point when all remaining effects were statistically significant or no further reduction was possible. The effect significance was analyzed with the likelihood-ratio test after obtaining the estimates of model parameters with the maximum likelihood method (ML) (Biecek 2013). The models were fitted in R 3.6.0 software (R Core Team 2019) with the *'lmerTest'* package (Kuznetsova et al. 2017). In cases of significant population effect the least-square means (estimated marginal means) were compared with the Tukey HSD test, using the *'emmeans'* package (Lenth 2019).

Comparisons of accumulated aboveground C between experimental sites and reference stands were performed based on the 95% confidence intervals.

Results

The population and site effects on the aboveground C accumulation were statistically significant in a common analysis across sites in both series, and the population × site interaction term was not significant (Table 3).

In the Pine85 series at the age of 22 years the greatest C accumulation was found in Choczewo (60.4 ± 1.0 Mg ha^{-1} (mean ± s.e.) and the smallest in Janów Lub. (31.0 ± 0.5 Mg ha^{-1}; Fig. 2, Table S3). Values at the Gołdap and Babki sites were by 23% and 8% lower than at the Choczewo site, respectively. On average, a group of best-performing provenances – no. 1, 3, 12 and 7 (all above 54.4 Mg ha^{-1}) had a C accumulation 31% greater than a group of the poorest-performing provenances – no. 21, 10, 31 and 28 (all below 41.6 Mg ha^{-1}).

Table 3 Information on the common garden trial sites analyzed in the study.

Model	Pine 85			Pine 96		
Source of variance	**AIC**	**logLik**	**p value**	**AIC**	**logLik**	**p value**
full model	5930.6	-2922.3		3190.3	-1559.2	
block(site)			0.2729			<0.0001
site			<0.0001			0.0039
pop. × site			0.0898			0.7590
population			<0.0001			<0.0001
reduced model	5930.4	-2924.2		3188.4	-1559.2	
block(site)[#]			-			<0.0001
site			<0.0001			0.0038
population			<0.0001			<0.0001

Note: [#] the effect was not included in the reduced model if the p value is missing.

Table 4 Diagnostic statistics for the mixed models used to analyze variation of carbon accumulation (Mg ha^{-1}) in the aboveground biomass within the Pine 85 and Pine 96 series (analysis of individual sites). AIC – Akaike information criterion, logLik –logarithm of the likelihood, p value – probability level.

Pine 85												
Model	**Babki**			**Choczewo**			**Gołdap**			**Janów Lub.**		
Source of variance	**AIC**	**logLik**	**p value**	**AIC**	**logLik**	**p value**	**AIC**	**logLik**	**p value**	**AIC**	**logLik**	**p value**
full model	1456.9	-687.46		1555.5	-738.78		1542.2	-732.1		1282.8	-600.42	
block			0.8065			0.7484			0.4441			0.1501
population			0.5162			<0.0001			0.0013			0.0001
reduced model	1454.98	-687.49		1553.66	-738.83		1540.79	-732.39		1282.90	-601.45	
population			<0.0001			<0.0001			0.0236			0.0076

Pine 96												
Model	**Babki**			**Bytów**			**Janów Lub.**			**Szczebra**		
Source of variance	**AIC**	**logLik**	**p value**	**AIC**	**logLik**	**p value**	**AIC**	**logLik**	**p value**	**AIC**	**logLik**	**p value**
full model	575.13	-253.56		818.26	-379.13		961.07	-450.53		787.04	-363.52	
block			0.4422			<0.0001			<0.0001			0.0687
population			0.0002			<0.0001			0.0463			<0.0001
reduced model	573.72	-253.86		849.01	-395.50		983.53	-462.76		788.35	-365.17	
population			0.0325			<0.0001			0.4966			<0.0001

Note: # the effect was not included in the reduced model if the p value is missing.

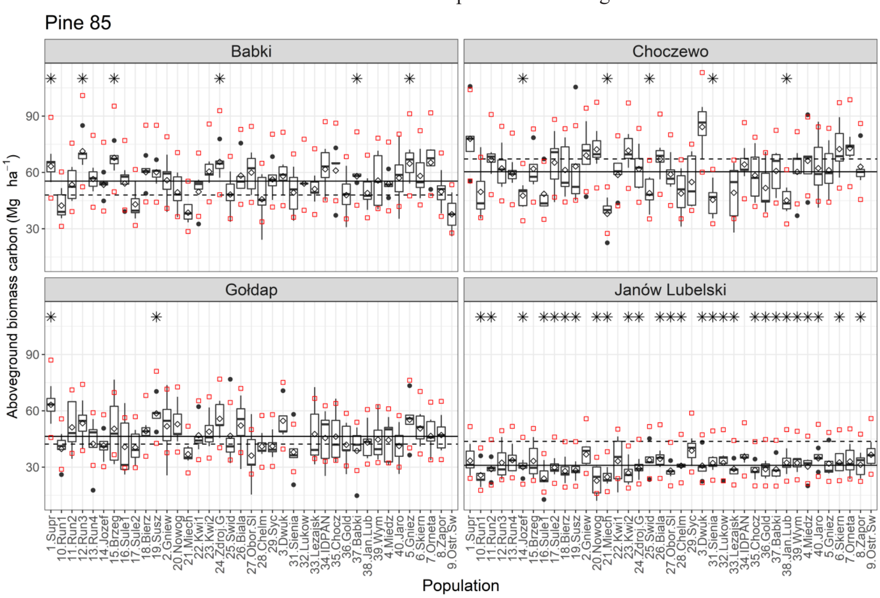

Figure 2 Boxplots of aboveground biomass carbon for tested populations at four experimental sites of the Pine85 series. A diamond shows the mean and a thick line within a box shows the median for each population. Small red squares show the values of aboveground carbon obtained with the models giving the smallest and greatest biomass estimates. A solid line shows the site mean, and a dashed line shows the mean for the reference stands at that site. Asterisks indicate values significantly different (greater or lower) from the reference stands.

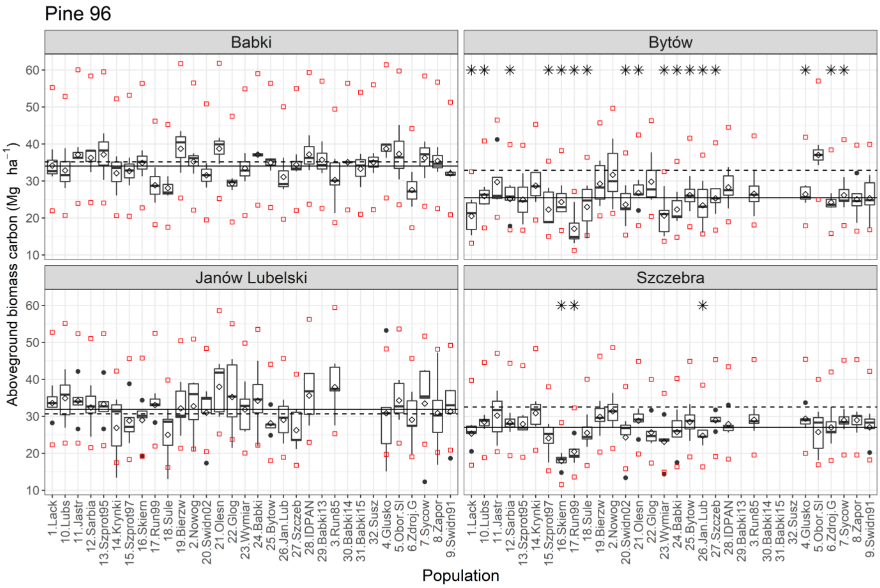

Figure 3 Boxplots of aboveground biomass carbon for tested populations at four experimental sites of the Pine96 series. A diamond shows the mean and a thick line within a box shows the median for each population. Small red squares show the values of aboveground carbon obtained with the models giving the smallest and greatest biomass estimates. A solid line shows the site mean, and a dashed line shows the mean for the reference stands at that site. Asterisks indicate values significantly different (greater or lower) from the reference stands.

In the analysis of aboveground C accumulation at individual sites of the Pine85 series the reduced model fitted better (according to the AIC) than the full model, except for the Janów Lub site (Table 4). Variation among populations was significant with percentage differences between the populations accumulating the most and the least C at each site amounted to 47% in Babki (pop. 12 vs. 9), 55% in Choczewo (3 vs. 21), and 43% in Gołdap (1 vs. 27), and 41% in Janów Lub. (29 vs. 20; Fig. 2).

In the Pine96 series at the age of 17 years the greatest C accumulation was found in Babki (34.0 ± 0.5 Mg ha^{-1} (mean ± s.e.) and the smallest in Bytów (25.5 ± 0.5 Mg ha^{-1}; Fig. 3, Table S3). Values at the Janów Lub. and Szczebra sites were lower by 6% and 21%, respectively, than at the Babki site. On average, a group of best-performing provenances – no. 2, 21, 11, 5, 19 and 28 (all above 32.1 Mg ha^{-1}) had 23% greater C accumulation than a group of the poorest-performing provenances¬ – no. 17 and 18 (below 25.5 Mg ha^{-1}).

In the analysis of aboveground C accumulation at individual sites of the Pine96 series the full model fitted better than the reduced model, except for the Babki site (Table 4), and significant variation among populations was found at all sites (Table 4). Percentage differences between the populations accumulating the most and the least C amounted to 54% in Bytów (pop. no. 5 vs. 17), 43% in Szczebra (2 vs. 16), 34% in Janów Lub. (20 vs. 18) and 29% in Babki (21 vs. 6; Fig. 3). However, no significantly different groups of populations were found with the Tukey HSD test at the Babki and Janów Lub. sites.

Compared to the reference stands, C accumulation in the common garden trials of the Pine85 series was on average greater by 15% in Babki, and 10% in Gołdap, and lower by 29% in Janów Lub. and 10% in Choczewo. These differences were statistically significant only at the Babki and Janów Lub. sites (Fig. 2, Table S3). Significant differences in C accumulation were also found between individual populations and the reference stands at each site in this series (Fig. 2). In Babki and Gołdap those differences were positive for the six and two populations, respectively (between 21% and 49% above the reference in Babki and between 39% to 49% above the reference in Gołdap). At the Choczewo site five populations and at the Janów Lub. site most of the populations (27 out of 39) performed significantly poorer than the reference stands (Fig. 2).

On average, C accumulation at the study sites in Bytów and Szczebra in the Pine96 series was significantly lower than in the reference stands by 23% and 17%, respectively (Fig. 3, Table S3). At the population level those differences were significant for three populations at the Szczebra site (between 24% and 45% lower than a reference), and for most populations (17 out of 29; between 19% and 48% lower than a reference) at the Bytów site (Fig. 3).

Discussion

In this study we investigated variation in the accumulation of carbon in standing aboveground biomass among the progeny of Scots pine clonal and seedling seed orchards in the common garden experiments planted at variable environments. We expected the examined seed sources to vary with respect to C accumulation, and specifically hoped to identify the progeny showing better growth and greater accumulation of C when compared to the commercial reference stands.

According to our expectation, we found statistically significant and large variation among the examined seed sources in the amount of C accumulated in their aboveground biomass. The average values for aboveground biomass found in our study were higher than reported in the literature at a similar age (Jagodziński et al. 2018, Jagodziński et al. 2014). However, it is important to note that, although we focused on the average C accumulation in the analysis, we have obtained a range of values for aboveground C accumulation based on a series of allometric equations fitted to our data. Because tree growth is affected by multiple factors, the allometric equations are often site-specific (Muukkonen 2007), and the use of equations developed for other site conditions should be considered a source of uncertainty. To account for this uncertainty, we used a series of allometric equations for ages and tree sizes similar to our dataset (see Fig. S1). Thus, it is informative to relate to the range of values the estimated C accumulation may take beside a specific point-estimate for the average value. When this uncertainty is included, the estimates of accumulated aboveground C for examined Scots pine stands are in the range from 28% lower to 34% higher than the average values we reported for the Pine85 series, and from 43% lower to 58% higher for the Pine 96 series (Fig. 2 and 3). Another element of uncertainty to C accumulation is associated with the conversion of aboveground biomass into carbon. In boreal and temperate trees the biomass is roughly 50% carbon (Thomas & Martin 2012), but this fraction differs among individual biomass components (Bert & Danjon 2006, Herrero de Aza et al. 2011, Laiho & Laine 1997, Tolunay 2009), and the share of biomass constituted by a given component changes throughout plant development (e.g. Chmura et al. 2017). To account for this, we used biomass fractions from the literature for trees at similar age to obtain the aboveground C estimates. Acknowledging those sources of uncertainty associated with the precision of C accumulation estimates, the differences in mean values between the most and the least productive populations at individual sites exceeded 41% in the Pine85 series and 29% in the Pine 96 series. This variation points to a great potential to select among the tested seed orchards with regard to the aboveground productivity for increased C accumulation in forest biomass.

Our second expectation to find the progeny performing better than the reference stands was only partially fulfilled. We offer at least two possible explanations of this observation. Firstly, the population plots at the trial sites were relatively small (Table 1). A stochastic loss of trees from the small plots, even at a scale that has no consequence for the average estimates of DBH or H, may negatively affect the summarized area-based estimates of productivity, and thus stand C accumulation. Secondly, the observed lack of significant differences between the improved and commercial stands may illustrate the "background improvement" of commercial stands. The reference stands we used in the study were planted with seeds harvested from the stands that were considered as above the average for a given region (the so-called "commercial seed stands"). They represent the first step of population selection that is commonly practiced in the Polish State Forests. Thus, the reference stands could not be treated as truly unimproved, because they represent some level of phenotypic selection. Similarly, the two experimental series used in this study represent the first generation of seed orchards, for which the maternal trees were only phenotypically-selected, and were not progeny-tested so far. The seed orchards were not thinned to remove inferior clones or families (rogued), and thus the genetic gain is somewhat lower than could be expected (Haapanen et al. 2016, Matziris 2005, Matziris 2000, Weng 2011, Weng et al. 2008). The 10-20% of gain in volume could be obtained from the first generation seed orchards without roguing (Carson et al. 1999, Eriksson et al. 2013, Haapanen et al. 2016, Matziris 2005, Matziris 2000), and perhaps a similar level of improvement could be expected from replacing poor-growing populations with the better ones (Butcher & Hopkins 1993). This indicates that selection intensity should be increased in order to enhance the aboveground biomass productivity and C accumulation in forest stands.

An important limitation to our conclusions about the lack of superiority of genetically improved material over the commercial stands is that the genetic and environmental effects were confounded for the reference stands. Thus, the differences between the improved and commercial seed stock were affected both by the variable site conditions and planting material used for reforestation in the local stands we used as a reference. These effects could not be separated and their relative size could not be estimated in commercial stands. In contrast, the statistical layout of the replicated common garden experiment for the seed orchard progeny allows for the proper estimation of genetic and environmental effects. Clearly, the environment affected both the average performance and the extent of variation among tested populations, although the population × site interaction was not significant. The site effect includes edaphic, moisture and climatic conditions. Variation among the tested populations was greatest at the Choczewo site in the Pine85 series and at the Bytów site in the Pine96 series. These sites were the most and the least productive for their series, respectively. However, both of them were located in the maritime climate zone, which seems to be highly diversifying for the adaptation and growth of Scots pine populations sampled within this study. This underlines the importance of establishing common garden tests in variable environmental conditions.

Conclusions

Increasing growth and biomass accumulation in forest stands may positively contribute to C sequestration and climate change mitigation. In a study comparing the progeny of Scots pine seed orchards we found a significant and large variation among the examined seed sources for C accumulation in aboveground biomass. This finding is promising for the potential to enhance C sequestration in forest stands through tree improvement. On the other hand, only a few of the investigated seed orchard progeny had C accumulation significantly greater than the reference stands, and some had a lower C accumulation, depending on the study site. This indicates that only a limited level of growth enhancement is possible as a result of phenotypic selection practiced so far in Polish forestry, which is similar for the first generation seed orchards and seed stands. Thus, for increased C sequestration in planted forests, selection would need to be intensified and followed by progeny testing of selected trees in variable environmental conditions.

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