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RESEARCH ARTICLE

Climate-Driven Productivity Responses and Implications for Genetic Adaptation and Breeding of Boreal Trees in Kazakhstan

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Abstract: Kazakhstan's boreal and forest-steppe forests form the southern ecotonal edge of the West Siberian taiga, where relatively small changes in heat and moisture can trigger disproportionate impacts on tree growth, mortality, and regeneration. Although forests cover only ~4% of Kazakhstan, they provide critical ecosystem services: stabilizing hydrological regimes, buffering microclimates, protecting agricultural lands from wind and water erosion, and supporting landscape resilience in drought-prone regions. Sustainable forest management therefore requires quantitative monitoring of forest productivity and carbon balance, not only descriptive assessments, to support both climate policy and adaptive silviculture. Over recent decades, Kazakhstan has experienced persistent warming and increasing hydroclimatic stress. Rising temperatures can lengthen the growing season and increase potential productivity, but warming also elevates atmospheric water demand and Vapor-Pressure Deficit (VPD), intensifying drought stress and increasing the likelihood of productivity collapse during extreme years. Globally, such "hotter droughts" have been linked to declining growth and higher tree mortality risk, especially in climate-sensitive ecotones. For boreal systems, drought effects may offset warming-driven gains and destabilize the net carbon sink. Productivity and carbon dynamics are also central to genetic adaptation and breeding. Tree populations often exhibit genetically structured variation in phenology, hydraulic traits, and growth responses to climate, producing distinct reaction norms across climatic gradients. Under climate change, selective pressures may shift from cold tolerance toward drought and heat tolerance, implying that breeding programs and seed-origin zoning must be updated to maintain forest performance and reduce maladaptation risk. However, for Kazakhstan, long-term quantitative relationships among climate drivers (temperature, precipitation, SPEI, VPD), productivity (NDVI, NPP, NEP), carbon pools (AGC, SoilC), and breeding-relevant adaptation patterns remain insufficiently established. This study addresses that gap by integrating multi-decadal climate datasets with satellite observations and carbon-cycle modelling to evaluate climate-driven productivity responses across five boreal regions of Kazakhstan (Akmola, Kostanay, North Kazakhstan, Pavlodar, East Kazakhstan) during 1990–2024. We test the expectation that (i) productivity shows an overall increasing trend under warming but (ii) drought years trigger strong negative anomalies in NPP and NEP, potentially switching forests from sink to source, and (iii) regional contrasts in climate elasticities delineate functional adaptive–breeding zones relevant for provenance selection and assisted gene flow. Aim. To quantify climate-driven changes in productivity and carbon balance of Kazakhstan's boreal forests (1990–2024) and interpret them in the context of genetic adaptation and breeding priorities of dominant tree species.

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Introduction

Forests in Kazakhstan, despite the extremely low overall forest cover (approximately 4% of the national territory), play a disproportionately important role in maintaining the stability of natural and agricultural landscapes. They stabilize soil and hydrological conditions, reduce the risks of wind and water erosion, regulate runoff within major river basins, and mitigate the impacts of extreme climatic events through the formation of local microclimates [1–6]. Under conditions of increasing climate variability and a rising frequency of extreme droughts, the need for quantitative, spatially explicit monitoring of forest ecosystem condition and functioning becomes particularly urgent, as such assessments form the basis for evidence-based decisions in forest management and climate policy.

Recent studies conducted in Kazakhstan further emphasize the importance of integrating ecological monitoring with plant adaptation research and sustainable management strategies. For example, seed priming with natural mineral materials has been shown to enhance antioxidant defense mechanisms and improve salt tolerance in barley seedlings, highlighting the potential of environmentally friendly approaches for increasing plant resilience to abiotic stress [7]. In addition, investigations of medicinal and endemic plant species have demonstrated the considerable biotechnological potential of native plant resources for sustainable agricultural and environmental applications, further supporting the need to conserve and effectively manage Kazakhstan's natural ecosystems [8, 9].

The forest fund of Kazakhstan is characterized by pronounced spatial heterogeneity and includes several major types of forest ecosystems formed under a sharply continental climate and strong latitudinal and altitudinal gradients (Fig. 1). Its structure comprises boreal forests of the northern and eastern regions, mountain forests of the Altai and Tien Shan ranges, riparian (tugai) forests along major river valleys, ribbon pine forests, as well as protective and artificially established forest plantations that primarily perform conservation and agro-landscape functions.

Boreal forests of northern and eastern Kazakhstan constitute the southern periphery of the West Siberian taiga and are mainly confined to the forest-steppe zone and the northern margins of the steppe. They are represented by pine, birch, larch, and spruce stands dominated by Pinus sylvestris, Betula pendula, Larix sibirica, and Picea obovata. These forests store the majority of aboveground and soil carbon within the national forest fund and make a key contribution to CO_2 uptake in the LULUCF sector. Due to their ecotonal position, boreal forests exhibit heightened sensitivity to climatic fluctuations and play a decisive role in regulating hydrological regimes and sustaining the stability of agricultural landscapes in northern Kazakhstan.

A distinctive subgroup within this system is formed by the ribbon pine forests of northern Kazakhstan, developed on sandy paleo-alluvial deposits. These unique forest massifs perform important protective functions by preventing deflation and soil degradation, while simultaneously serving as a significant object of forest management. Their stability is closely linked to moisture availability and drought frequency, making ribbon pine forests particularly vulnerable to ongoing climatic change.

Alongside natural forests, protective and artificial plantations, such as shelterbelts, field-protective, and water-protective forests, play an important role in stabilizing agricultural landscapes and combating erosion and desertification. Although these plantations generally contain lower biomass and carbon stocks than natural forests, their functional importance under the arid and semi-arid conditions of Kazakhstan is exceptionally high.

The analytical assessment "Forests and Climate Change in Kazakhstan" demonstrated that, despite the high ecological significance of forests, the forestry sector has long remained peripheral within national climate strategies. This occurred despite the substantial mitigation potential of forests through CO_2 sequestration in the LULUCF sector and their critical role in adapting rural areas to drought, land degradation, and desertification [10–12]. That assessment systematized information on forest resource structure and institutional arrangements of forest management and identified major climate risks and policy

directions related to forest restoration and protective afforestation [13–16]. Nevertheless, quantitative relationships between long-term climate trends, forest productivity, carbon balance dynamics, and adaptive characteristics of major tree species remain insufficiently developed in the national context [17].

Boreal forests of northern and eastern Kazakhstan, as the most extensive and carbon-dense forest massifs in the country, function under conditions of a sharply continental climate and in close proximity to dry steppes and semi-deserts [18]. The dominant forest-forming species create complex ecotonal communities in which even relatively small changes in thermal or moisture regimes can lead to disproportionally large shifts in growth, mortality, and regeneration processes [19, 20]. Over the past 30–40 years, Kazakhstan has experienced persistent climatic changes, including an increase in mean annual temperature by 1.4–1.8°C, more frequent summer droughts, rising Vapor-Pressure Deficit (VPD), altered precipitation regimes during the growing season, and an increased frequency of extreme drought events (SPEI ≤ −1.0) [21–24]. These trends are capable of substantially reshaping selective pressures in boreal populations, shifting adaptive advantages from cold tolerance toward drought and heat tolerance [25].

Contemporary research in forest ecology and genetics indicates that productivity (NPP), carbon fluxes and stocks (NEP, AGC, SoilC), and resilience to climatic stress are closely linked to population genetic structure, reaction norms, and mechanisms of local adaptation [26, 27]. For Pinus sylvestris, Larix sibirica, Betula pendula, and other boreal species, genetically determined differences have been documented in growth rates, phenology, cavitation resistance, root system architecture, and drought responses [28–30]. However, for the boreal forests of Kazakhstan, integrated studies remain lacking that simultaneously link multi-decadal dynamics of productivity and carbon pools, key climatic drivers, and the interpretation of these patterns in terms of local adaptation and seed-zoning or breeding frameworks [31].

The aim of this study is to quantitatively assess climate-driven changes in productivity and carbon balance of the boreal forests of Kazakhstan over the period 1990–2024 and to interpret these changes in the context of genetic adaptation and breeding priorities of the major forest-forming species, while accounting for institutional and policy dimensions of forest management [32].

Materials and Methods

The study covered five boreal regions of northern and eastern Kazakhstan: Akmola, Kostanay, North Kazakhstan, Pavlodar, and East Kazakhstan.

These regions lie within 51–550 N and 65–850 E, representing the southern periphery of the West Siberian taiga and forming transitional zones toward steppe and dry-steppe ecosystems. The climate is strongly continental with hot, short summers and long, cold winters. Moisture conditions range from relatively humid East Kazakhstan to more arid parts of Pavlodar and Akmola regions.

Dominant soils include sod-podzolic, grey forest, dark chestnut, and alluvial-forest types (Fig. 1). The main forest-forming species are Pinus sylvestris, Betula pendula, Larix sibirica, and Picea obovata.

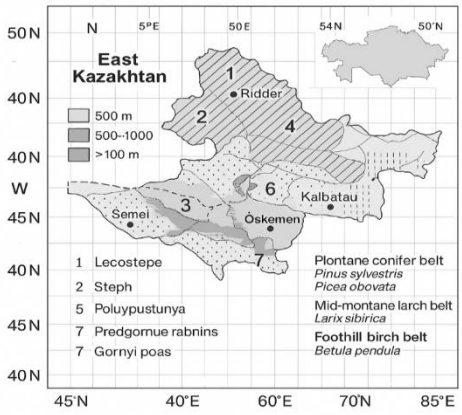

Fig. 1: Natural vegetation zones of Kazakhstan with the position of forest-steppe and boreal forest areas (1 – Forest steppe, 2 – Steppe, 3 – Semi-desert, 4 – Desert, 5 – Foothill plains, 6 – Mountain zone, 7 – Lowland (floodplain) forest)

The map shows major vegetation belts (forest-steppe, steppe, semi-desert, desert, foothill plains, mountain zone, and floodplain forests) and highlights the five boreal regions analyzed (Akmola, Kostanay, North Kazakhstan, Pavlodar, East Kazakhstan). The figure provides the biogeographic context for interpreting productivity gradients along the moisture and continentality transition. Region boundaries are administrative; forest cover is indicated by the national forest mask used for satellite averaging.

Climate Data and Drought Indicators. Climate variables were obtained from three independent sources: ERA5 (ECMWF) for air temperature, precipitation, VPD and PET; CRU TS 4.06 for independent validation of interannual temperature and precipitation anomalies; and Kazhydromet for national meteorological archives used for calibration.

The following climate metrics were calculated: mean temperature for the growing season from May to September; summer temperature anomaly defined as the difference between the annual temperature and the 1990–2020 baseline; accumulated precipitation during the growing season; the Standardized Precipitation Evapotranspiration Index derived from the balance between precipitation and potential evapotranspiration; and growing degree days above five degrees Celsius.

Drought intensity thresholds were defined as follows: values of the Standardized Precipitation Evapotranspiration Index less than or equal to minus one indicated drought; values less than or equal to minus one point five indicated severe drought; and values less than or equal to minus two indicated extreme drought. Special attention was given to the drought years 1998, 2010 to 2012 and 2021.

Satellite NDVI Data. Vegetation activity was assessed using two long term NDVI datasets: AVHRR GIMMS NDVI3g version one with an eight kilometre resolution covering the period from 1982 to 2015, and MODIS NDVI MOD13Q1 with a two hundred fifty metre resolution covering the period from 2000 to 2024. Preprocessing included cloud masking, smoothing using the Savitzky Golay filter, and generation of maximum value composites for the months from May to September. NDVI values were averaged across forested pixels identified using national forest cover maps and land use data.

Estimation of Productivity. Net primary production was estimated using the light use efficiency model, where maximum light use efficiency was set between zero point forty five and zero point fifty five grams of carbon per megajoule for coniferous species, and between zero point thirty and zero point thirty five grams of carbon per megajoule for birch. Temperature limitation was represented by an exponential function centred at an optimum temperature of sixteen to twenty degrees Celsius, with a temperature sensitivity parameter of four to six degrees Celsius. Vapour pressure deficit limitation was described by an exponential decay function, with a critical vapour pressure deficit of one point zero to one point two kilopascals.

Net ecosystem production was calculated as the difference between net primary production and heterotrophic respiration. Heterotrophic respiration was modelled using an exponential temperature response function with a base respiration rate at ten degrees Celsius between one point two and one point seven tonnes of carbon per hectare per year and an activation energy parameter between two hundred forty and two hundred sixty Kelvin.

Aboveground and Soil Carbon. Aboveground carbon was assessed using regional allometric relationships, empirical relationships between NDVI and biomass expressed as a linear function, and an assumed carbon fraction of fifty percent in dry biomass. Soil carbon in the upper thirty centimetres was modelled using a first order decay equation in which soil carbon content depends on carbon inputs and a decomposition rate. Initial soil carbon values ranged between twenty five and seventy tonnes of carbon per hectare.

Statistical Analysis. To evaluate climatic controls of net primary production variability, standardized multiple regression was applied. The standardized form allowed direct comparison of the contributions of temperature, precipitation and the Standardized Precipitation Evapotranspiration Index across regions. Model performance was evaluated using the root mean square error, the coefficient of determination, the Nash Sutcliffe efficiency and ten fold cross validation with MODIS net primary production used as the reference dataset.

As part of the research, a full inventory of all clones growing in the clone archives was conducted. It was established that the average survival rate of clone archives No. 1 and No. 2 as of 2022 was 70.1% and 67.7%, respectively. The total number of ramets across both sites was 3,286, with each clone represented by 11 to 58 ramets (trees genetically identical to the original clone).

According to the weighted average score of sanitary condition, the plus-tree clones were classified as weakened, with scores of 1.7 and 1.6 for clone archives No. 1 and No. 2, respectively. The proportion of ramets without visible signs of weakening accounted for 41.1% of all individuals at the study sites.

During the field inspection of plus-tree clones, mechanical stem damage was identified, including bark stripping of various sizes. In many cases, bark stripping extended down to the cambium, resulting in visible traces of resin exudation. It can be assumed that such damage is repeatedly caused by wild ungulates (roe deer), for which the thin bark on the lower part of the stem serves as a source of additional nutrients. The proportion of trees with such mechanical damage in clone archives No. 1 and No. 2 was 56.8% and 44.7%, respectively. Severe stem damage (up to 2 m in height and exceeding half the stem diameter) was most common in clone archive No. 1, where it affected 20.9% of all trees. In clone archive No. 2, the proportion of severely damaged trees was twice as low (10.3%).

The expansion of the damaged area around the entire stem circumference and complete destruction of the bast (phloem) may disrupt the downward transport of organic compounds, reduce plant stability and vitality, and ultimately lead to tree mortality.

Initially, a selection-genetic assessment and molecular-genetic passporting were performed for 15 plus-tree clones of Scots pine (Pinus sylvestris). Figure 7 presents the biometric characteristics and survival rates of the studied clones.

Long-term trends in NDVI, NPP, NEP, AGC, and SoilC were evaluated using the Mann–Kendall trend test with Sen's slope estimator to provide robust monotonic trend estimates under non-normality. Differences between drought years and non-drought years were tested using bootstrap confidence intervals for mean anomalies and non-parametric comparisons where appropriate. Climate controls of NPP were quantified using standardized multiple regression; multicollinearity was assessed using Variance Inflation Factors (VIF), and residual autocorrelation was checked using Durbin–Watson statistics. Model performance was evaluated with RMSE, R^2, Nash–Sutcliffe efficiency, and 10-fold cross-validation, using MODIS NPP as a reference dataset for validation.

Results

NDVI Dynamics

All five regions showed a positive trend in the Normalized Difference Vegetation Index between 1990 and 2024. The strongest increase was observed in East Kazakhstan, where NDVI rose from approximately zero point fifty five to between zero point sixty eight and zero point seventy. North Kazakhstan maintained consistently high NDVI values in the range of zero point fifty to zero point fifty eight. Kostanay demonstrated moderate growth with pronounced year to year variability. Akmola and Pavlodar exhibited weaker increases and the greatest interannual fluctuations. Significant declines in NDVI were recorded during the years 1998, 2010 to 2012 and 2021, corresponding to strong negative values of the Standardized Precipitation Evapotranspiration Index.

Changes in Carbon Stocks. Across the boreal forests of Kazakhstan, aboveground carbon increased from approximately sixty to eighty tonnes of carbon per hectare, representing an increase of about thirty to thirty five percent. Soil carbon increased by between five and ten tonnes of carbon per hectare, depending on the region (Table 1, Fig. 2).

Table 1: Trends in Aboveground Carbon (AGC) and Soil Carbon (SoilC) in 1990–2024

№	Region	AGC 1990 (т C·ha⁻¹)	AGC 2024 (т C·ha¹)	ΔAGC	SoilC 1990 (т C·ha¹)	SoilC 2024 (т C·ha¹)	ΔSoilC
1	East Kazakhstan	70–75	90–95	+20	65–75	75–85	+10
2	North Kazakhstan Region	65–70	85–88	+18	60–70	68–75	+8
3	Kostanay	55–60	72–76	+15	55–65	59–68	+6
4	Akmola	50–55	65–68	+12	45–55	50–58	+5
5	Pavlodar	48–52	58–63	+10	40–50	45–54	+5

The most intensive increase in AGC and SoilC is observed in East Kazakhstan and North Kazakhstan, which corresponds to more favorable hydrothermal conditions and a higher proportion of mesophytic coniferous and mixed forests.

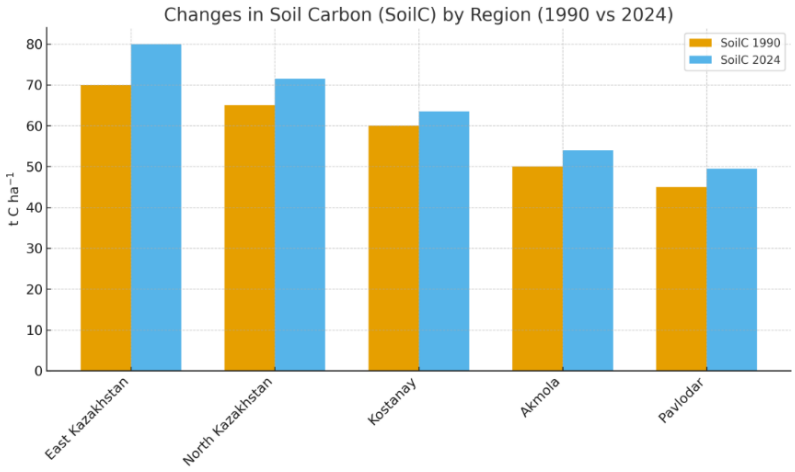

Fig. 2: Changes in AGC and SoilC by region (1990 vs. 2024)

Description: Bar charts by region, with paired bars for AGC and SoilC.

Paired bars compare AGC and SoilC for each region, illustrating long-term accumulation of carbon stocks. Values represent regional means over forested pixels; SoilC refers to the 0–30 cm layer. The figure emphasizes spatial contrasts, with higher carbon stocks in East and North Kazakhstan and lower stocks in more arid regions. Error bars (if available) should show uncertainty (e.g., ±95% CI or ±SD).

Long-term trends in NPP and NEP. NPP. Average NPP values in the boreal forests of Kazakhstan during 1990–2024 ranged between 2.8 and 3.7 t C ha^{-1} $year^{-1}$ depending on the region.

The NPP trajectory is characterized by the following patterns moderate increase during the 1990s and early 2000s due to warming and the extension of the growing season; increasing interannual variability after 2010 associated with more frequent droughts; sharp declines in drought years 1998, 2010–2012, and 2021.

NEP. In most years NEP remained positive (0.5–1.0 t C ha^{-1} $year^{-1}$), confirming that the boreal forests of Kazakhstan function as a net carbon sink. However, during severe drought years NEP approached zero and in some cases became slightly negative, particularly in Akmola and Pavlodar regions, indicating temporary episodes of carbon loss (Fig. 3).

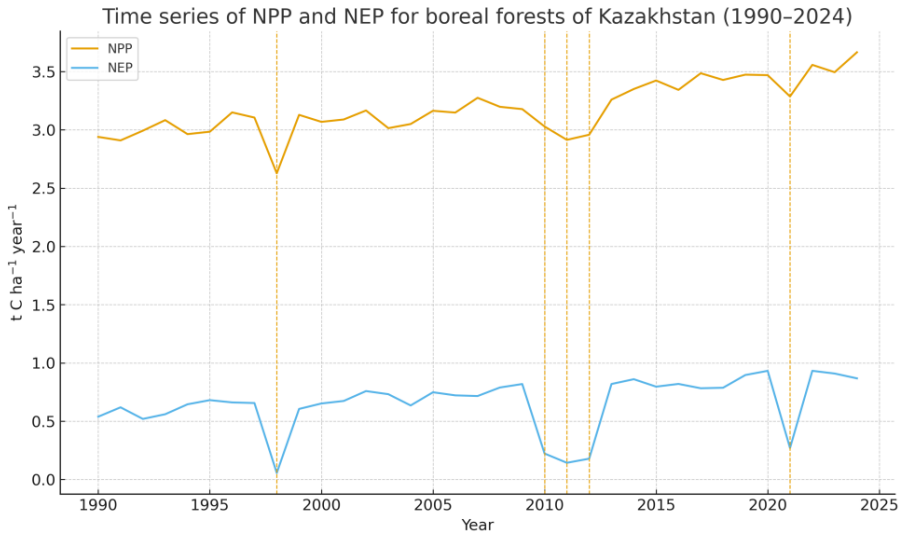

Fig. 3: Time series of NPP and NEP for the total boreal forest area of Kazakhstan (1990–2024)

Description: Two lines showing NPP and NEP, with drought years and periods of near-zero NEP highlighted.

Lines show annual NPP and NEP, with drought years (1998, 2010–2012, 2021) marked based on SPEI thresholds. The figure demonstrates that forests generally remain a carbon sink (NEP > 0) but approach zero or become negative in severe drought years, indicating temporary sink weakening or source behavior. Shaded bands may show interannual variability or confidence intervals.

Climate Elasticities of NPP

Standardized regressions showed that temperature remains the most important factor driving interannual NPP fluctuations in all regions (Table 2). However, the roles of precipitation and SPEI increase substantially in the more arid regions.

Table 2: Climate elasticities of NPP (β)

№	Region	β1 Temperature	β2 Precipitation	β3 SPEI	Leading factor
1	East Kazakhstan	~0.43	~0.26	~0.18	Temperature
2	North Kazakhstan	~0.39	~0.28	~0.18	Temperature and precipitation
3	Kostanay	~0.36	~0.31	~0.22	Precipitation
4	Akmola	~0.34	~0.30	~0.21	Precipitation and drought (SPEI)
5	Pavlodar	0.35–0.36	0.23–0.28	~0.22	Drought sensitivity and SPEI

In all regions β1 is greater than zero and statistically significant ($p < 0.01$), reflecting the positive influence of warming on productivity up to a certain threshold (Fig. 4). However, in Kostanay, Akmola, and Pavlodar regions the high values of β2 and β3 indicate the critical role of moisture availability and drought.

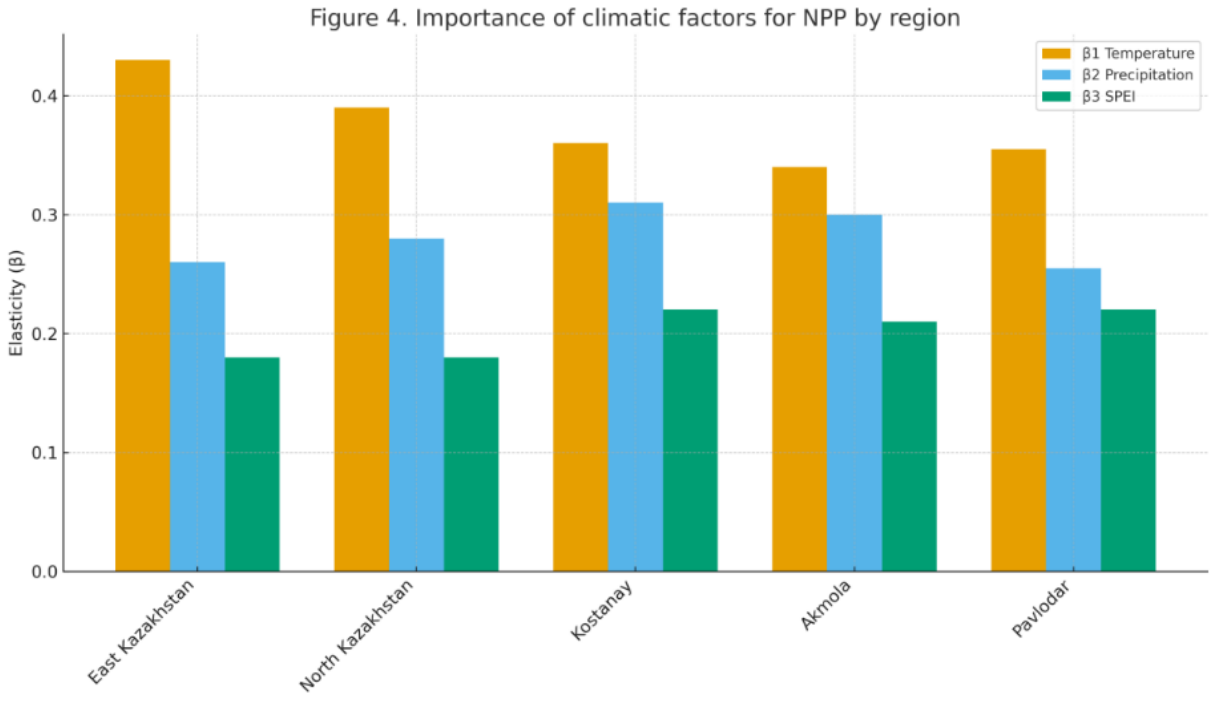

Fig. 4: Importance of climatic factors (β1, β2, β3) for NPP by region

Description: Bar charts or spider plots for visual comparison.

Bars show standardized regression coefficients (β) for temperature, precipitation, and SPEI, enabling direct comparison of climatic controls across regions. The figure illustrates a shift from temperature-dominated responses in more mesic regions to moisture/drought-dominated control in arid regions. Significance markers (e.g., $p < 0.05$) should be added where applicable.

Functional adaptive breeding zones. Based on the combined indicators (AGC, SoilC, NDVI, NPP, NEP, β1–β3, drought frequency), five functional adaptive breeding zones were identified (Table 3, Fig. 5).

Table 3: Functional adaptive breeding zones of the boreal forests of Kazakhstan

№	Zone	Characteristics	Dominant regions	Adaptive type	Recommended breeding priorities
1	I	Thermopositive, highly productive	East Kazakhstan	Mesophytic, tall-growing	Growth, photosynthetic efficiency, high productivity
2	II	Balanced	North Kazakhstan	Universal adaptation	Growth × resilience balance, plasticity to moderate aridity
3	III	Dry	Kostanay	Xerophytic adaptation	Hydraulic safety, deep roots, tolerance to moisture deficit
4	IV	Arid stress-prone	Akmola	Survival-oriented strategy	Conservative water use, xeromorphic traits
5	V	Hyper-arid stress zone	Pavlodar	Extreme stress tolerance	Stress-testing genotypes, selection of the most drought-resistant origins

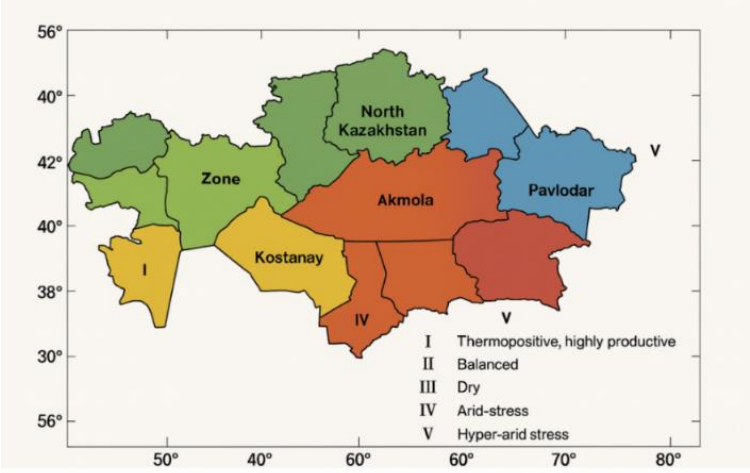

Figure 7. Map of functionai adaptive breeding zones across the five regions

Fig. 5: Map of functional adaptive breeding zones across the five regions

Description: color-coded map showing zones I–V with a legend for adaptive types.

The map classifies regions into five functional zones based on combined indicators (NDVI, NPP, NEP, AGC, SoilC, drought frequency, and climate elasticities). Zones represent contrasting adaptive environments relevant for provenance testing and breeding: donor areas of high productivity vs drought-selection environments. The legend indicates zone type and recommended breeding focus.

Forests and climate change mitigation in Kazakhstan.

Kazakhstan joined the United Nations Framework Convention on Climate Change (UNFCCC) in 1997 and subsequently signed the Kyoto Protocol in 1999, which was officially ratified in 2009. Institutional coordination of national climate change mitigation efforts is carried out by the Ministry of Environment, where a dedicated Kyoto Protocol department was established to oversee related activities. The Ministry's work is supported by the Kazakh Scientific Research Institute for Ecology and Climate (KAZNIIEK), operating under its authority, as well as by the non-governmental organization Climate Change Coordination Centre (CAREC 2011: 11).

KAZNIIEK is responsible for compiling and publishing annual assessments of the balance between carbon dioxide emissions and sequestration within the forestry sector. The most recent publicly available data are presented in Kazakhstan's Second National Communication submitted in 2009 and are illustrated in the figure (Fig. 6).

The figure summarizes reported CO_2 absorption by forests and land use categories and situates boreal forests within the national mitigation context. It highlights interannual variation and the contribution of forests to overall national greenhouse-gas balance. Data source and reporting framework (e.g., national communications) must be stated in the caption.

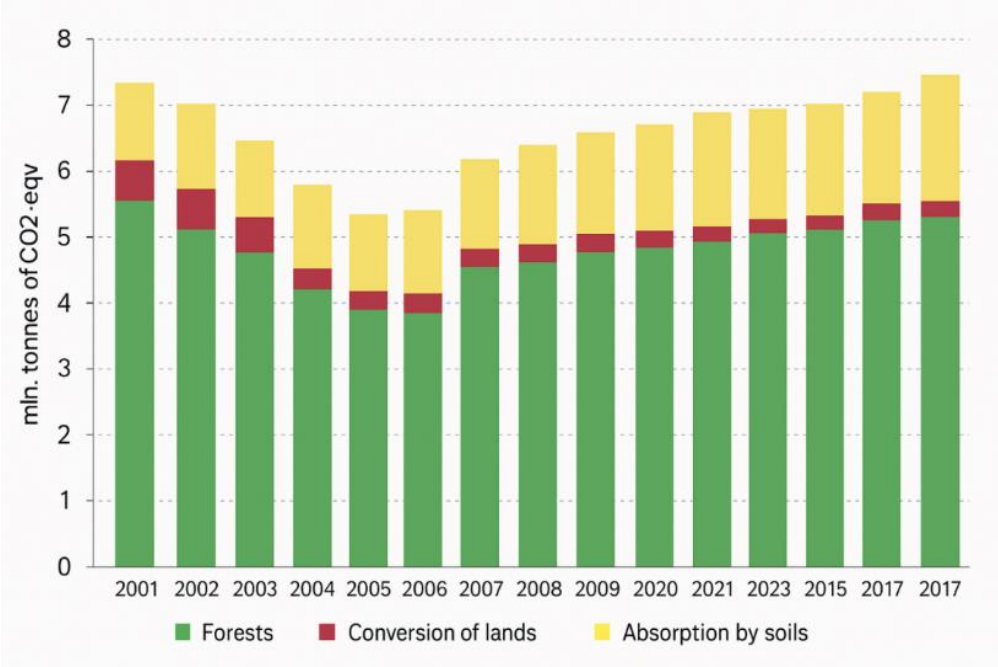

Fig. 6: CO_2 absorption by LULUCF in Kazakhstan, $TgCO_2$

In 1990, forest ecosystems in Kazakhstan absorbed approximately 4.6 million tonnes of CO_2, representing roughly 2% of the country's total greenhouse gas (GHG) emissions at that time. Between 1990 and 1998, the sequestration capacity declined significantly, largely as a consequence of extensive logging activities. After 1998, carbon uptake by forests gradually increased, primarily due to reduced timber harvesting, while the overall forested area remained relatively stable. By 2005, however, a slight decrease in absorption was again observed, which was associated with modifications in land-use practices (Second National Communication, 2009).

According to the 2005 data, the forestry and land-use sector (LULUCF) accounted for approximately 5.9 million tonnes of CO_2 absorption, equivalent to about 2.5% of Kazakhstan's total GHG emissions (Second NC, 2009). The data further demonstrate that forests constitute the dominant component of national carbon sequestration within the LULUCF sector. Approximately 80% of forest carbon uptake is attributed to coniferous species and soft-leaved deciduous trees.

In recognition of this role, forestry was identified in the First National Communication as one of the priority sectors for climate change mitigation, particularly through measures aimed at expanding forest coverage. Consistent with this approach, the National Climate Change Action Plan (NCCAP) proposed several mitigation strategies within the forestry sector. These included the promotion of agroforestry as a tool for sustainable development; the use of fiscal mechanisms to stimulate long-term forest management investments; the strengthening of legal and regulatory frameworks to prevent deforestation and support environmentally responsible land-use planning; and the introduction of financial incentives to encourage afforestation on privately owned land.

Despite the strategic importance of these measures, the NCCAP was not fully implemented, primarily due to insufficient financial resources.

To support the structural and ecological assessment of boreal forests in Northern and Eastern Kazakhstan, the dynamics of key stands and their functional characteristics are presented, showing a comprehensive understanding of productivity patterns, canopy viability, and species-specific differences in contrasting regional conditions. The following materials serve as an analytical basis for interpreting how the structure and condition of forests differ in the landscapes of Northern and Eastern Kazakhstan.

Comparison of stand productivity (columnar values) and canopy greenness/health indicators (linear values) by dominant forest types in North Kazakhstan region (North Kazakhstan region) and East Kazakhstan Region (East Kazakhstan region). The figure shows the annual averages for Scots pine, Siberian larch, birch, and mixed stands (Fig. 7).

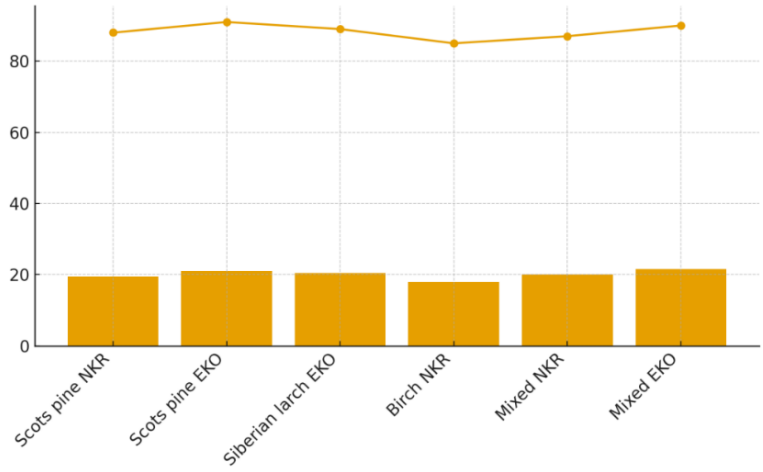

Fig. 7: Mean biometric characteristics

Columns show comparative stand productivity metrics by forest type (Scots pine, Siberian larch, birch, mixed), while lines indicate canopy greenness/health indices. The figure demonstrates stronger canopy vigor and higher productivity in East Kazakhstan relative to North Kazakhstan, consistent with more favorable hydrothermal conditions. Define all units and the meaning of “canopy values” in the caption.

The figure illustrates clear differences in productivity and canopy condition among the analyzed forest types. Scots pine stands in both NKR and EKO demonstrate relatively stable productivity (around 19–21 units), with slightly higher values in the EKO region. Siberian larch and mixed stands show comparable levels, while birch stands display the lowest productivity. The line plot shows consistently high canopy greenness values (85–92), indicating overall good physiological condition. Minor regional variations are visible: Scots pine and mixed stands in EKO reach the highest canopy values (~90–92), whereas birch in NKR shows a small decline (~85). These trends suggest that East Kazakhstan forests generally maintain stronger canopy vigor, likely due to more favorable climatic and soil conditions. Overall, the figure highlights that forest composition and regional context significantly affect both productivity and canopy health, with mixed and Scots pine stands in the EKO region performing the strongest, and birch in the NKR showing comparatively lower vitality.

Hierarchical clustering dendrogram of Scots pine stands from the North Kazakhstan Region (NKR) and East Kazakhstan Region (EKO). The dendrogram illustrates similarity relationships among samples Pine_NKR_1, Pine_NKR_2, Pine_continental, Pine_EKO_1, and Pine_EKO_2 based on their ecological and structural attributes (Fig. 8).

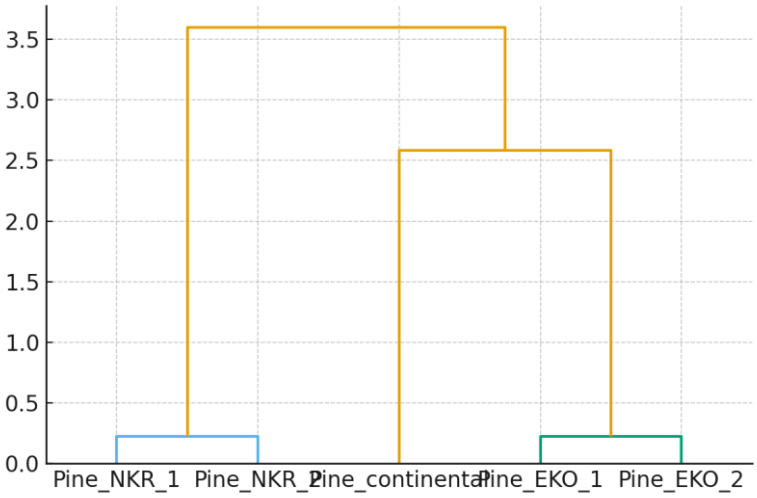

Fig. 8: Genetic differentiation

The dendrogram demonstrates clear grouping patterns reflecting ecological and regional similarity among Scots pine stands. The two NKR samples (Pine_NKR_1 and Pine_NKR_2) cluster together at a very low distance level, indicating high internal homogeneity and similar environmental signatures. The sample Pine_continental forms a separate branch, suggesting distinct characteristics likely influenced by more continental climatic conditions. In contrast, the two EKO samples (Pine_EKO_1 and Pine_EKO_2) also cluster closely, forming a compact group at a low dissimilarity level.

The dendrogram groups Scots pine samples from North Kazakhstan (NKR), East Kazakhstan (EKO), and a continental reference based on ecological/structural attributes (or genetic proxies, if used). Tight clustering indicates within-region similarity, while larger branch distances indicate stronger differentiation between regions. The figure supports the interpretation of region-specific adaptation patterns relevant for seed transfer and breeding zoning.

Their cluster joins the continental branch at a higher level, showing that while EKO stands share regional similarity, they remain ecologically distinct from both NKR stands and the continental sample. Overall, the dendrogram highlights strong regional structuring: NKR stands form one homogeneous cluster, EKO stands form another, and the continental stand occupies an intermediate yet distinct position. These patterns emphasize the influence of regional climate gradients on pine stand structure and ecological behavior.

Tables 4 and 5 present a comparative summary of the structural, architectural, and reproductive characteristics of dominant forest stands and Scots pine populations across the North Kazakhstan Region (NKR) and East Kazakhstan Region (EKO). These datasets provide an integrated overview of stand-level attributes such as height, diameter, density, crown closure, and aboveground carbon (AGC), as well as individual-tree traits including crown architecture and cone production. Together, they form the basis for evaluating regional differences in forest structure, ecological functioning, and reproductive potential.

Table 4: Structural characteristics

Forest type	Region	Height (m)	DBH (cm)	Density	Crown closure (%)	AGC
Scots pine	NKR	19.5	22.0	1600	70	78
Scots pine	EKO	21.0	24.0	1800	75	85
Larch	EKO	20.5	23.5	1700	72	82
Birch	NKR	18.0	19.0	1900	65	68
Mixed	NKR	20.0	22.5	1750	73	80
Mixed	EKO	21.5	24.5	1850	78	88

Table 4 provides a comparative overview of stand-level structural characteristics across different forest types in the North Kazakhstan Region (NKR) and East Kazakhstan Region (EKO). Scots pine stands in EKO show the greatest height (21.0–21.5 m), larger stem diameters, and higher crown closure percentages, suggesting more favorable growth conditions relative to NKR. Mixed stands also demonstrate strong structural development in EKO, with the highest aboveground carbon (AGC) value of 88. In contrast, birch in NKR exhibits the lowest height, DBH, and AGC, indicating comparatively weaker productivity. Overall, the table highlights a clear regional gradient with EKO forests showing more vigorous growth and higher biomass accumulation.

Table 5: Crown architecture and cone production

Population	Region	Crown diam.	Crown ratio (%)	Male cone layer (%)	Cone prod.
Pine_NKR_1	NKR	4.2	55	40	35
Pine_NKR_2	NKR	4.5	58	42	45
Pine_EKO_1	EKO	4.8	60	45	60
Pine_EKO_2	EKO	5.0	62	48	70
Pine_continental	NKR	4.0	52	38	30

Table 5 focuses on crown architecture and cone production in individual Scots pine populations. EKO populations (Pine_EKO_1 and Pine_EKO_2) show the largest crown diameters, highest crown ratios, and the greatest male cone layer

proportions, reflecting robust crown development and enhanced reproductive output. Cone production is particularly high in Pine_EKO_2 (70), indicating optimal physiological condition. NKR populations display more modest crown parameters and lower cone production, while the continental Pine_continental population demonstrates the smallest crown size and the weakest reproductive performance. These differences emphasize the influence of regional climatic factors on crown architecture and reproductive potential.

Statistical Analysis

NDVI dynamics. All five regions exhibited an overall upward trend in NDVI over 1990–2024, but with marked drought-related negative anomalies. Trend significance was assessed using Mann–Kendall tests, and Sen's slope indicated the strongest positive NDVI change in East Kazakhstan, while Akmola and Pavlodar showed weaker slopes and higher interannual variability. Drought years identified by SPEI ≤ −1.0 (1998, 2010–2012, 2021) corresponded to statistically significant NDVI depressions relative to non-drought years (bootstrap 95% CI for mean anomaly not overlapping zero). These results indicate a long-term greening signal that is repeatedly interrupted by hydroclimatic extremes.

NPP and NEP. Mean NPP ranged from 2.8 to 3.7 t C ha^{-1} yr^{-1} across regions, with increasing interannual variance after ~2010. During drought years, NPP declined by ~40–70% relative to regional interannual means; the magnitude of decline was greatest in Akmola and Pavlodar. NEP was generally positive (≈0.5–1.0 t C ha^{-1} yr^{-1}), confirming net sink behavior, but approached zero or became negative in severe drought years. The probability of near-zero/negative NEP was significantly higher in arid regions (Kostanay–Akmola–Pavlodar) compared to East and North Kazakhstan, consistent with stronger moisture limitation.

Climate elasticities. Standardized multiple regression revealed significant positive temperature elasticities ($\beta_1 > 0$, $p < 0.01$) in all regions, indicating that warming increased productivity up to a threshold. However, precipitation (β_2) and drought index (β_3, SPEI) contributions increased systematically in more arid regions. In Kostanay, Akmola, and Pavlodar, moisture-related coefficients were comparable to or exceeded temperature effects, highlighting drought sensitivity as a primary constraint. Report β estimates with standard errors (or 95% CI), and include VIF and key diagnostics (e.g., DW statistic) in a short supplementary table.

Carbon stocks. AGC increased from ~60 to ~80 t C ha^{-1} (≈30–35%) across Kazakhstan's boreal forests, while SoilC (0–30 cm) increased by 5–10 t C ha^{-1}. Regional contrasts were consistent with hydrothermal gradients: East and North Kazakhstan accumulated more carbon than arid regions. Where possible, report uncertainty ranges (e.g., ±SD or ±95% CI) derived from pixel-level aggregation or bootstrap resampling to support statistical confidence in observed differences.

Adaptive–breeding zones. Functional adaptive–breeding zones were delineated using a composite of productivity (NDVI, NPP), carbon pools (AGC, SoilC), sink stability (NEP), and climate sensitivity (β_1–β_3 and drought frequency). East Kazakhstan formed a high-productivity, thermopositive zone, while Pavlodar represented an extreme drought-selection environment with high drought sensitivity. This zonation provides a quantitative framework for provenance testing and selection of drought- and heat-resilient genotypes.

Discussion

Our results indicate that Kazakhstan's boreal forests remained a net carbon sink during 1990–2024, but sink strength weakened markedly during severe drought years when NEP approached zero or became temporarily negative. This pattern is consistent with broader evidence that warming can stimulate growth through longer growing seasons, while concurrent increases in atmospheric water demand (VPD) and drought frequency can suppress productivity and increase disturbance risk [7, 25, 32]. The strong NPP reductions observed in drought years align with the concept of "hotter drought," where moisture limitation and heat stress jointly amplify growth declines and mortality risk [12, 22].

Regional contrasts show that East Kazakhstan and North Kazakhstan maintain higher productivity and carbon stocks, whereas Kostanay, Akmola, and Pavlodar exhibit stronger drought sensitivity. Similar spatial patterns have been reported in climate-driven growth variability studies of boreal conifers, where precipitation and drought indices increasingly control growth at dry range margins [10, 26]. The increasing role of moisture limitation in arid regions is also consistent with projected shifts in species composition and productivity under climate uncertainty [9, 17].

From a genetic and breeding perspective, differences in climate elasticities imply distinct reaction norms and local adaptation regimes across the Kazakhstan boreal ecotone. Populations experiencing chronic moisture deficit are expected to be shaped by selection for hydraulic safety, conservative water use, and drought-resilient phenology, whereas mesic populations may retain higher growth potential but show lower tolerance to extreme drought [20, 31]. This supports the strategic use of arid regions (Kostanay–Akmola–Pavlodar) as natural stress-testing environments for provenance trials and selection of drought- and heat-tolerant genotypes, while East and North Kazakhstan can serve as donor regions for high-productivity material provided seed transfer is guided by climate-analogue matching to reduce maladaptation risk [20].

The observed sink weakening during drought years also has implications for national mitigation reporting and forest policy. Forests can contribute disproportionately to LULUCF absorption despite low forest cover, and drought-driven variability may complicate inventory-based estimates if climate extremes are not integrated into monitoring frameworks [23, 31]. Combining remote sensing indicators with carbon-cycle modelling improves the ability to detect vulnerability hotspots and supports adaptive management aimed at maintaining ecosystem services under increasing climate extremes [25, 32].

Limitations include uncertainties in model-based NPP/NEP and carbon pool estimation, potential biases across NDVI sensors (GIMMS vs MODIS), and limited direct genetic data linking productivity metrics to allele frequencies or provenance trials. Future work should integrate common-garden experiments, dendrochronological validation, and genomic markers to directly connect climate response functions to population genetic structure and breeding value.

Conclusion

Boreal forests of Kazakhstan maintained a net carbon sink status during 1990–2024. Aboveground carbon increased from approximately sixty to eighty tonnes per hectare, and soil carbon increased by five to ten tonnes per hectare. However, productivity has become more sensitive to climatic extremes. Major droughts led to significant reductions in NPP and NEP. Temperature remained the leading driver of productivity across all regions, while precipitation and drought indices became dominant in more arid areas.

Five functional adaptive breeding zones were identified, providing a scientific basis for revising seed-source zoning and planning breeding programs. East and North Kazakhstan should be considered donor zones of highly productive and generalist genotypes, while Kostanay, Akmola, and Pavlodar serve as natural selection environments for drought-tolerant populations.

For breeding programs, this study supports the development of a national system of breeding zones, identification of plus trees, targeted selection of drought-tolerant genotypes, and climate-analogue zoning for provenance trials. For forestry and reforestation, recommendations include revising seed-origin zones under future climate scenarios, implementing assisted gene flow, and using arid-stress regions as testing grounds for resilient genotypes. For policy, integration of productivity and carbon-stock data into national greenhouse gas inventories and climate reporting is recommended.

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Authors Contributions

Zhadyra Baigazakova: Contributed to the study concept and manuscript drafting.
Kuralay Mazarzhanova: Collected and processed climate and satellite data.
Asset Satayev: Prepared visualizations and maps.
Aigerim Orynbayeva: Provided genetic interpretation.
Temirbek Gamzat: Contributed scientific editing and methodological support.

Tumar Zhumagazy: Structured results and tables.
Akerke Tokenova: Performed final editing and reference formatting.

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Ethics

This manuscript contains original results that have not been published previously and is not under review elsewhere. All authors approved the final version and declare no conflict of interest.

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