

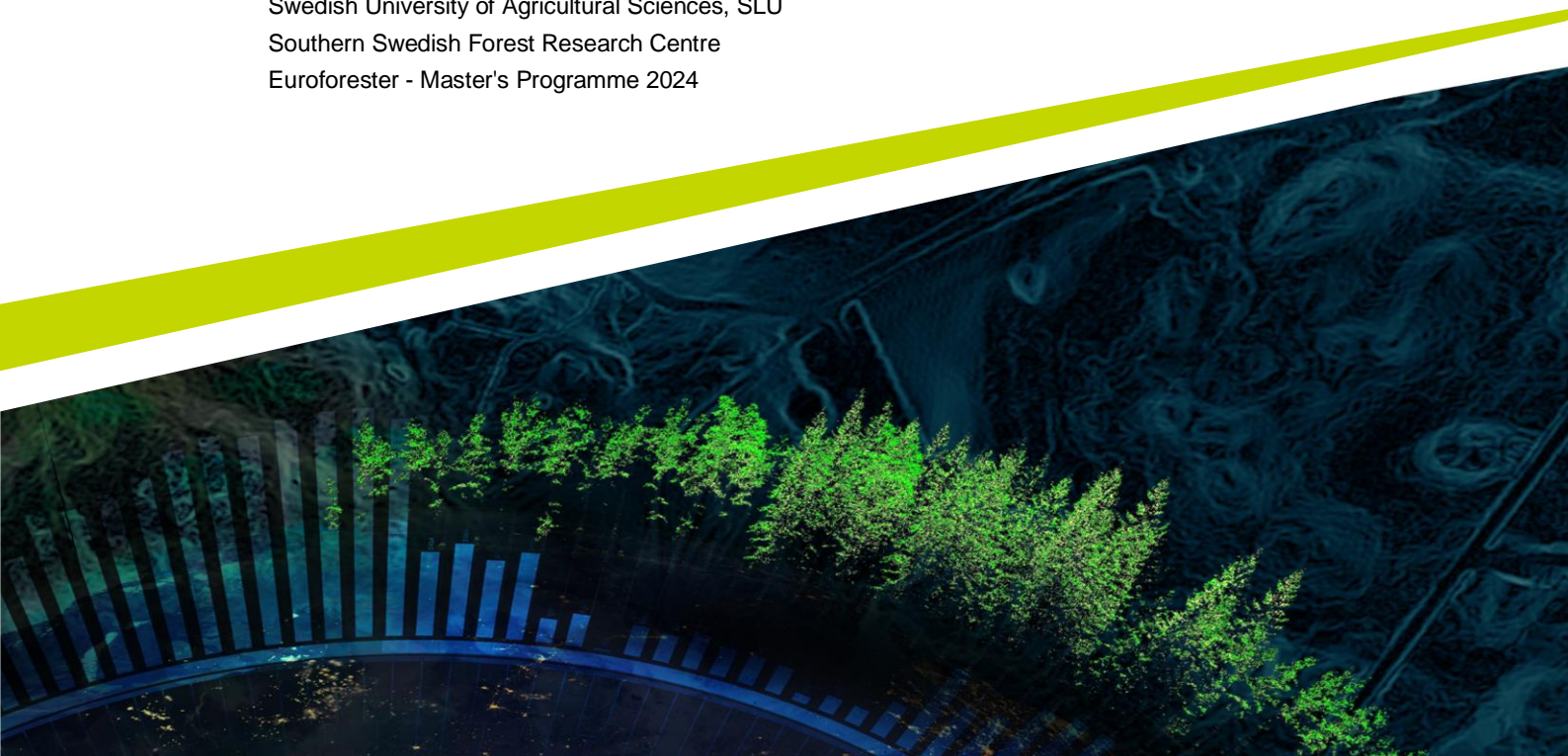


Genetic variability of male flowering in Silver birch (*Betula pendula*) seed orchards

*Zmienność genetyczna produkcji kwiatostanów męskich na plantacjach nasiennych brzozy brodawkowatej (*Betula pendula*)*

Adam Isio

Degree project • 30 hp
Swedish University of Agricultural Sciences, SLU
Southern Swedish Forest Research Centre
Euroforester - Master's Programme 2024



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Credits: 30 hp
Level: A2E
Course title: Master's thesis in Forest Science
Course code: EX0984
Programme/education: Euroforester - Master's Programme 2024
Course coordinating dept: Southern Swedish Forest Research Centre

Keywords: *Betula pendula*, seed orchard, male flowering variability, transfer distance

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Abstract

This study investigates the variability of male flowering in silver birch (*Betula pendula*) across three seed orchards located in northern Poland. The primary focus is on the variation in catkin count among and within clones and the relationship between flowering and latitudinal and longitudinal transfer distances. The research aimed to analyze the extent of flowering variability and to evaluate the impact of northward transfer, which is hypothesized to enhance male inflorescence production due to the longer photoperiod associated with northern latitudes.

The study addressed two main hypotheses: (i) there is substantial variability in male flowering both among different clones and within the same clone, and (ii) northward transfer of genotypes positively affects the frequency of male inflorescence, with longer transfer distances leading to increased inflorescence production. Data were collected on the catkin counts of various clones planted in the seed orchards, and statistical analyses were performed to assess the relationship between transfer distance and flowering intensity.

Results indicated significant variability in male flowering among and within clones, confirming the first hypothesis. Additionally, a positive correlation between northward transfer distance and catkin production was observed, supporting the second hypothesis. These findings highlight the importance of considering both genetic factors and geographic transfer distances in the management and selection of silver birch for seed orchards, aiming to optimize reproductive success and genetic diversity.

Keywords: *Betula pendula*, seed orchard, male flowering variability, transfer distance

Abstrakt

Niniejsze badanie bada zmienność w kwitnieniu kwiatostanów męskich brzozy brodawkowatej (*Betula pendula*) w trzech sadach nasiennych zlokalizowanych w północnej Polsce. Głównym celem jest zbadanie różnic w liczbie kwiatostanów między klonami i w ich obrębie oraz związku między ilością wyprodukowanych kwiatostanów a odległościami transferu w kierunku północnym i południowym. Celem badania była analiza zakresu zmienności kwitnienia oraz ocena wpływu transferu na północ, który według hipotezy ma zwiększać produkcję męskich kwiatostanów z powodu różnicy w szerokości geograficznej.

Badanie dotyczyło dwóch głównych hipotez: (I) istnieje znaczna zmienność kwitnienia męskiego zarówno między różnymi klonami, jak i w obrębie tego samego klonu, oraz (II) transfer genotypów na północ pozytywnie wpływa na produkcję męskich kwiatostanów, przy czym dłuższe odległości transferu prowadzą do zwiększonej produkcji kwiatostanów.

Wyniki wskazały na znaczną zmienność kwitnienia męskiego między klonami i w ich obrębie, potwierdzając pierwszą hipotezę. Ponadto zaobserwowano pozytywną korelację między odległością transferu na północ a produkcją kwiatostanów męskich, co wspiera drugą hipotezę. Wyniki te podkreślają potrzebę uwzględniania zarówno czynników genetycznych, jak i geograficznych (odległość transferu) w zarządzaniu i doborze brzozy brodawkowatej do plantacji nasiennych, mając na celu optymalizację reprodukcji i zróżnicowania genetycznej.

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Abbreviations

DBH	Diameter at breast-height
SO	Seed orchard
STD	Standard deviation
SLU	Swedish University of Agricultural Sciences

1. Introduction

1.1. Characteristics, distribution and habitat

Silver birch (*Betula pendula* L. Roth) is a medium-sized tree, which grows up to 30 m in height and has a broad pyramid shaped crown. Its average maximum age is ca 100 years, but some trees can live as much as 150 years. The most distinct features of the silver birch are white and shiny bark which can be peeled off and the downwards drooping branches, which distinguish it from downy birch (*Betula pubescens*).

As a monoecious species, it produces both male and female catkins, with the female catkins appearing in spring. The male catkins are roughly 5-6 cm long, with a yellow-brown colour and can usually be found on the end of branches in groups of 2-4. Male catkins, which are essential for fertilizing the female catkins and enabling seed production to develop in the summer a year before flowering and remain visible throughout winter, until they release pollen in April or May within days of the female catkins. After pollination the female catkin develops into 1-4 cm cylindrically shaped aggregates containing numerous small, winged fruits (i.e. seeds) in August that are then wind dispersed (Praciak et al., 2013).

The distribution of silver birch covers all of Europe from the Mediterranean to the very north of Europe and stretches east into Russia with a more continuous distribution in northern parts of its distribution and more patchy distribution in the south and western parts of its range (Fig. 1). Due to its wide distribution, the silver birch shows significant morphological diversity, leading to the description of various subspecies and varieties (Thórsson et al., 2001).

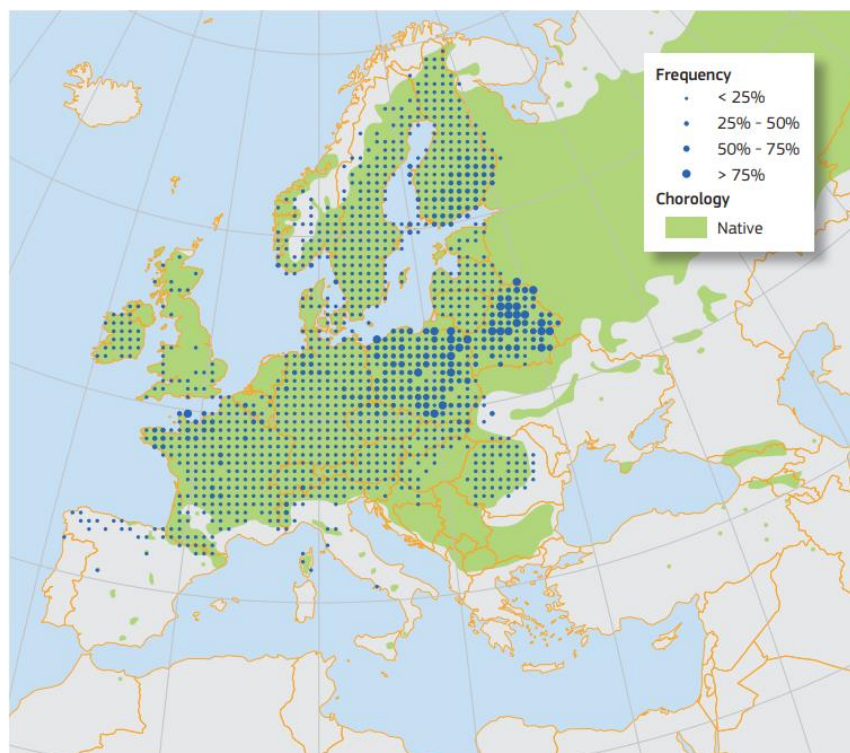


Figure 1. Map of silver birch distribution and frequency in Europe (Beck et al., 2016)

Silver birch is considered a pioneer species due to its fast-growing characteristics, small and wind-dispersed seeds, adaptability to varying soil types and can tolerate a wide range of temperatures. This makes silver birch a choice species both in artificial and natural reforestation and natural regeneration, as it can grow in habitats that are inaccessible to other tree species (Beck et al., 2016). Silver birch thrives on fairly fertile, well-drained, light soils, especially more acidic soils (Mitchell et al., 1974).

1.2. Importance for forestry, industry and ecology in Europe

In northern and eastern Europe, silver birch is one of the most important broadleaf tree species. In countries such as Belarus, Latvia and Estonia birch constitute more than 20% of the total standing volume of forests (FAO, 2020). Birch is an excellent source of hardwood (veneer and interior work) however it remains popular as a species due a plethora of uses other than its economical values.

Birch plantations can also be used as a protective habitat for seedling of frost sensitive species such as Norway spruce (*Picea abies*) or European beech (*Fagus sylvatica*) (Praciak et al., 2013). Apart from the positive effects it has on

neighbouring trees its presence also has been observed to increase biodiversity such as lichens (Vakkari, 2009) and birds (Felton et al., 2011). Silver birch is used extensively in urban and peri-urban settings, along roadsides, and within parklands due to its aesthetic appeal and high resilience to varied conditions of urban and peri-urban environments.

In Sweden and Finland, silver birch contributes to approximately 13% and 16% of the growing stock (Riksskogstaxeringen, 2023; Natural Resources Institute Finland 2023) respectively, which makes it the most important broadleaf tree in Fennoscandia. Most of the growing stock comes from natural regeneration and occurs most commonly in mixed conifer stands. Planted even-aged stands established with improved material from the birch breeding program are common in Finland and occur in Sweden (Hynynen et al., 2010). In north-western regions of Scandinavia a subspecies of downy birch called mountain birch (*Betula pubescens ssp. Tortuosa*) replaces silver birch due to its better adaptation to cold climate and wet site conditions that are more common towards the north (Atkinson, 1992).

Birch wood is popular in the forest industry for its use in pulp and paper, carpentry and manufacturing of wood products such as veneer, plywood and furniture, and can also be used as fuel. Currently, there is a strong demand for high quality stocks on the Baltic region timber market. Apart from finding use in the European wood products industry and pulp and paper industries, other commercial values of birch have been discovered for the food and beverage industry. In various regions across Europe, Asia, and North America birch sap continues to be tapped, sold, and consumed as part of traditional practices (Papp et al., 2014). The pharmaceutical and cosmetics industry also relies on betulin, a potential anticancer drug candidate sourced from extracts of the bark of silver birch (Fälåmaş, 2011). Birch bark has also been used in many traditional crafts such as basket weaving, canoe building, and decorative items. Woodcarvers also appreciate the aesthetic value and workability of the wood.

1.3. Genetic Variability of Silver Birch

The genetic variability of silver birch is an often-discussed topic due to the species' importance in the wood industry of Northern Europe. Due to their effective seed and pollen dispersal, genetic variability of neutral traits that don't affect the individual's fitness exhibits pronounced levels within populations, while the differentiation among population is low (Palmé et al., 2003; Maliouchenko et al., 2007). In Scandinavia large phenological differences among populations are present due to the adaptation of populations to local climate

conditions and the length of the growing season at their respective latitudes (Vakkari 2009). The adaptive features which vary among populations include critical night length (the shortest night length to trigger growth cessation), stem form which heavily influence the trees height growth and volume and resistance against browsing mammals (Vakkari, 2009; Viherä-Aarnio & Heikkilä, 2006). Viherä-Aarnio et al. (2012) observed that the most optimal latitudinal transfer distance to maximize yield is from 0° to 2° towards the north. Lee et al. (2015) similarly reported higher growth rates of silver birch in the UK with transfers of around 2° northward. White birch (*Betula papyrifera* Marsh.) has been observed to grow well when transferred up to 4° north from its seed origin latitude of 48°N (Tedla et al., 2019). Furthermore, the growth, biomass and biomass allocation were specifically affected by longer photoperiod regimes instead of the higher atmospheric CO₂ concentration, which suggests that white birch can benefit from longer photoperiod regimes during the growing season when relocating seeds to northern regions. However further northward transfers didn't seem to increase the growth of white birch which may suggest limited phenotypic plasticity (Tedla et al., 2019).

Longitude has been observed to have an effect on the leaf flushing of silver birch in Poland with eastern provenances generally flushing earlier (Wojda 2004). This observation could possibly suggest that other traits such as male catkin production could be similarly affected by longitude for differentially sourced birch clones especially when comparing clones adapted to the more oceanic climate of north-west Poland and clones from continental climate conditions occurring in the north-east part of the country.

1.4. Seed production and inflorescence abundance

Seedlings from improved seed sources are needed to plant well-growing and high-quality birch stands. In Fennoscandia, most of the seeds for commercial purposes are produced in seed orchards. Seed orchards (SOs) are maintained plantations consisting of carefully selected genotypes with one or more desired phenotypic traits, dedicated to the large-scale production of genetically enhanced reproductive material (seeds) for seedling cultivation.

Since 1970's in Finland, birch seeds have been produced in different greenhouse situations that have served to enhance production and logistics of harvest (Lepisto, 1973). The greenhouse environment allows for better control of cross fertilization of known genotypes of interest and thereby reduces the likelihood of cross contamination by wild pollen, increases seed size, makes it possible to increase volume of harvest, and makes seed harvest weather independent i.e.

produces seeds are not lost during unfavourable weather due to controlled conditions. Throughout years there were different types of orchards established containing different number of clones ranging from 2 to more than 100 clones used both for breeding and seeds production.

The Finnish SO concept was introduced to Sweden in 1980's with the establishment of two greenhouse SOs in Sävar, northern Sweden. These orchards were designed to produce seeds for middle Sweden up to latitude 65 and for northern Sweden north of latitude 65. Selected genotypes were moved to Sävar from the respective regions. After several years in operation, SO for central Sweden produced satisfactory numbers of seeds while there were almost no seeds from genotypes selected for northern Sweden (Rosvall, 1986).

In the early 1990s, a semi-closed greenhouse (a greenhouse with features of both open and closed greenhouses) SO was established in Ekebo in southern Sweden. The genotypes in the SO were selected from southern Sweden i.e. between latitude 56°N and 60°N. Ekebo SO is located at the latitude 55.5°N. Here trees are planted in the pots and are moved to greenhouse for pollination. After pollination seeds ripen outside. Seed productivity in Ekebo has varied a lot over the years and among clones. As long as the production was covering very low demand no special attention was put on the flowering phenomenon.

Currently, the demand for improved birch seedlings is increasing which cannot be covered by current seed production. Inflorescence and seed production hasn't been examined closely enough with regards to the genotypic variation (within and among clones) and latitudinal differences when transferring planting material to understand what might be causing lower seed yields.

It can be theorized that the variation in productivity among clones, and among SOs is due to the effect of the local climate, transfer distance, i.e. the origin of a specific clone, and the location of the SO. The types of SO (greenhouse and open pollinated) also likely to have an effect on the seed output.

Higher male catkin production has been observed to greatly increase pollination efficiency (Ranta et al. 2008). That's why it is imperative to look into the conditions under which male catkins are produced in higher numbers and the effect of seed transfer distance. Understanding which genotypes can be transferred at further distances can lead to optimizing current and future seed and seedling transfers. With the rapidly changing climate, there's an increasing possibility of using forest cultivation material transferred northward within the European Union. Seeds and seedlings from more southern regions could potentially benefit the forest industry of Fennoscandian countries like Sweden or Finland where

phenotype variation is more pronounced. That is why there is a need to broaden our knowledge about more southern seed origins for silver birch.

1.5. Study Aim

The aim of this study was to analyse the variability in flowering among clones and within clones planted in three silver birch seed orchards located in the northern part of Poland and to analyse the effect of latitudinal transfer. The research hypotheses were: (i) there is substantial variability in male flowering among and within clones, and (ii) northward transfer of genotypes giving a longer photoperiod has a positive effect on frequency of male inflorescence, i.e. longer transfer distance results in greater inflorescence production.

2. Methodology

2.1. Seed orchards and clones

Data used in this research originates from three silver birch clonal seed orchards (SO) located in northern and north-western Poland. The climate of the region is temperate oceanic with mild summers due to cool ocean currents, and wet and cloudy winters. The mean annual temperature is 9,5°C with the lowest temperatures occurring in February (-18°C) and highest in July (30°C). Total annual precipitation is around 500-600 mm with the lowest precipitation being in February (39 mm average) and highest in July (94 mm average). The annual growing season (when the daily mean temperature is above 5°C) lasts around 225-230 days. The seed orchard in Świerczyna (53°45' N) was planted in the year 2012 in a 6 x 6 meter spacing on an area of 4.2 hectares. The area was divided into 3 blocks. The SO in Kwidzyn (53°65' N) was planted in 1995 with a 6 x 6 meter spacing with an area of 3.5 hectares and 3 blocks (one of which hasn't been measured). The SO in Jastrowie (53°40' N) was established in 1985 with a 5 x 5 meter spacing and 5 separate blocks on a 5.2 ha area. In each SO, each clone was randomly assigned to block and planting position (randomized complete block design).

The number of clones in each seed orchard was 33 for Świerczyna, 34 for Kwidzyn and 36 for Jastrowie. The clones were selected from planted or natural stands as so-called plus-trees i.e., selected trees that are considered better than surrounding ones in height, diameter and external quality traits. There was an overlap of 19 clones between SO in Kwidzyn and Jastrowie. This allowed for direct comparisons between the same clones with different transfer distances. Each clone within the selected seed orchards was geo-referenced using a local positioning system (Block, row, plant) and labelled with its corresponding code (ranging from '9930' to '10172') which allowed for accurate identification. Clones have been transferred from North-West and North-Eastern parts of Poland with latitudes of origin ranging from 54°55' N to 52°63' N with southward transfer distances of up to 1°09' of latitude (in Świerczyna SO) and northward transfer distances of up to 1°01' of latitude (in Kwidzyn SO) (Fig. 2).

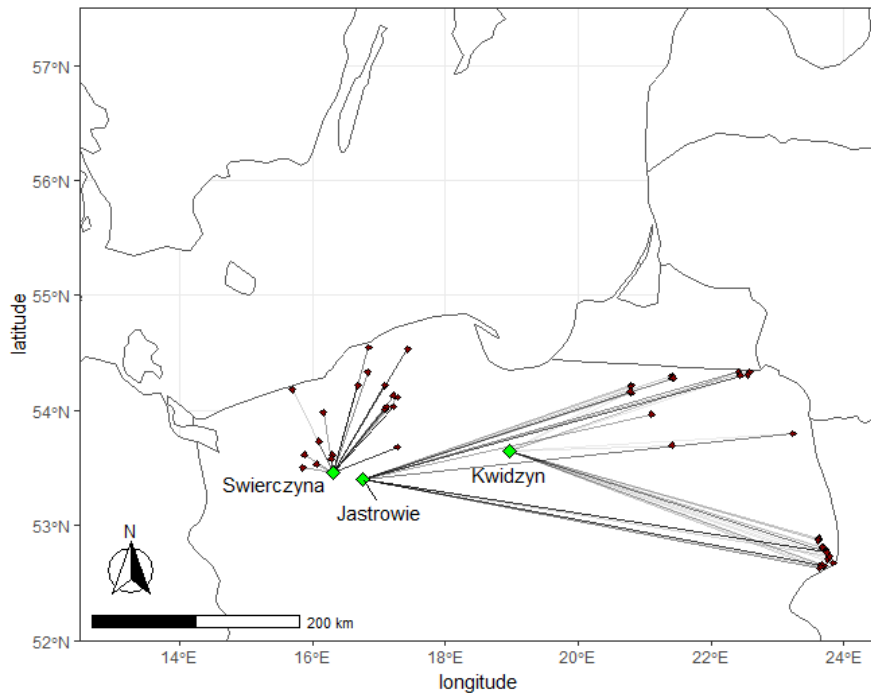


Figure 2. Locations of studied seed orchards (◆) with corresponding clone sources (◆).

The longitudinal origin of the clones ranged from 15°70' E to 23°84' E. Clones in Świerczyna SO were sourced from longitudes ranging from 15°70' E to 17°43' E (West Poland) while both Kwidzyn SO and Jastrowie SO had clones sourced from 20°78' E to 23°84' E (east Poland). There is a noticeable climatic difference between these longitudes. North-West of Poland is characterized by a more oceanic climate while North-East of the country has more of a continental influence on its climate. These climatic differences on the longitudinal axis between the sources of the clones presented a unique opportunity to study the effect of the longitudinal transfer distances on male catkin production.

2.2. Inventories

The inventories for this study were done during winter 2024, when the SOs were 13-years-old – Jastrowie, 29-years-old – Kwidzyn and 39-years-old - Świerczyna. The following traits were measured for each tree in SOs except block 3 at Kwidzyn which was excluded from measurements. The number of trees measured per SO varied from 182 trees in Kwidzyn, to 453 in Jastrowie and 885 in Świerczyna.

The number of male catkins were visually assessed for the whole crown of the tree. The assessment of catkins was also stratified to bottom, middle and top of

the crown, and a cardinal direction axis i.e. north, south, east and west. Each assessment was done in a four-grade scale quantifying abundance of male catkins on trees or its part: 0 – no catkins; 1 – minimal number of catkins; 2 – moderate number of catkins; 3 – plentiful number of catkins. The number corresponding to the abundance of male catkins present on the crown is referred to as the male catkin score.

Crown vitality was visually assessed using a scale dividing trees into 4 separate categories based on crown structure: 0 - exploration, 1 - degeneration, 2 - stagnation, 3 - resignation) (Roloff, 1989)

Apart from the aforementioned observations diameter at breast height (DBH) was measured for each tree using standard tree calipers. Mean tree height from each seed orchard was sourced from the Polish State Forest database with most recent entries being updated in 2023 (Forest Data Bank, 2023).

2.3. Data Analysis

In order to mitigate problems arising from the categorical nature of the original "male catkin score", a weighted arithmetic mean of male catkin count for each tree was computed. This involved utilizing the data collected from different parts of the tree crown, including those facing towards each cardinal direction (North, East, South, and West), as well as data about catkin count in the bottom, middle, and top sections of the crown.

The formula used for calculating the weighted mean was:

$$C_n * W_n + C_e * W_e + C_s * W_s + C_w * W_w + C_b * W_b + C_m * W_m + C_t * W_t$$

Where: C – male catkin count score within each measured part of the crown (n – north, e – east, s – south, w – west, b – bottom, m – middle, t – top), W - weights corresponding to each measured part of the crown ($W_n, W_e, W_s, W_w = 0.15$; $W_b, W_t = 0.1$; $W_m = 0.2$)

This equation assigned appropriate weights to each part of the crown based on its significance in contributing to the overall catkin count. By incorporating data from diverse crown segments, the resulting weighted average transformed the original ordinal catkin count data into continuous values ranging from 0 to 3. This conversion enabled a better exploration of the variability among clones, while also enabling deeper insight into the relationship between catkin production and DBH.

Descriptive statistics were used to summarize the phenotypical data and geographical data of clones in the complete dataset as well as within each SO. Latitudinal transfer distance was calculated for each clone by subtracting its latitude of origin from the latitude of the SO. This was done to ensure that north-to-south transfers had negative values while south-to-north transfers values would be positive. Correlations were calculated to examine the relationships between transfer distance (with differentiation between northward and southward transfers) and male catkin abundance as well as other characteristics such as DBH, crown vitality, and catkin count in different parts of the crown.

Analysis of variance (ANOVA) was done to test for significant differences in catkin count among and within the individual clones that were in common for SO in Kwidzyn and Jastrowie. Clones with a sample size of <5 were excluded from these analyses.

The linear mixed-effects model used in the ANOVA analysis was:

$$Y_{ijkl} = \mu + SO_i + Block_j + Clone_k + \epsilon_{ijkl}$$

Where: Y_{ijkl} - predicted male catkin count score; μ - overall mean male catkin count score; SO_i - fixed effect of the SO; $Block_j$ - random effect of the block; $Clone_k$ - fixed effect of the clone; ϵ_{ijkl} - error term accounting for unexplained variability in the male catkin count

The interaction effect between SO and Clone was tested however the results proved to be statistically insignificant (p-value > 0.05)

Tukey post-hoc tests were applied to identify specific differences between SOs and clone means when the ANOVA results were significant. The differences between groups were considered as significant at the p-level of 0.05.

The analysis and data presentation was created using R programming language.

3. Results

3.1. Clonal variability

Analysis of the data revealed notable variability among clones of silver birch in inflorescence production. The consistently high variability within most clones suggest a considerable degree of variability in inflorescence production among ramets of single clones.

Figures 3 and 4 show variability of the male inflorescence production among clones. This gradual increase in mean values across the clones in both figures is indicative of the consistent variability observed within the populations. Świerczyna SO consistently shows an increase in male inflorescence counts from 0 to 3, despite large standard errors, whereas the other two SOs exhibit greater variability and inconsistency in productivity among the clones (Fig. 4).

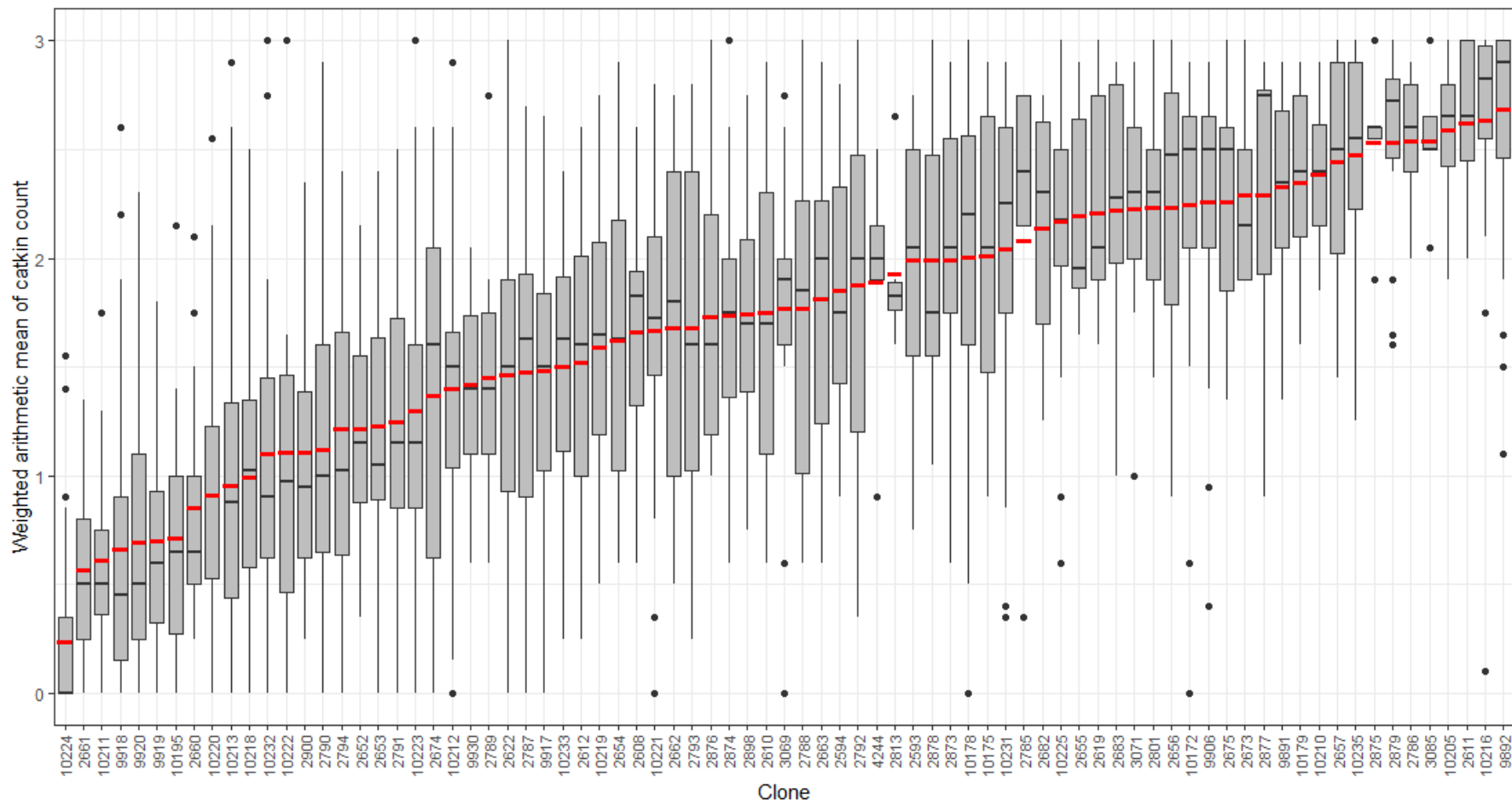


Figure 3. Weighted arithmetic means of male catkin count with medians (black horizontal lines), arithmetic means (red horizontal lines) and outliers (black dots) of each clone group

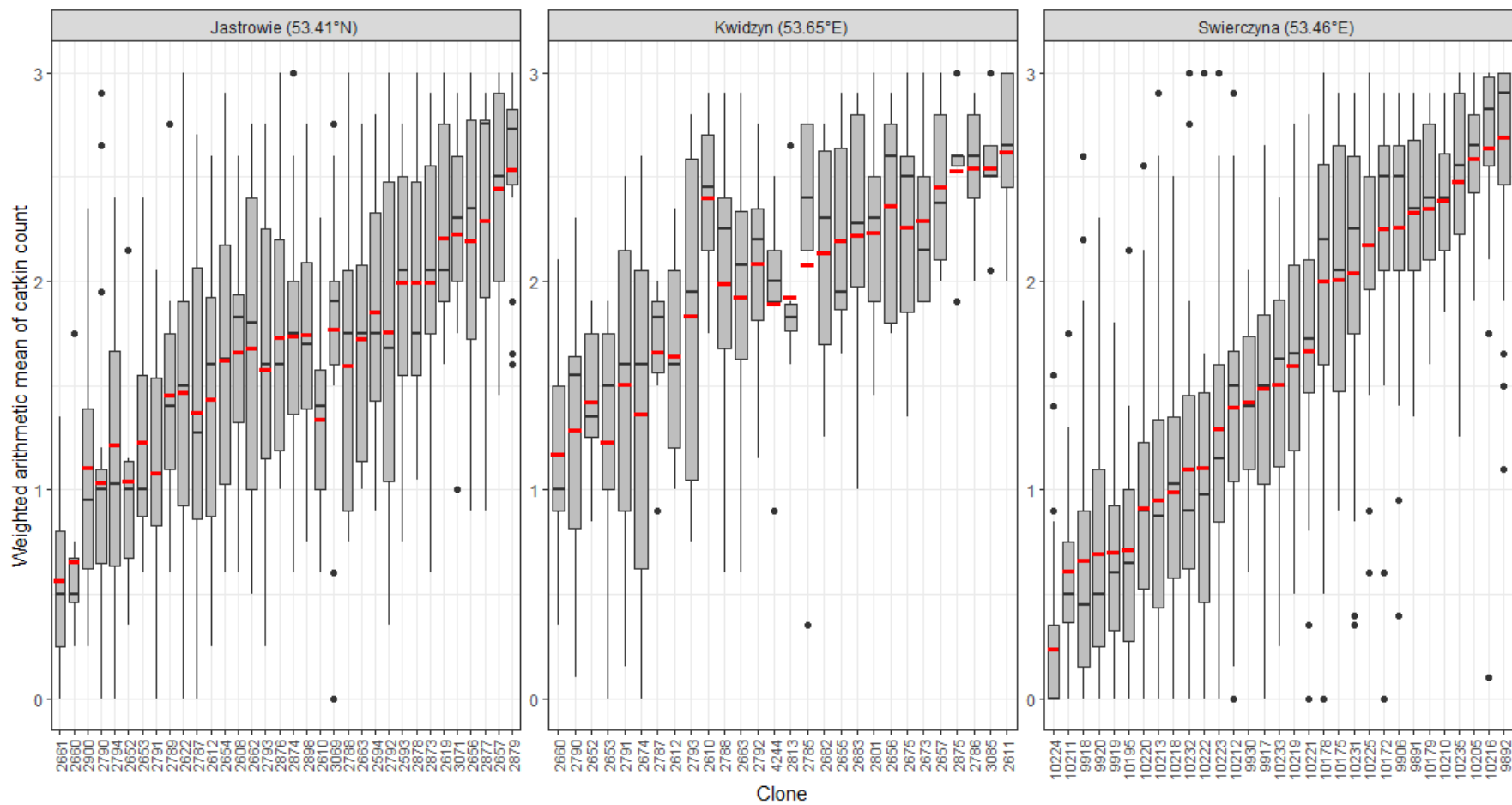


Figure 4. Weighted arithmetic means of male catkin count with medians (black horizontal lines), arithmetic means (red horizontal lines) and outliers (black dots) of each clone group in the three analyzed SOs.

Besides the observed variability in male catkin production, some clones consistently exhibited no male catkins while others displayed varying degrees of catkin abundance. Clones with a higher frequency of ‘0’ values (indicating the score with absence of male catkins) tended to have fewer ramets with the maximum score of ‘3’ (trees with abundant male catkins). More clones transferred from northern seed origins (southward transfer) were observed to not produce any male catkins (Fig. 5).

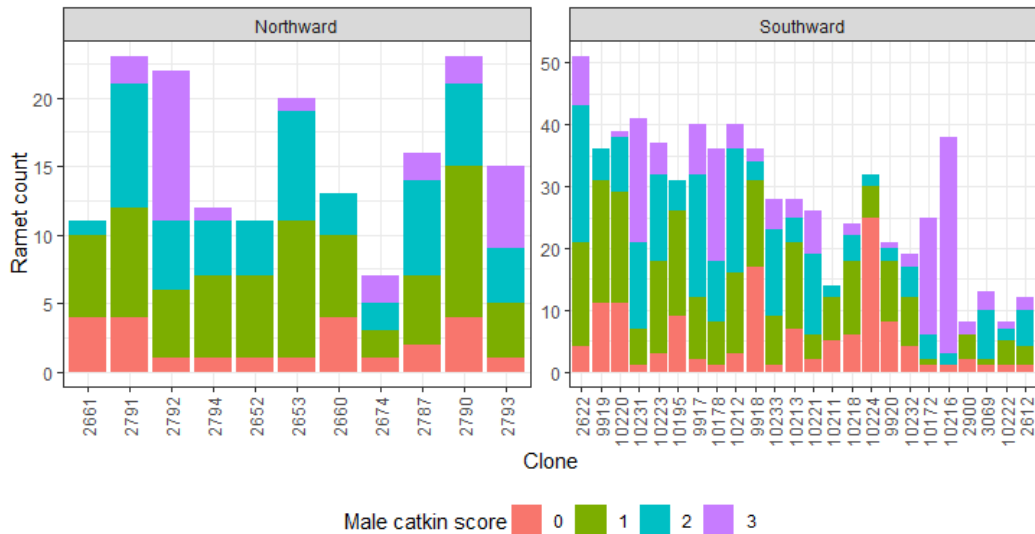


Figure 5. Ramet count of clones with different male catkin scores based on the direction towards which seedlings were transferred from their seed origin location.

The most ‘0’ values were observed in Świerczyna SO which is the youngest analysed SO and is comprised of only clones transferred southward. In comparison, Jastrowie and Kwidzyn SOs have very little clones exhibiting no male catkin production, however their ramet count of each clone is considerably lower than in Świerczyna SO (Fig. 6).

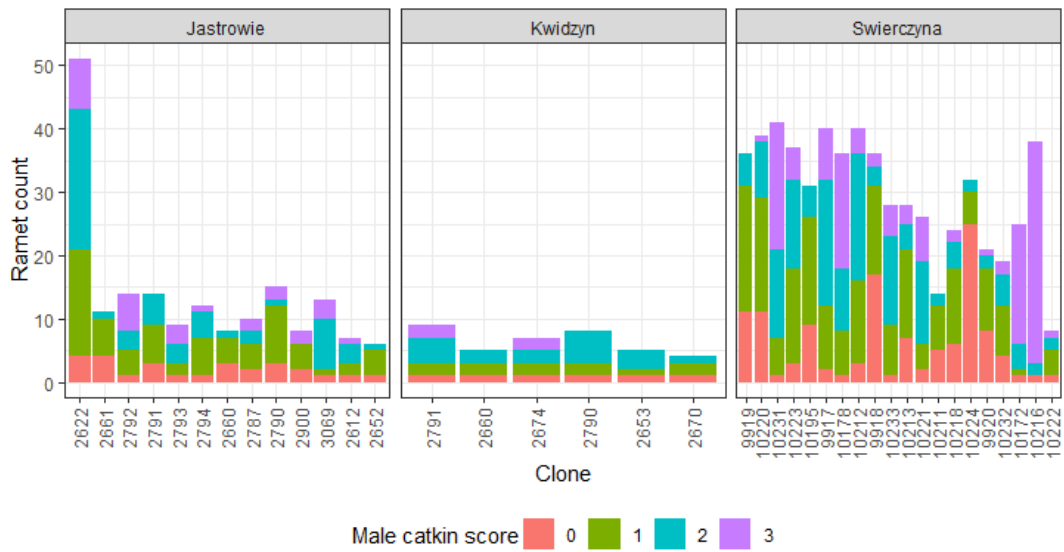


Figure 6. Ramet count of clones with instances of no male catkins found in their crowns (male catkin score of '0') in the three analyzed SOs

Among the 19 overlapping clones between Kwidzyn and Jastrowie SOs, 17 of them consistently exhibited higher male catkin scores in the Kwidzyn SO compared to Jastrowie SO (Fig. 7). A notable characteristic of clones at Kwidzyn SO was their longer northward transfer distances and shorter southward transfer distances compared to the Jastrowie SO (Fig. 8a & Fig. 8b). Despite this difference in transfer distances, a high correlation coefficient of 0.87 occurred between male inflorescence values in the two SOs, suggesting that the performance of the clones does not significantly differ between SOs.

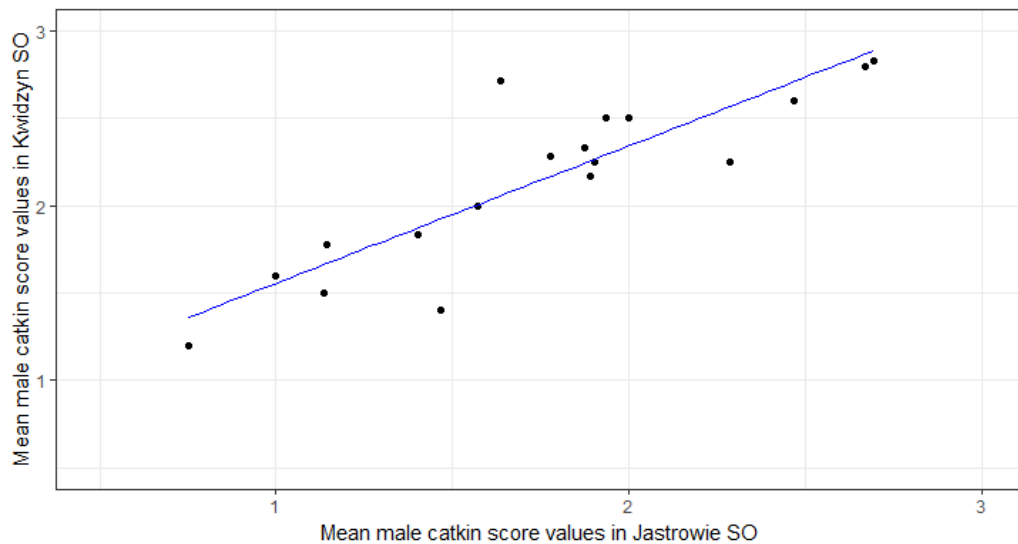


Figure 7. Mean male catkin score of 19 clones of both Jastrowie SO and Kwidzyn SO plotted against each other.

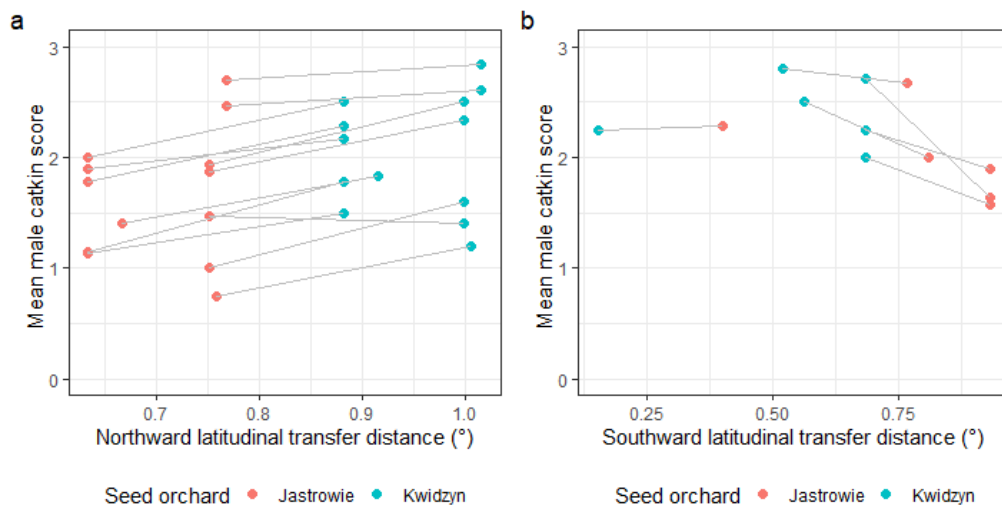


Figure 8. Mean male catkin scores in clones present in both Jastrowie SO and Kwidzyn SO depending on transfer distance. Clones transferred from a higher to lower latitude (Southward transfers) have a negative transfer distance value. Grey lines connect the same clones in two different SOs.

Analysis of variance (ANOVA) of the 19 overlapping clones between Kwidzyn and Jastrowie SOs shows that the SOs had an insignificant effect on the male catkin count score ($p=0.1895$). The clones also varied significantly among each other in regards to their catkin count score ($p<0.05$). Blocks did not influence the response variable ($p=0.8950$). There was no significant interaction between blocks and clones ($p=0.999$) (Table 1).

Table 1. Analysis of variance (ANOVA) results for the effects of SO (Site) and Clone on male catkin count score.

	df	Male catkin count score	
		F	p
Site	1	10.6236	0.1895
Clone	18	5.6565	<.0001

The Tukey post-hoc test resulted in the classification of the 19 clones into 9 different groups: "a", "ab", "abc", "abcd", "abcde", "bcde", "cde", "de", "e" (Fig. 9). This grouping indicates significant differences in male catkin production among the clones.

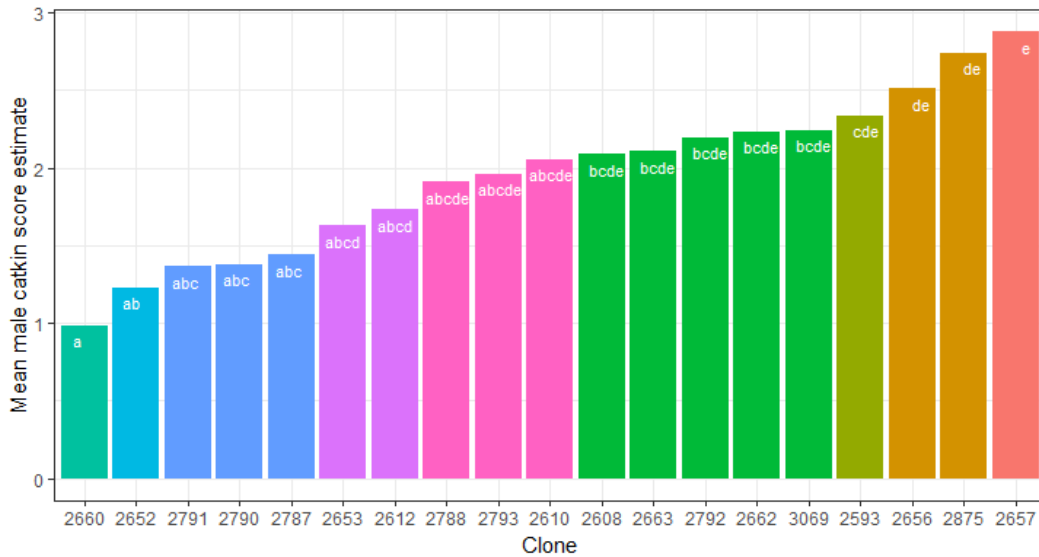


Figure 9. *s* LS-mean estimates of male catkin score for clones found in both Jastrowie and Kwidzyn SO, showcasing distinct groups identified through the Tukey post-hoc test, with labels and colors indicating the various clusters.

3.2. Latitudinal Transfer distance

Statistical analysis showed that the direction and distance of transfer of clones had an effect on male catkin production. Clones that were transferred northward (SO located north of location of origin) had an increase in male catkin count scores with longer transfer distances. A correlation coefficient (Pearson) of 0.32 ($p=0.046$) suggests the increase in transfer distance had a positive effect on the catkin count (Fig. 10a).

The clones that were transferred southward (SO south of clone origin location) have been observed to produce relatively high catkin numbers when their transfer distance is low ($0-0.3^\circ$) with a gradual decrease of productivity with further transfers. A correlation coefficient (Pearson) of -0.24 ($p=0.067$) also suggests a weak negative correlation between the transfer distance and catkin production (Fig. 10b).

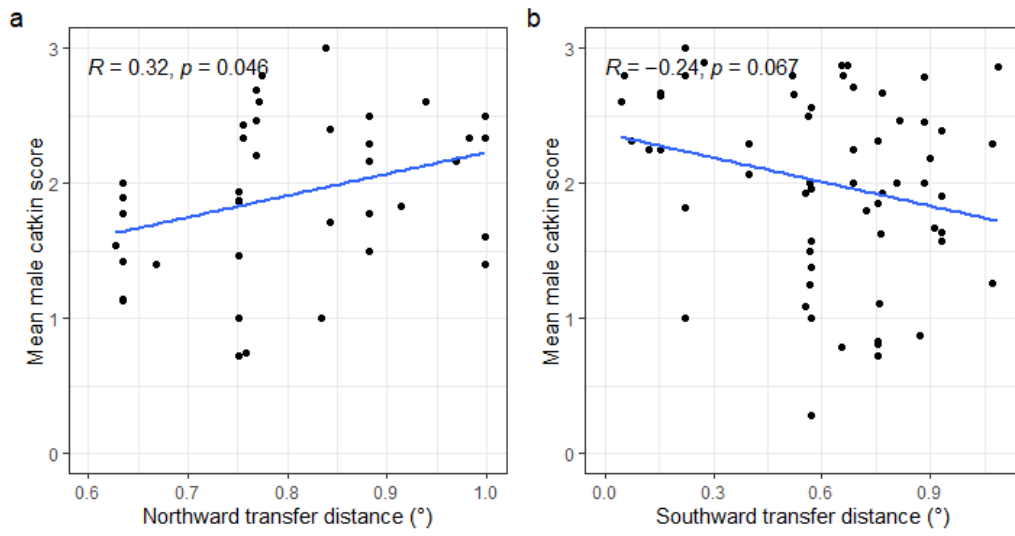


Figure 10. a - Mean male catkin score of clones and their distance of transfer from latitude of origin to latitude of SO (Northward). b - Mean male catkin score of clones and their distance of transfer from latitude of origin to latitude of SO (Southward). Correlation coefficients and their respective p-values are shown.

3.3. Cardinal directions

There was a very small difference in the abundance of male catkins depending on the direction the part of the crown was facing. The highest values of catkin abundance were present in Kwidzyn which is the SO located the most towards the east. The other two SOs (Świerczyna and Jastrowie) didn't differ significantly from each other and the catkin counts in all parts of the crown were relatively similar. Catkin production seems to be slightly influenced by the cardinal direction the trees crown is facing, with northward and eastward-facing crown sections generally producing more flowers (Fig. 12).

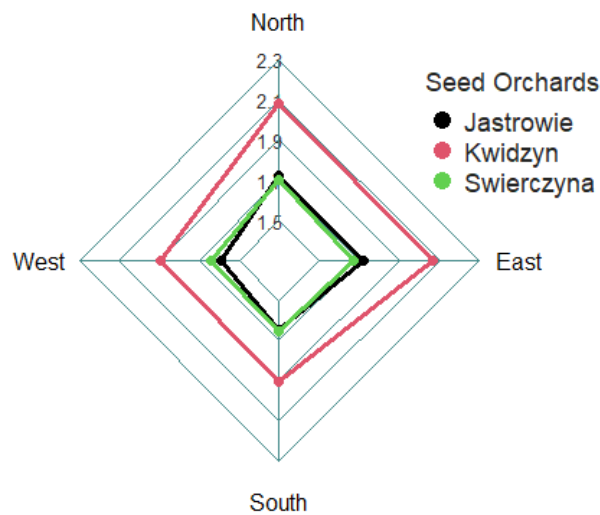


Figure 11. Mean male catkin score in parts of tree crowns facing four cardinal direction in the three SOs

3.4. Crown vitality

Analysis of the data revealed that crown vitality influenced the male catkin count score. With decreasing crown vitality (nearing '1') the abundance of flowers also decreased. The correlation between the two traits was -0.2. We observed that higher inflorescence counts tended to correspond to better crown vitality. While this relationship isn't strong it suggests a tendency for trees with healthier crowns to exhibit higher levels of reproductive productivity (Fig. 13).

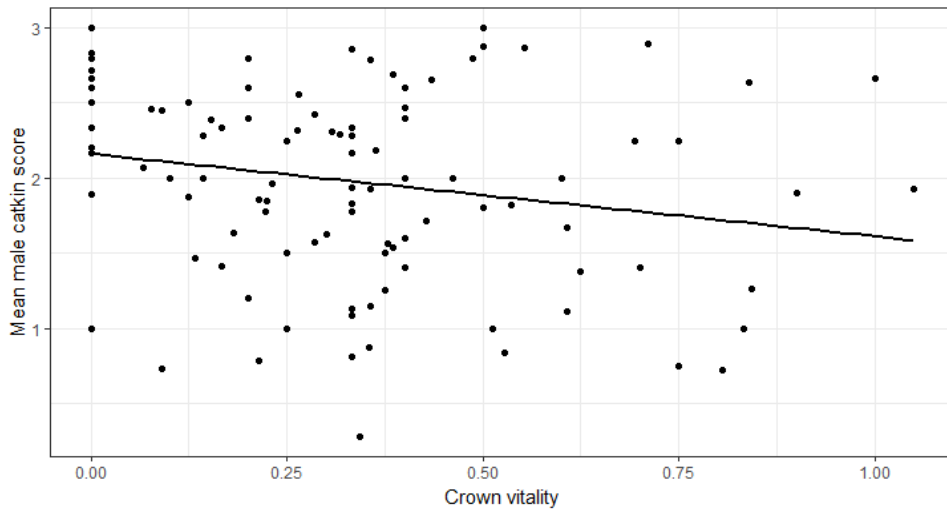


Figure 12. Mean male catkin count score of of different clone groups depending on their mean crown vitality.

3.5. DBH

Size of the tree appeared to affect inflorescence production. Trees with higher DBH values tend to show higher male inflorescence production in the crown than trees with lower DBH. This trend implies that larger, more mature trees tend to exhibit greater reproductive activity compared to smaller counterparts (Fig. 14)

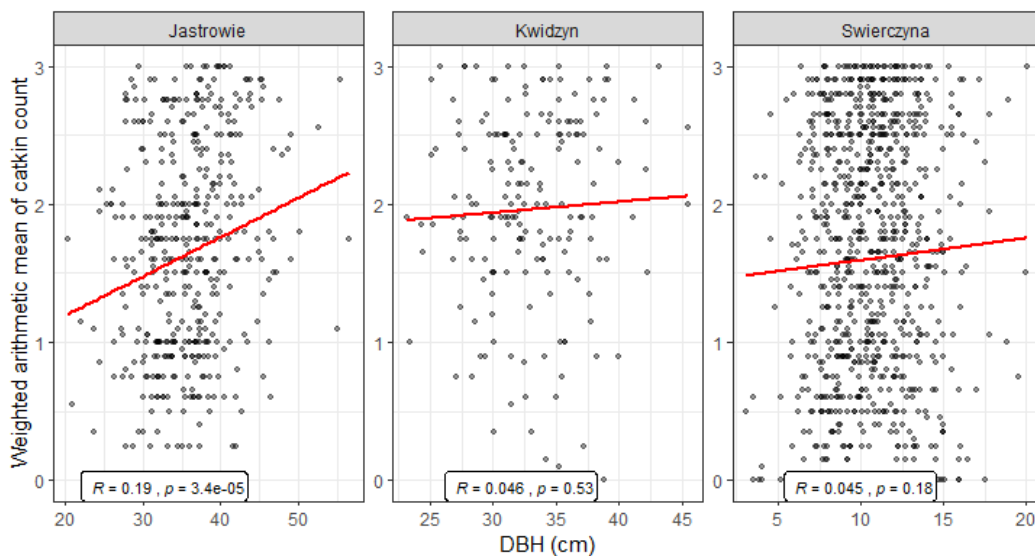


Figure 13. Weighted arithmetic means of male catkin count and DBH of each tree in three SOs with correlation coefficients (R) and their respective p-values (p).

The strength of the observed trend varied among the three SOs. In the Jastrowie SO, where DBH values exhibited the highest variability due to the orchard's older

age, the correlation between DBH and male inflorescence production was most pronounced; correlation coefficient = 0.19, p-value = 3.4e-05.

In contrast, while similar trends were evident in the Kwidzyn and Świerczyna SOs, the correlations were weaker, with higher p-values of 0.53 for Kwidzyn and 0.18 for Świerczyna. These differences may be attributed to variations in SO age, tree density, environmental conditions, or other factors influencing tree growth and reproductive behaviour.

3.6. Longitudinal transfer distance

Further westward transfers proved to negatively impact the catkin count of clones in Jastrowie and Kwidzyn SO with correlations coefficients of $R=-0.43$ and $R=-0.35$ respectively and p-values lower than 0.05. In Świerczyna SO the opposite effect was observed with a correlation coefficient of $R=0.32$ and p-value of 0.12 (Fig. 15).

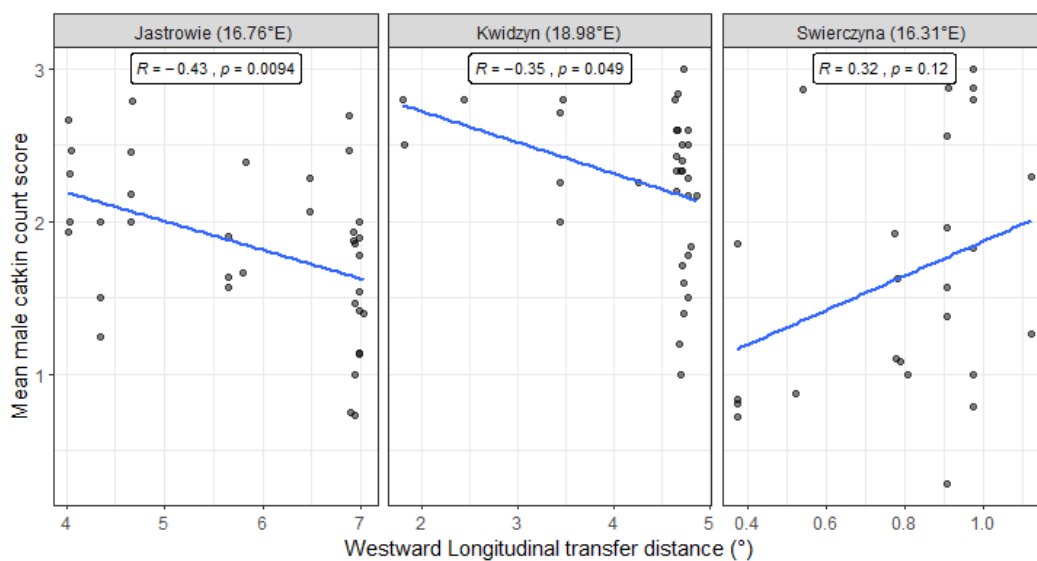


Figure 14. Mean male catkin count scores of different clone groups and their distance of transfer from longitude of origin to longitude of SO (Westward) in the three analyzed SOs. Correlation coefficients and their respective p-values are shown.

When comparing the catkin abundance among the 19 overlapping clones in Kwidzyn and Jastrowie SO the majority of clones reached higher catkin count scores in the nearer SO (Kwidzyn SO). A small yet consistent decrease of male catkin count score was observed in relation to the distance of the longitudinal transfer (Fig. 16).

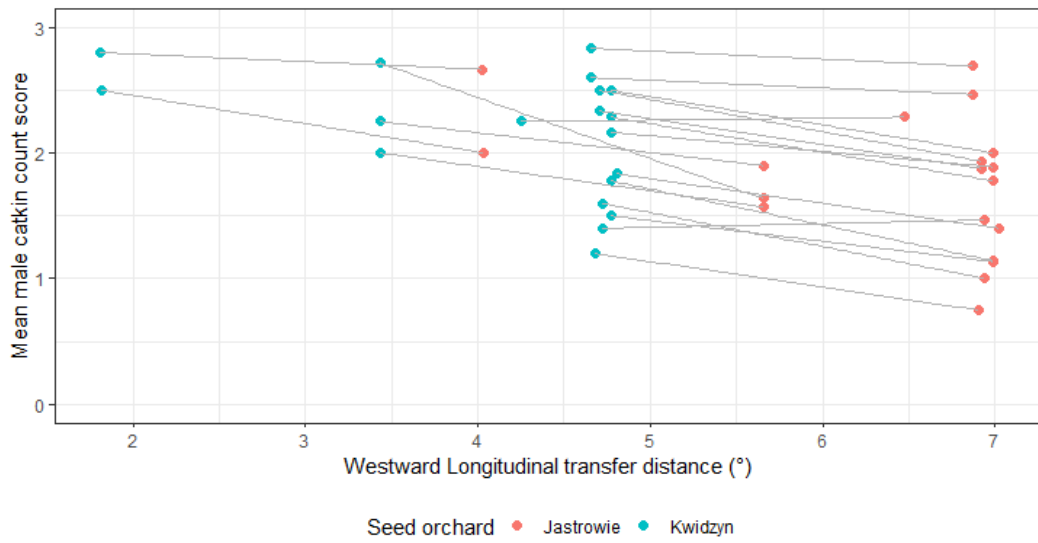


Figure 15. Mean male catkin count score of clones present in both Jastrowie and Kwidzyn SO and their distance of transfer from longitude of origin to longitude of SO (Westward). The same clones are connected by grey lines.

4. Discussion

4.1. Variability in male flowering

This study showed that the variability in male flowering in silver birch is quite substantial. Large differences in the amount of male catkins were observed both within and between the observed clones. The question to ask is how much of this variability can be attributed to differences in the adaptability of clones to photoperiod lengths versus annual fluctuations of flowering among clones? The lack of chronological data regarding flowering can be considered a limitation to this study. Especially considering the findings of Clark et al. (2004) who suggested that a significant portion of individuals exhibit approximate synchronization in their reproductive cycles, while others deviate from this pattern. Consequently, in a given year, a specific tree might dominate seed production, whereas in another year, a different tree takes on this role. This alternation can mitigate interannual variations in seed production across the population. The clonal differences in male flowering might influence pollination efficiency which in turn affects reproductive potential (Ranta et al., 2008).

The observed gradual distribution of clones in male inflorescence productivity from '0' to '3' in Świerczyna SO suggests a more uniform response among the clones in this particular SO. This could be attributed to the fact that the clones in this SO originate from similar climatic conditions, with their latitudes and longitudes being quite local to each other. The homogeneity in their environmental backgrounds likely contributes to the more consistent productivity levels observed. Another reason could be the young age and short height of clones in Świerczyna SO which allowed for an accurate assessment of their catkin count. It is reasonable to infer that the older and taller clones in Kwidzyn SO and Jastrowie SO contribute to a higher degree of measurement errors.

In contrast, the more irregular distribution patterns seen in the other two SOs, with larger differences in catkin count variability among clones, might be present due to the more diverse climatic origins of the clones. These differences could reflect

varying degrees of adaptation and response to the local environmental conditions of the SOs.

The data also shows that there was a higher frequency of clones with no catkins observed in Świerczyna SO compared to the other two SOs. This is the youngest SO in the study. This may suggest that some clones haven't yet began to reproduce since silver birch can start reproducing between 5-30 years of age (Atkinson, 1992). Alternatively, the lower inflorescence production can be attributed to the latitudinal transfer distance (average of -0.46° for southward transfers) which could further explain the influence of photoperiod differences and the adaptation of birch to local climate conditions on the reproductive capabilities.

Nilsson (2001) highlights that phenological traits, such as the timing of budburst and growth cessation, vary significantly among populations from different latitudes. For both scots pine (*Pinus sylvestris* L.) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm), northern populations tend to exhibit earlier budburst and growth cessation compared to southern populations. Trees from northern origins also tend to flower earlier and have greater cold hardiness, which can lead to differences in reproductive timing and success when transferred to different latitudes.

4.2. Transfer distance

While the male catkin production of southward transferred genotypes in general was observed to be higher than in the case of northward transfers, the trend line indicated the loss of catkin production with increasing transfer distance towards the south. On the other hand, the trend for northward transfers was increasing with distance which may suggest that photoperiod differences could positively influence flowering. Based on our findings it's safe to say that transferring seedlings up to 1° northward most likely will have a positive effect on their reproductive capabilities, while the opposite can be said about southward transfers of the same distance.

The influence of latitudinal transfer on the variability of catkin production in silver birch aligns with findings in other tree species, underscoring the significant impact of latitude on tree productivity and phenological traits.

Berlin et al. (2016) observed that scots pine seedlings transferred across latitudes showed differences in growth, phenology, and survival. Southern provenances struggled in northern climates due to climate adaptation mismatches. This

indicates that similar mismatches could influence catkin production in silver birch, with latitude affecting the timing and quantity of catkin development.

Liziniewicz et al. (2023) found that Norway spruce seedlings demonstrated variability in growth and phenology when transferred across latitudinal gradients. Southern provenances grew faster but were more frost-sensitive in more northern, harsher environments. This pattern suggests that latitudinal transfer in silver birch could lead to variable catkin production, with northern transfers potentially producing catkins earlier but facing increased frost risk.

These studies collectively highlight that latitudinal transfer affects growth and phenological traits of other species, due to differences in climatic adaptation. For silver birch, this implies that catkin production and related reproductive traits may exhibit significant variability based on the latitude of origin and planting location. Understanding these effects is crucial for optimizing forestry practices and improving the reproductive success of transferred seedlings.

While higher reproductive potential of silver birch might be correlated with clones originating from more southern latitudes, it is worth noting that transferring clones towards the north can also increase the risk and frequency of moose browsing (Viherä-Aarnio & Heikkilä, 2006). It is important to research this topic in the future, because increased browsing may prove to be a decisive factor when deciding to transfer seedlings towards northwards.

4.3. Limitations of the study

A big limitation of this study was the small amount of overlapping clones among the analysed SOs. A precise assessment of variability requires large amounts of data with the same clones with different growing conditions which this study lacks. With only 19 overlapping clones and limited ramet counts for each clone the results of the analysis could be considered not precise enough. Comparing the same genotypes subjected to different environmental conditions (especially photoperiod) was one of the main focuses of this study. However, due to the limited number of overlapping clones, it was challenging to draw any robust conclusions. The small sample size of overlapping clones reduced the statistical power of the analysis and potentially obscured subtle differences or interactions that might have been detected with a larger sample.

Secondly, the northward and southward transfer distances of clones were relatively low. Transfer distances of the north-south axis weren't longer than 1° (a rather small distance when considering photoperiod to be the driving factor of the male catkin production). A wider range of clone transfer distances should have

been utilized to better analyze the influence of latitudes. On the other hand, transfers on the east-west axis were almost entirely limited to westward transfers, with just a couple insignificant clones being transferred from western origins towards the east. While the range of transfer distances on the longitudinal axis is larger there is no comparison the eastward transfers which greatly hinders the value of the analysis.

Thirdly, the visual method of gathering the male catkin count score data was imprecise. There is no way of knowing about any inconsistencies within the gathered data. Each SO differed from the others when it comes to the height of the trees, which limited the amount of catkins seen from below on the tall crown. This could unpredictably influence the subjective grading of the researcher. More precise methods of acquiring such data should be considered in the future.

Another limitation is the complete lack of chronological data regarding the analyzed clones. Without knowing the year-to-year variation of catkin numbers making conclusions based on the male catkin counts in one year is limited. Considering that clones could be synchronized, there is no way of knowing if the clones with instances of male catkin count scores equal to zero are exhibiting these undesirable traits due to their lack of adaptability to the new latitude or just happen to be having one unproductive year.

The role of climate conditions on silver birch variability in catkin production is not well known but its definitely worth looking into. No specific data about photoperiod lengths was used to explain the clonal variability. The study didn't investigate the effects of environmental conditions such as meteorology, air temperature, and edaphic factors on the variation of catkin production. The influence of these and other factors on pollen production remains largely unknown (Ranpal et al., 2022).

4.4. Management implications

Transferring silver birch clones from northern origins to southern SOs consistently resulted in lower male catkin production. This suggests that northern-adapted clones may struggle to achieve optimal reproductive performance in southern environments. As such, forestry managers should exercise caution when planning north-to-south transfers and consider alternative strategies that might mitigate these adverse effects.

In contrast, moving seedlings from southern origins to northern locations showed a notable increase in male catkin production, up to a certain point. This indicates that southern-adapted clones can be used by forest managers in the future to

increase male catkin production in slightly cooler northern climates with longer photoperiod during vegetation season.

Male catkin production in silver birch increases the pollination capabilities, which in turn increases the reproductive abilities of silver birch. When analyzing variability it is possible to find outstanding clones capable of increased catkin production. Identifying and planting these clones in SOs at specific latitudes and conditions could support sustainable seed production. Planting progenies of these clones in forestry practices could enhance natural regeneration and help maintaining healthy, productive silver birch populations.

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Appendix 1: Spatial distribution of silver birch clones within SO plots

This appendix presents three figures (Fig. 17; Fig. 18; Fig. 19) visualizing the spatial distribution of silver birch clones within the seed orchard blocks. The key observation from these figures is that there is no noticeable effect of the position of silver birch clones on male catkin production. Additionally, the spatial distribution of clones with the lowest male catkin score suggests that light availability, determined by the clone's position within the plot, does not significantly influence catkin production.

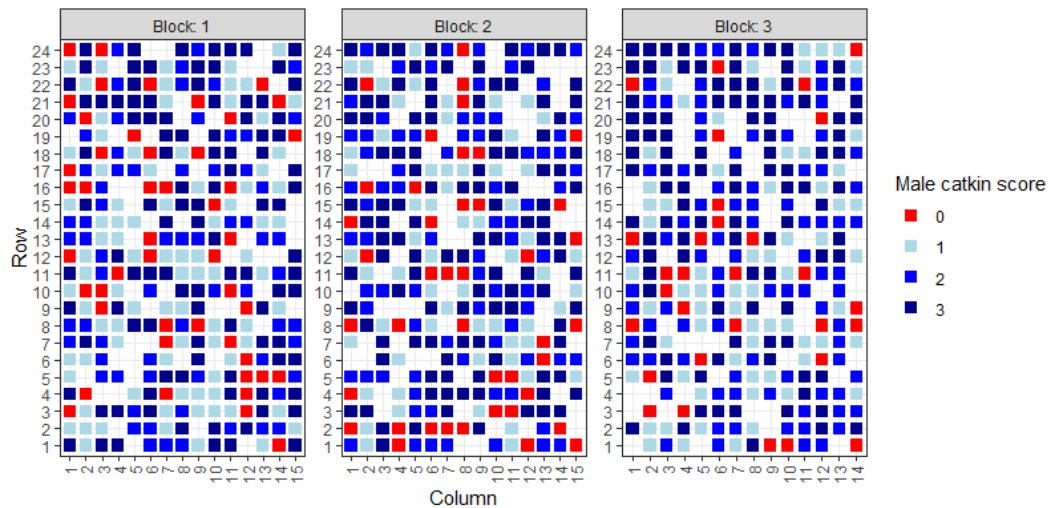


Figure 16. Spatial distribution of male catkin scores within three blocks in Świerczyna SO.

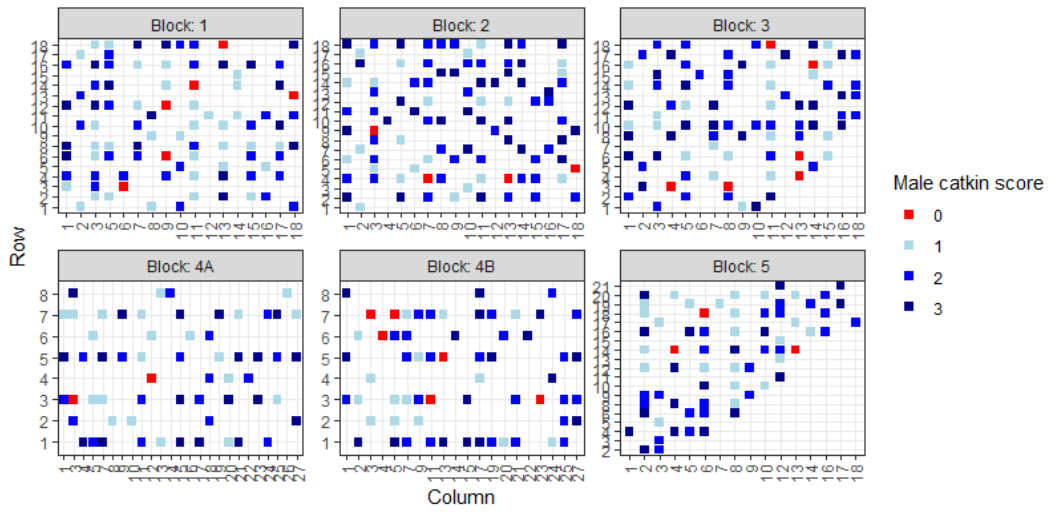


Figure 17. Spatial distribution of male catkin scores within six blocks in Jastrowie SO.

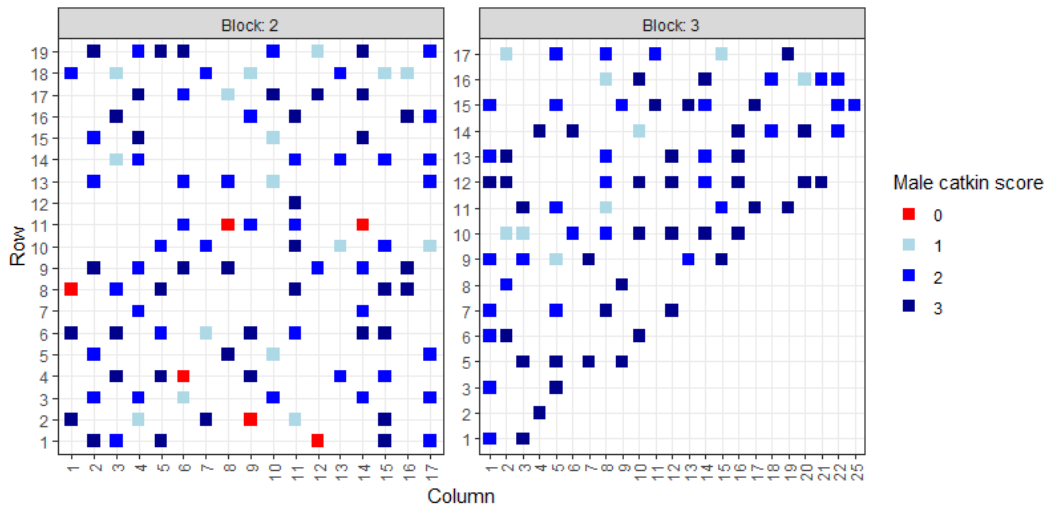


Figure 18. Spatial distribution of male catkin scores within two blocks in Kwidzyn SO.