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Changes in Pleistocene vegetation and climate of Ukraine in the range of 1.8-0.4 million years

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Abstract. On the basis of the analysis of the results of detailed palynological studies of Pleistocene deposits in Ukraine, the correlation between climatic changes and vegetation dynamics was retraced in the range of 1.8-0.43 million years. The curve of paleoclimate changes was constructed and analyzed. It was shown that certain climatic characteristics

were inherent for each stage of the nature development, which was reflected in the composition of vegetation. It was found that temperature and humidity fluctuations also occurred during each stage. The evidence of this is the reconstructed micro-rhythm in the development of vegetation of each stage. The main features of vegetation composition were determined for four warm and five cold stages of nature development, and a pattern of vegetation changes was retraced during each stage. The dynamics of vegetation cover of the Prydonetska Plain, different parts of the Prydniprovsk Lowland, the Prydniprovsk Upland, the Near Black Sea Lowland, and the Podil'ska Upland vegetation during the specified geological time was reconstructed. General and regional distinctions of the composition of vegetation cover were revealed, and the influence of the main climatic factors such as temperature and humidity on the character of its changes was retraced. The stages characterized by the warmest and wet climatic conditions and the most cold and dry ones were established. It was substantiated that the climatic conditions of the Sula period were less severe than in the subsequent stages of the fall of temperature. The existence of refugiums of thermophilic flora in the Sula period within separate regions of Ukraine was established. The existence of vegetation zonality was substantiated not only in warm stages, but also in cold periods of the Early Neopleistocene.

Key words: vegetation cover, climate, Pleistocene, Ukraine

Зміни плейстоценової рослинності та клімату України в інтервалі 1,8-0,4 млн. років

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Анотація. На основі аналізу результатів детальних палінологічних досліджень плейстоценових відкладів України простежено взаємозв'язок кліматичних змін та динаміки рослинності в інтервалі 1,8-0,43 млн. р. Побудовано та проаналізовано криву змін палеокліматів. Показано, що для кожного етапу розвитку природи властиві певні кліматичні характеристики, що знайшло відображення у складі рослинності. Встановлено, що коливання температури та вологості відбувались також і в межах кожного етапу. Свідченням цього є реконструйована мікроритмічність у розвитку рослинності кожного етапу. Визначено основні риси складу рослинності для чотирьох теплих та п'яти холодних етапів розвитку природи та простежено характер змін рослинного покриву протягом кожного з етапів. Реконструйовано динаміку рослинного покриву Придніпровської рівнини, різних частин Придніпровської низовини, Придніпровської височини, Причорноморської низовини, Подільської височини протягом зазначеного геологічного часу. Виявлено загальні та регіональні відміни складу рослинного покриву та простежено вплив основних кліматичних чинників – температури та вологості на характер його змін. Встановлено етапи, що характеризувались найбільш теплими та вологими кліматичними умовами, та найбільш холодними і посушливими. Обґрунтовано, що кліматичні умови сульського часу були менш суворими, ніж у наступні етапи похолодань. Встановлено існування рефугіумів термофільної флори в сульський час у межах окремих регіонів України. Обґрунтовано існування рослинної зональності не лише у теплі етапи, а і у холодні періоди нижнього неоплейстоцену.

Ключові слова: рослинний покрив, клімат, плейстоцен, Україна

Introduction. The dynamics of the Pleistocene vegetation in time is inextricably linked with the rhythmic changes in the climate primarily due to the interchanges of glacial and interglacial periods. Vegetation reacts sensitively even to minor climate change. In the interval considered within the plain part of Ukraine, five cold (Berezan, Illichivsk, Priazovya, Sula, Tiligul) and four warm (Kryzhanivka, Shyrokyne, Martonosh, Lubny) stages of nature development occurred.

During the warm stages, the pedo-complexes consisting of soils of early and late optimum and the final stage of pedogenesis were formed. In the most complete sections, soils of optimums were separated by thin loessial layers, which is the evidence of inter-staging falls of temperature. During the cold stages in the non-glacial zone, loess and loessial loams were accumulated, in the strata of which immature embryonic soils formed during short-term inter-stage warming were retraced. Each of these stages differs in terms of temperature as well as the degree of irrigation and humidification of the climate, which was reflected in the composition of vegetation.

According to the International Stratigraphic Scale 2018 (ISS), the stages of nature development in the range of 1.8-0.8 million years are dated to Calabrian, and in the range of 0.8-0.43 million years – Middle Pleistocene. According to the stratigraphic scheme of the Quaternary deposits of Ukraine (Stratygrafichnyj kodeks Ukraïny Redaktor P.F. Gozhyk, 2012), the paleogeographical stages of the first interval are dated to Eopleistocene, and the second interval – Early Neopleistocene. The purpose of this research is to establish the patterns of vegetation dynamics within the plain part of Ukraine related to changes in climatic parameters during the specified geological period, not only at the level of separate stages of nature development, but also within each stage; determination of general and regional differences of vegetation cover within individual regions of Ukraine; construction of paleoclimate curve according to palynological data.

Materials and methods. The main method of the research was a spore-pollen analysis. The material for the performed reconstructions was the analysis of the results of detailed palynological studies of the Pleistocene deposits in 16 sections located within the Donets folded structure, the Dnieper-Donets and the Black Sea depressions (Sirenko, 1994, 2017a, b), the central, northern and southern parts of the Ukrainian shield (US) (Sirenko, 2002, 2009a, 2017b), as well as the Volyn-Podil'ska Plate (Sinenko, 2009b), and, correspondingly, within three modern vegetation

zones: steppe, forest-steppe and mixed forests (Fig. 1). In the process of the research, not only spore-pollen charts but also the cyclograms of the ecological structure of the complexes constructed for each section were analyzed, which allowed not only to reconstruct a type of vegetation, but also gave an opportunity to draw conclusions about the nature of climate change in certain periods.

In addition, the data of palynological studies of Pleistocene deposits by S.I. Turlo (Sirenko, Turlo, 1986) and N.P. Gerasimenko (Gerasimenko, 2004, Matviishyna, Gerasimenko, Perederii, Brahin, Ivchenko, Karmazynenko, Nahirnyi, Parkhomenko, 2010) were analyzed.

Main results. The features of the vegetation composition of Ukraine in the range of 1.8-0.8 million years, which corresponds to Calabrian according to the International Stratigraphic Scale (ISS), are closely linked to global trends in climate change. According to A.A. Velichko with co-authors (Velichko A.A., Pisareva V.V. Faustova M.A., 2011), the tendency to falling of temperature intensified in the range of 1.8-0.8 million years. At that time, in Western Europe glaciation spread to Scandinavia and Northern England. Significant aridization of climate occurred about 1.8 million years resulted in the depletion of vegetation. In particular, the role of mesophyllous plants decreased in the composition of vegetation in the territory of the European part of Russia and Ukraine, including the changed composition of herbaceous cenoses from miscellaneous herbs to more xerophilous miscellaneous herbs–orach and mugwort–orach. The role and taxonomic diversity of thermophilic and broad-leaved species of moderately warm zone in forest groups also decreased.

During the Berezan period (1.8 million years) the forest-steppe type of vegetation predominated within Ukraine, while in the southern and southeastern regions (Sirenko, Turlo, 1986, Gerasymenko, 2004) the area occupied by herbaceous cenoses increased. In the Prydonetska Plain and area near the Azov Sea (Sirenko, Turlo, 1986), their main components were representatives of Chenopodiaceae and Asteraceae families, in the central part of the Prydniprovsk Upland – Poaceae. The last region and the western part of the Prydniprovsk Lowland were characterized by meadow-steppe cenoses and locations with a few aquatic and coastal aquatic plants: Sparganium sp. and Typha sp. The herbaceous groups of the southern part of Ukraine included xerophytes and halophytes of Frankeniaceae family (Sirenko, Turlo, 1986), which may indicate the existence of saline vegetation.

The main component of thinned forests was

Pinus spp. subg *Diploxylon* with a small impurity of *Betula* spp., and in humid places – *Alnus* spp. Broad-leaved forests were mainly represented by *Quercus robur*, and the forest groups of the north-western part of the Prydniprovskia Lowland included *Tilia cordata*, *Corylus avellana* and very rare – single *Juglans regia*.

According to N.P. Gerasimenko (Matviishyna, Gerasimenko, Perederii, Brahin, Ivchenko, Karmazynenko, Nahirnyi, Parkhomenko, 2010), the most humid conditions, and, correspondingly, the greater representation of deciduous plants in

cover of the southern and south-eastern regions (domination of xerophilic herbaceous groups) and the central, northeastern and western regions (prevalence of broad-leaved –coniferous, oak–pine and mixed forests). Within the area near the Azov Sea, the Donets Basin and the area near the Black Sea, forest groups were confined to the river terraces.

The vegetation cover of the Early Kryzhanivka period was characterized by insignificant taxonomic diversity of deciduous plants (*Alnus* spp., *Betula* spp., *Quercus* spp., *Tilia* spp.) and a fairly significant

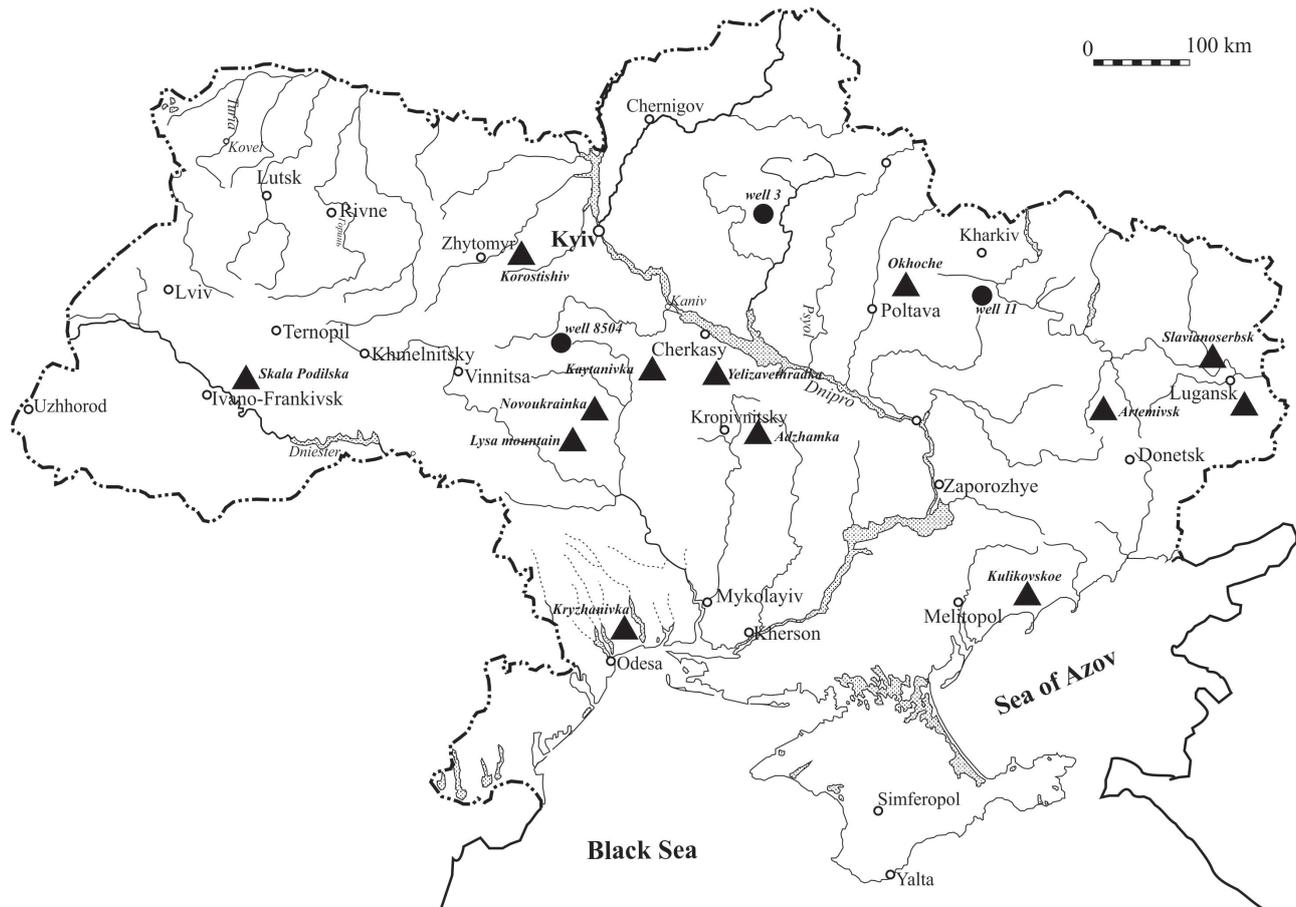


Fig. 1. The scheme of location of Pleistocene deposit sections in Ukraine, studied by the method of spore-pollen analysis (according to O.A. Sirenko).

forest groups, as well as miscellaneous herbs in the composition of herbaceous cenoses existed in the Middle Berezan, and the most arid and cold – in the Late Berezan.

The general tendencies of aridization and fall of temperature that occurred at the beginning of Calabrian influenced the vegetation composition of both cold and warm stages.

The characteristic features of Kryzhanivka vegetation might include the presence of dark conifers (mainly *Picea* spp. sect *Eupicea*) in the forests of almost the whole territory of the platform Ukraine, as well as the bright differentiation of vegetation

representation (depending on the relief) of conifers and herbs. Thermophilic plants in forests were represented by few *Juglans* spp.

In the Middle Kryzhanivka period, humidity of climate and heat supply probably increased, which resulted in the expansion of the representation of deciduous plants, especially broad-leaved species: such as *Fagus sylvatica*, *Fagus* sp., *Tilia platyphyllos*, *T. rubra*, *Carpinus betulus*, *C. orientalis*, *Ulmus laevis*, *Ulmus* sp. and shrubs: *Corylus* spp., *Elaeagnus* sp., *Rhamnus* sp., *Euonymus* sp. in forests. Birch forests and thickets (*Salix* spp. and *Alnus* spp.) grew on various forms of relief.

In the central part of the Prydniprovskia Upland, there were probably freshwater basins where *Typha* spp. and *Sparganium* spp. grew. The thermophilic elements in forests existed in small quantities and were predominantly represented by *Juglans cinerea*, and only single *Pterocarya stenoptera* and *Juglans nigra* grew in the valleys near the Azov Sea and the Black Sea regions, and *Myrica* sp. – along liman shores.

Forests predominated in the vegetation cover of the Prydniprovskia Upland and the Prydniprovskia Lowland, while herbaceous cenoses, the main component of which were various Asteraceae and miscellaneous herbs – on the Prydonetska Plain. The dominant part of the deciduous forests was *Quercus* spp. in most regions of Ukraine and *Tilia cordata* – only within the northwestern part of Prydniprovskia Lowland and the central part of the Prydniprovskia Upland.

A certain fall of temperature and climate irrigation occurred in the Late Kryzhanivka period, which caused a reduction of broad-leaved and thermophilic species in the forest groups. Significant areas were occupied by pine forests with a small impurity of *Quercus* spp.

and *Tilia cordata* as well as birch light forests within the Prydniprovskia Upland and the Prydniprovskia Lowland. *Picea* was not already met in woods. Within the southern regions and the Prydonetska Plain the area occupied by herbaceous cenoses, in whose composition the role of *Chenopodiaceae* significantly increased, expanded even more as compared to the Middle Kryzhanivka period.

In the Illichivsk period further fall of temperature (Fig.2) and aridization of climate occurred, which resulted in the fact that the vegetation was notable for impoverished composition not only compared with Kryzhanivka, but also to Berezan. In the structure of vegetation cover of the whole territory of plain Ukraine, the role of herbaceous cenoses, which consisted mainly of the representatives of Poaceae, Chenopodiaceae and Asteraceae families, increased. The composition of arboreal groups also grew poorer due to mainly broad-leaved and thermophilic plants.

Birch-pine light forests and grass-orach-mugwort cenoses occupied approximately equal proportions in the vegetation cover of the Prydniprovskia Lowland. In the northwestern part of the Prydniprovskia Lowland, the area of forest groups slightly

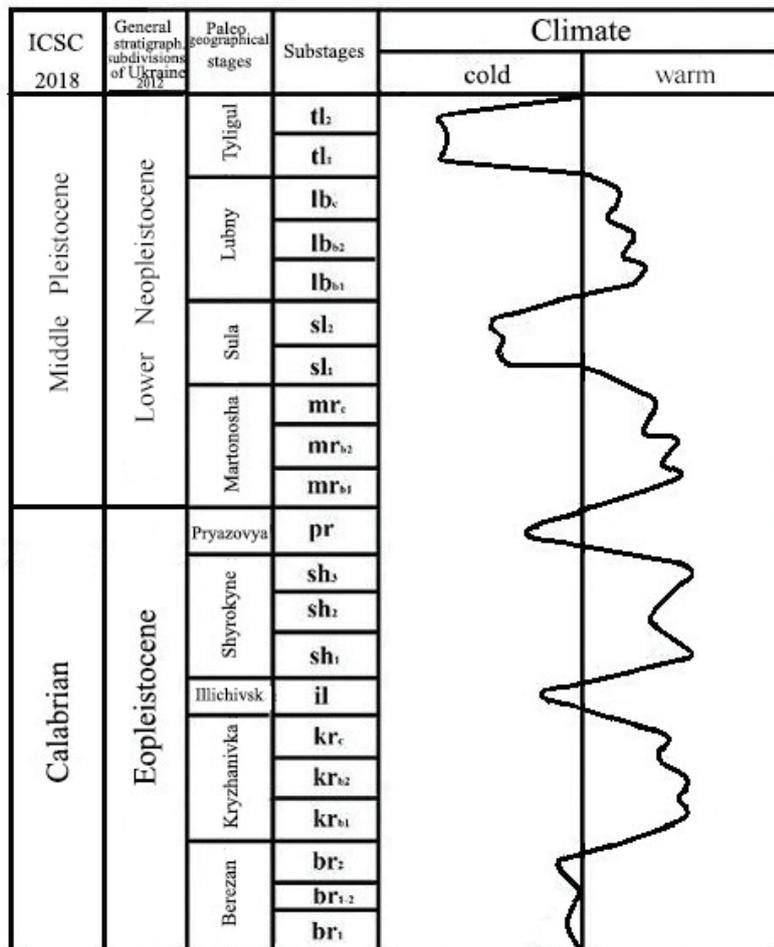


Fig. 2. The curve of changes in heat supply during the stages of nature development in Ukraine in the range of 1.8-0.4 million years.

expanded, and single *Tilia cordata* occurred in their composition. In the forest groups of the coastal areas of the Eastern Azov Sea, the role of *Quercus robur* slightly increased in comparison with the central regions.

In the structure of vegetation cover of the northwestern part of the Prydniprovskaya Upland, pine forests and herbaceous groups, the main component of which was Asteraceae, occupied approximately equal areas.

Within the Prydonetska Plain mugwort-orach cenoses dominated, and valley forests sometimes included *Tilia cordata* and *Ulmus*, and very rarely single *Juglans* (Sirenko, Turlo, 1986). Pine forests with single *Quercus robur* grew on river terraces.

In the Early Shyrokyne period significant warming occurred (Figure 2) and climate humidity slightly increased in comparison not only with the Illichivsky period but also with the Kryzhanivka period. The above-mentioned climate changes caused increase in a number, generic and specific diversity of thermophilic species and heat-loving pine species of *Haploxyton* subgenus in the forests of the Shyrokyne period, as compared with Illichivsk and Kryzhanivka vegetation. At the same time, the structure of Shirokinsky vegetation still included a large part of herbaceous cenoses, which was typical for the previous stages of nature development.

In the Early Shyrokyne period coniferous-deciduous forests with a significant share of *Tilia* spp. and thermophilic plants dominated within the Prydniprovskaya Lowland, the northern part of the Prydniprovskaya Upland and the Podil'ska Upland. Forests also dominated in vegetation cover of the central part of the Prydniprovskaya Upland but their area declined as compared with the Kryzhanivka period.

In pine-broad-leaved and mixed forests *Tilia cordata*, *Quercus robur* and *Q. pubescens* were sub-dominant, and also *Tilia platyphyllos*, *Fagus sylvatica*, *Carpinus betulus*, *Juglans cinerea* and *Juglans regia* grew. The undergrowth consisted of *Corylus* spp. and *Thelycrania* sp. The grass cover of forests consisted of ferns and floating plants at humid sites. It is also possible to assume the existence of lime groups at isolated sites. Herbaceous cenoses occupied small areas and mainly consisted of Asteraceae and Chenopodiaceae, and meadow grasses on relief depressions. Compared to the Kryzhanivka period, the role of Potamogetonaceae and Sparganiaceae water and coastal water plants decreased in the composition of plant groups.

Within the Prydniprovskaya Lowland broad-leaved and coniferous forests also included *Ulmus laevis*, and *Pterocarya* sp. from the thermophilic plants.

Compared to one-year-old forest groups of adjacent regions, the role of *Carpinus betulus* increased.

Within the territory near the Azov Sea broad-leaved groups with a significant participation and specific diversity of walnut tree: *Juglans sieboldiana*, *J. cinerea*, *J. mollis* existed in river valleys. Single *Rhus* sp. grew at more arid sites. The composition of dominants among deciduous plants of a moderately warm zone did not change as compared with the forests of the central regions.

Despite the fact that a forest-steppe type of vegetation predominated in the southern regions of Ukraine and Donets Basin (Sirenko, Turlo, 1986) in the Early Shyrokyne period, the representation of forests in the structure of vegetation cover was higher than in the subsequent Late Shyrokyne period.

Insignificant fall of temperature and climate aridization that occurred in the Middle Shyrokyne period led to a reduction in the vegetation cover of broad-leaved and thermophilic plants and the expansion of areas occupied by herbaceous groups. Particularly, herbaceous cenoses including multiple Asteraceae prevailed in the structure of vegetation cover of the Prydonetska Plain and the central part of the Prydniprovskaya Lowland. Thermophilic species consisted of oak-pine light forests occurred very rarely and in small quantities.

A forest type of vegetation was only typical for the north-western part of the Prydniprovskaya Lowland. Within this region vast areas were occupied by mixed forests. In their composition *Betula* spp. dominated deciduous species, and also *Carpinus betulus*, *Tilia cordata*, *Ulmus laevis* and *Juglans regia* occurred in small quantities, which was no longer typical for the forest groups of the Late Shyrokyne period.

In the Late Shyrokyne period the temperature regime of climate increased again but in comparison with the Early Shyrokyne period, the degree of humidity decreased. In connection with this, forest groups were characterized by a significant number of broad-leaved and thermophilic plants but in comparison with the Early Shyrokyne period, they differed in smaller taxonomic varieties. In the structure of vegetation cover in practically all regions of Ukraine a part of herbaceous groups increased including miscellaneous herbs in their composition: Apiaceae, Ranunculaceae, Lamiaceae, Fabaceae, Plantaginaceae, Polygonaceae, and Rosaceae. In the central and northeastern regions of Ukraine arboreal and herbaceous cenoses occupied almost equal areas, and in the southern regions (Sirenko, Turlo, 1986) herbaceous groups prevailed.

The Priazovya stage was characterized by significant aridization and fall of temperature (Figure

2), which resulted in the impoverishment of both arboreal and herbaceous groups. In the southeastern and southern regions of Ukraine (Sirenko, Turlo, 1986), the steppe type of vegetation predominated. Significant areas were covered with grass-mugwort-orach cenoses, and grass-miscellaneous herbs within the Prydonetska Plain. In the vegetation cover of the Middle and Lower Prydniprovia herbaceous cenoses also dominated, and a few arboreal groups existed only along the valleys and river terraces and mainly consisted of pine, oak, ulmus and hazel (Sirenko, Turlo, 1986). Within the southwestern part of the Prydniprovskaya Upland, a significant part of vegetation cover belonged to pine and birch-pine light forests with a small impurity of oak. In the territory of the Prydniprovia near Kyiv both pine light forests (Sirenko, Turlo, 1986) and different miscellaneous herb-mugwort groups (Gerasymenko, 2004) existed in various durations of the Priazovya period.

The Martonosha period was characterized by the dampest climate for the investigated geological time, which was very clearly appeared in the vegetation cover of the entire territory of Ukraine. In the central, northeastern and western parts of the region, a forest type of vegetation dominated. And only within the southern regions of Ukraine and Donets Basin, the wooded steppe prevailed. The forests of the Martonosha period were characterized by the considerable participation of coniferous species including thermophilic pine species of *Haploxylon* subgenus, a large variety of broad-leaved species in the moderately warm zone and thermophilic elements. In contrast to the forest groups of the Shyrokyne period, the role of small-leaved species of a temperate zone increased in Martonosha forests, which together with the growth of the participation of conifers might indicate a slight fall of temperature during the Martonosha period.

The Martonosha period is characterized by the long-winded climatic optimum and, correspondingly, the weak differentiation of vegetation cover in the periods of formation of early and late optimal Martonosha soils. This feature is characteristic mainly for the vegetation cover of the central and northwestern parts of the Prydniprovskaya Lowland as well as the northern part of the Prydniprovskaya Upland, and it is associated with high humidity, under which Martonosha soils were formed in these regions. And only in the regions with more arid conditions of the formation of Martonosha soils (the southern and central parts of the Prydniprovskaya Upland, the Prydonetska Lowland) the differences in the conditions of the formation of early and late optimum

soils, as well as the final stage of Martonosha soil formation more distinctly appeared.

Within the Prydonetska Plain in the Early Martonosha period the forest-steppe type of vegetation predominated. Large areas were occupied by herbaceous groups with the participation of Chenopodiaceae and Asteraceae. Hygrophytes and herbaceous groups as well as sphagnum mosses grew along river valleys and shore.

The composition of mixed and pine-deciduous forests was quite variegated: *Pinus* spp. sect *Eupitys* (dominated), *P.* spp. sect *Cembrae*, *Picea* sect. *Eupicea*, *Carpinus betulus*, *Quercus robur*, *Quercus* sp., *Tilia cordata*, *T. platyphyllos*, *Corylus avellana*. Thermophilic plants were represented by *Juglans cinerea* and *Juglans* sp. Deciduous species of the temperate zone *Alnus glutinosa*, *A. incana*, *Betula* sp. sect *Albae* in forests occupied a smaller area compared to broad-leaved plants of moderately warm zone. Ferns Polypodiaceae participated in the grass cover of forests.

During the first inter-stage fall of temperature, a forest-steppe type of vegetation also predominated, but the role of *Betula* spp. significantly increased in the composition of arboreal formations, while the role of ferns decreased in the grass cover of forests.

In the Middle Martonosha period the temperature again increased but in comparison with the Early Martonosha period, the humidity slightly reduced. The role of herbaceous groups consisted mainly of Chenopodiaceae and Asteraceae increased in the composition of vegetation cover. Compared to the Early Martonosha period, a number of thermophilic plants increased in the forests but their specific composition as well as the composition of broad-leaved species practically did not change. The undergrowth consisted of *Corylus avellana*. The role of deciduous plants of the temperate zone *Betula* and *Alnus* diminished in the composition of forest groups, while *Ulmus* spp. quite often occurred.

The second inter-stage fall of temperature was characterized by compared with the first one greater lowering of temperature regime and humidity of climate, which caused impoverishment of both arboreal and herbaceous groups that already occupied much larger areas. A few arboreal groups mainly consisted of *Pinus* sect *Eupitys* with a small impurity of *Tilia cordata*, *Quercus robur*, *Corylus avellana*, and thermophilic plants were not found there. The composition of herbaceous cenoses became poorer due to herbs and hygrophytes.

In the Late Martonosha period a slight increase in the temperature occurred as compared with the

period of formation of a loess-type layer. The main components of a few arboreal groups located on lowered relief elements were mostly *Pinus* sect. *Eupitys* and *Betula* with a small participation of *Quercus robur*. Within the region of research large areas were occupied by herbaceous cenoses. In their composition as compared with the Middle Martonosha period, the share of miscellaneous herbs reduced.

The conditions of high humidity that existed during the formation of Martonosha soils in the Prydniprovskaya Lowland leveled differences in the structure of vegetation cover during the periods of soil formation of the early and late optimum of Martonosha pedogenesis. Within the specified region, the forest type of vegetation dominated during the Martonosha period. In the central part of the Prydniprovskaya Lowland, pine and oak-pine forests occupied mostly watershed areas, while broad-leaved–coniferous forests grew on lowered relief elements. In addition to *Pinus* spp., *Picea* spp. sect. *Eupicea* played a significant role in their composition. Few *Carpinus betulus* were found in forests of the Early Martonosha period but *Tilia platyphyllos* and *Ulmus laevis*, which were typical the Prydonetska Plain, were absent. In general, except for the indicated differences, a deciduous component of forests was similar to the forest groups of the Prydonetska Plain. Thermophilic plants in forests were represented by *Juglans cinerea* and *Juglans* sp.

Herbaceous groups occupied insignificant areas and grew predominantly in forest glades; dominants in their composition were various Asteraceae with a small impurity of miscellaneous herbs. Mosses and ferns occurred in the grass cover of forests.

The forests of the northwestern part of the Prydniprovskaya Lowland were distinguished by a more diverse composition of broad-leaved trees of a moderately warm zone. In particular, in addition to the taxonomy already mentioned, various forest elements included *Carpinus betulus*, *Quercus pubescens*, *Tilia dasystyla*, *T. platyphyllos*, *Ulmus laevis*, *U. campestris*, and *Juglans nigra*. As opposed to the forests of the Prydonetska Plain and the central part of the Prydniprovskaya Lowland, *Tilia cordata* was subdominant in the forests but not *Quercus*. A significant role in forest groups also belonged to *Betula* sp. sect. *Albae*. The grass cover of the forests consisted of *Lycopodium* sp and Polypodiaceae. Few herbaceous groups grew in forest glades.

A slight fall of temperature occurred during the formation of loess-type loam that separates the soils of the early and late optimum Martonosha pedogenesis. This led to an increase in the number of *Betula* in

forests and a reduction in the taxonomic diversity of broad-leaved trees.

During the Late Martonosha period, the area occupied by herbaceous vegetation increased. In the forests, the share of broad-leaved trees decreased and thermophilic plants disappeared, while a number of plants increased in the temperate zone.

There were no sharp changes in the composition of vegetation in the central part of the Prydniprovskaya Upland during the Early and Middle Martonosha periods. The main differences consisted in the fact that the most generic and specific diversity of broad-leaved species of temperate-warm zone and thermophilic elements were typical for the middle Martonosha forests: *Carpinus betulus*, *C. orientalis*, *Tilia cordata*. (dominated), *Tilia platyphyllos*, *Tilia dasystyla*, *Tilia* sp., *Quercus robur* L., *Q. pubescens*, *Fagus sylvatica*. The elevated elements of relief were occupied by pine-oak and mixed forests with *Pinus* sp. sect. *Eupitys*, *P. sp.* sect. *Cembrae* and *P. sp.* sect. *Strobus*, *Betula pendula*, and *Betula* sp. Pine-deciduous forests including *Ulmus campestris*, *Juglans cinerea*, *J. regia*, *Juglans* sp. grew near ponds and in the lowered elements of relief. The undergrowth consisted of *Corylus* sp., *Thelycrania* sp., Caprifoliaceae, Grossulariaceae, *Vitis* sp., Moraceae. Lime groups probably existed. *Betula pubescens*, *Alnus glutinosa*, and *A. incana* grew along the banks of ponds and in wetlands. The grass cover of forests consisted of ferns and mosses. The specific composition of pines did not change in comparison with Martonosha forests in adjacent regions. As opposed to the forest groups of the Prydniprovskaya Lowland, *Picea* spp. sect. *Eupicea* did not grow in the forests of the central part of the Prydniprovskaya Upland. Herbaceous groups occupied insignificant areas, and dominants in their composition (the representatives of Asteraceae family) did not change as compared to the Prydniprovskaya Lowland, whereas the proportion and diversity of mesophilous herbs and Poaceae increased.

In the Late Martonosha period the share of forests decreased in vegetation cover and the composition of forests changed. Pine–broad-leaved forests and lime groups interchanged with oak-pine forests including *Fagus* and oak forests, the edicator of which was *Quercus robur*. Mixed forests with various *Betula* spp. and a small impurity of *Carpinus betulus*, *Tilia cordata*, *Tilia dasystyla*, and *Quercus pubescens* grew only on lowered relief elements. Thermophilic plants did not grow in forests.

As a result of the growing fall of temperature, on the second half of the Late Martonosha period the forests became poorer due to *Carpinus betulus*

and *Tilia dasystyla*, and predominantly consisted of *Betula* spp. and *Pinus* spp. with a small impurity of *Quercus robur* and *Tilia cordata*.

During the Martonosha period within the northern part of the Prydniprovskaya Upland almost all the area was occupied by pine, birch-pine and mixed forests. In contrast to one-age forest groups of the central part of the Prydniprovskaya Upland, a part of *Betula* increased in their composition, a number of thermophilic elements decreased, and the taxonomic diversity of broad-leaved species of moderately warm zone decreased. Among deciduous forests, *Tilia cordata* was subdominant, and a small part of the forests included *Tilia platyphyllos*, *Carpinus betulus*, *Fagus* sp., *Quercus robur*, *Quercus* sp., *Ulmus* sp., *Corylus* sp. A quite significant part in the composition of vegetation cover belonged to *Sphagnum* sp. and Polypodiaceae. Small herbaceous groups were presented by the plants of Chenopodiaceae, Poaceae, Asteraceae families and miscellaneous herbs as well as *Artemisia* spp. genus.

Martonosha forests of the Podil'ska Upland were similar in composition to the forest groups of adjacent regions. The most distinctive features were the most specific variety of pines *Pinus* sp. sect *Eupitys*, *P.* sp. subg *Diploxylon* (dominated), *P.* sp. sect *Banksia*, a significant part of the heat-loving species of *Pinus* sp. sect *Cembrae*, *P.* sp. sect *Strobus*, which was probably due to the influence of the Carpathian Mountains, as well as the most specific variety of thermophilic species of Juglandaceae family: *Pterocarya stenoptera*, *Juglans cinerea*; *J. regia*, *J. nigra*, *Juglans* sp.

In the Early Martonosha period mixed and pine-broad-leaved forests occupied large areas. A characteristic feature of the forests was the wide representation of deciduous plants of the temperate-warm zone in their composition, notably *Quercus* spp., *Carpinus betulus*, *C. orientalis*, *Ulmus laevis*, *Rhamnus* sp., *Corylus* sp. Representatives of the Tiliaceae family such as *Tilia dasystyla*, *T. cordata*, *Tilia* sp. were dominant in a deciduous component of the forests. Probably, separate lime groups could also exist within the region of the research. The forests also included *Pinus* spp., *Betula* spp., *Alnus* spp., *Salix* spp. The composition of vegetation cover consisted of Polypodiaceae, *Sphagnum* sp., *Bryales* sp. Herbaceous cenoses occupied small areas and consisted of miscellaneous herbs, Poaceae, Asteraceae and Cyperaceae.

In the Middle Martonosha period, forest groups also dominated in the structure of vegetation cover of the investigated region but their area reduced in comparison with the Early Martonosha period.

Probably, under the influence of climate humidity decrease, hydrophilous plants such as *Salix* spp., *Pterocarya stenoptera*, *Juglans nigra* disappeared from the forests; dominants of the deciduous component of the forests also changed, notably, the leading positions already belonged to *Quercus* spp. By the number of broad-leaved and thermophilic species these forests predominated over the Early Martonosha forests. The herbaceous cover of the forests also included few Polypodiaceae and *Lycopodium* sp. On the contrary, in the structure of vegetation cover the areas occupied by herbaceous groups expanded, and a part of plants of Chenopodiaceae and Asteraceae families increased in their composition.

In the Sula period aridization and fall of temperature intensified but according to palynological (Sirenko 2017b) and malacofaunistic (Kunitsa, 2007) data, climatic conditions of the Sula period were less severe than in the subsequent stages of the fall of temperature. The composition of forest groups became poorer due to heat-loving pine species, broad-leaved species of moderately warm zone and thermophilic elements. Asteraceae were dominant in herbaceous cenoses, and Chenopodiaceae had a subordinate value.

A steppe type of vegetation existed within the Prydniprovskaya Plain. Among the herbaceous groups, Chenopodiaceae and Asteraceae were dominant. Meadow-steppe cenoses and a few forest groups consisted of *Pinus* sect. *Eupitys*, *Alnus* sp., *Betula* spp., *Ulmus* sp. spread on the wettest areas.

The central part of the Prydniprovskaya Plain is characterized by a forest-steppe type of vegetation. Watersheds were covered with pine forests including *Quercus robur*, and *Tilia cordata* within the northwestern part of the region. Significant participation in the structure of vegetation cover belonged to herbaceous cenoses consisting of Poaceae, Asteraceae, Chenopodiaceae. Birch-pine and coniferous forests as well as meadow-miscellaneous herb groups grew on lowered relief elements. Within the northwestern part of the Prydniprovskaya Lowland refugia with single *Juglans* sp. existed.

The distinctive features of vegetation cover of the central part of the Prydniprovskaya Upland might consist in participation in arboreal formations *Tilia cordata*, *Alnaster*, cf. *manshuricus*, miscellaneous herbs, aquatic and coastal aquatic plants. Within the specified region there were certain distinctions in the structure of vegetation cover in the Early and Late Sula periods.

In the structure of vegetation cover of the Early Sula period arboreal groups were dominants including,

in addition to usual pine, isolated thermophilic pine species. The deciduous component of forests was mainly represented by *Betula verrucosa* with a small impurity of *Quercus robur* and *Tilia cordata*. Miscellaneous herb groups and *Alnus* spp. as well as helophyte cenoses including *Sparganium* spp., *Typha* spp., and *Sphagnum* spp. distributed in humid places on lowered relief elements.

In the Late Sula period the proportion of herbaceous cenoses, the main component of which was Chenopodiaceae with miscellaneous herbs, increased in the structure of vegetation cover. As opposed to the Early Sula period, a number of hydro- and hygrophytes significantly decreased while a part of the representatives of Betulaceae family increased in forest groups, and *Alnaster* and *Corylus* appeared. *Tilia cordata* singly occurred in forests, and *Juglans* in river valleys.

Forest type of vegetation predominated in the territory of the northern part of the Prydniprovsk Upland. Pine and birch-pine forests no longer included heat-loving pine species. Besides *Pinus* spp. and *Betula* spp. the forests occasionally included *Alnus* sp. and *Tilia cordata*, and *Juglans* sp. sometimes occurred in refugiums.

In the Sula period pine and mixed forests dominated in the central part of the Podil'ska Upland, and included, as compared to forest groups in other regions of Ukraine, the largest part of broad-leaved species. On lowered relief elements deciduous groups including various Betulaceae, *Quercus robur* and *Tilia cordata* as well as individual *Tilia platyphyllos* grew. Single *Juglans* survived in isolated refugiums. Compared to the Martonosha period, the representation of gramineous-herb and mugwort groups expanded in the structure of vegetation cover.

Thus, the palynological data indicate that in the Sula period within the platform Ukraine there was a clearly defined plant zoning. Within the Prydniprovsk Plain and the southern regions of Ukraine, the steppe type of vegetation predominated. The southern and northern boundaries of the forest-steppe zone were within the limits of the modern forest-steppe zone, while the western part was shorter. In the northern part of the Prydniprovsk Upland and probably the central part of the Podil'ska Upland a forest zone existed.

In the western, northwestern and partly central regions of Ukraine there were refugiums near ponds where broad-leaved and thermophilic species grew. Higher humidity could level to some extent global climate fluctuations and influence the composition of vegetation cover.

In Lubny period, warmth and humidity increased

again but, compared to the Martonosha period, the intensity of increase was lower. In contrast to the Martonosha period, the role of conifers reduced in the composition of vegetation, the participation of deciduous species increased in temperate and temperate warm zones (mainly due to *Quercus robur* and *Tilia cordata*), a number of thermophilic elements significantly decreased, and the role of herbaceous groups including miscellaneous herbs in their composition expanded.

Temperature and humidity fluctuations occurred within the territory of platform Ukraine during the Lubny period, which affected the nature of vegetation cover in the Early, Middle and Late Lubny periods.

In the Early Lubny period herbaceous groups with the participation of Chenopodiaceae, Asteraceae, Rosaceae, miscellaneous herbs, aquatic and coastal aquatic plants predominated within the Prydniprovsk Plain. Arboreal groups had a subordinate value but as against before Sula period, they occupied larger areas. Depending on the relief, birch-pine light forests with a small amount of *Picea* sect. *Eupicea* and oak-lime-hardbeam groups including *Carpinus betulus*, *Fraxinus* sp., *Quercus robur*, *Quercus* sp., *Tilia cordata*, *T. platyphyllos*, and *Corylus avellana* occurred. Single *Juglans* sp. grew in valley forests, and *Typha angustifolia* and *Alnus glutinosa* – along the banks of ponds.

Inter-stage fall of temperature that occurred during the formation of a thin loess-type layer caused impoverishment of forest groups due to disappearance of thermophilic and hydrophilic plants (*Juglans*, *Tilia*, *Carpinus*). This period was also characterized by an increase in irrigation that resulted in the expansion of areas occupied by herbaceous cenoses, in the composition of which a share of miscellaneous herbs reduced, while *Artemisia* spp. played a significant role.

In the Middle Lubny period a degree of humidity decreased. As a result, the role of *Quercus* increased in the composition of few arboreal groups. Certain changes occurred in the structure of forest groups as compared with the Early Lubny period. In oak-pine and pine-deciduous forests with *Corylus avellana* and *Elaeagnus* sp. hygrophilous plants such as *Carpinus betulus*, *Fraxinus* sp., *Picea* sect. *Eupicea* no longer occurred in undergrowth. Herbaceous cenoses, dominants in which were Chenopodiaceae family, prevailed in the composition of vegetation cover.

The second inter-stage fall of temperature was more intensive compared to the first one. The edificators of small forest groups were *Pinus sylvestris* and *Betula pendula*. Thermophilic and broad-leaved

species no longer entered into the composition of forests. Herbaceous cenoses, which occupied a significant part of the region of the research, also became poorer mainly due to miscellaneous herbs and hygrophilic plants.

In the Late Lubny period there was a slight increase in the humidity of climate, which led to a wider participation of birch-pine forests with a small impurity of *Quercus robur* as a part of vegetation cover and an increase in the role of miscellaneous herbs in the composition of herbaceous cenoses.

Climatic fluctuations retraced during the Lubny period also influenced the structure of vegetation cover of the Prydniprovskia Lowland. In the Early Lubny period large areas were covered with mixed forests including *Pinus* spp. sect. *Eupitys*, *Betula pendula*, *Picea* spp. sect. *Eupicea*, *Quercus robur*, *Corylus avellana* within the central part of the region. Thermophilic species did not enter into the composition of forests. Herbaceous groups occupied small areas and mainly consisted of Asteraceae, Chenopodiaceae and miscellaneous herbs. Polypodiaceae were present in the grass cover of forests.

Under the influence of inter-stage fall of temperature, the proportion of herbaceous cenoses including Poaceae, Polygonaceae, and Cyperaceae increased in the structure of vegetation cover. Compared to the Early Lubny period, the composition of few arboreal groups did almost not change.

In the Middle Lubny period, a forest-steppe type of vegetation predominated. In comparison with the Early Lubny period, the areas of forests decreased, and a number of *Pinus* and *Picea* diminished.

In the Late Lubny period the area of birch-pine forests increased in the composition of vegetation cover but the deciduous species of the temperate-warm zone (*Quercus* and *Corylus*) were already absent. Herbaceous groups occupied small areas and consisted predominantly of Poaceae, Asteraceae and miscellaneous herbs. Similar patterns of vegetation changes during the Lubny period were also retraced within the northwestern part of the Prydniprovskia Lowland. The differences consisted in the presence of *Carpinus betulus* and *Juglans regia* in the composition of forests in the Early Lubny period, pronounced representation of deciduous plants of the temperate-warm zone in the forests of the Middle Lubny period, especially *Tilia cordata*, as well as the appearance of *Ulmus campestris* and *Ulmus laevis*.

In the Early Lubny period a forest-steppe type of vegetation predominated within the Prydniprovskia Upland. Birch-pine and mixed forests occupied larger areas compared to herbaceous groups. Besides the

representatives of Pinaceae and Betulaceae families, numerous broad-leaved species such as *Quercus robur*, *Q. pubescens*, *Tilia cordata*, and *T. platyphyllos* grew in forests. Sometimes *Carpinus betulus*, *Fagus sylvatica*, and *Juglans cinerea* occurred in the composition of forest groups. The undergrowth consisted of *Corylus avellana* and *Rhamnus* sp. Meadow-steppe groups mainly consisted of miscellaneous herbs. Cyperaceae, *Typha* sp., and *Sparganium* sp. grew in ponds and along their banks.

Climate aridization, which occurred in the Middle Lubny period, led to the reduction in the area occupied by forests. Instead, a large part of the investigated territory was occupied by steppe cenoses mainly consisting of Asteraceae, Poaceae and Chenopodiaceae. Miscellaneous herbs only extended at wet sites. As compared with the Early Lubny period, a number of *Quercus robur* increased in forests but *Juglans cinerea* no longer occurred.

In the Late Lubny period within the region of the research there was a significant number of freshwater reservoirs with Potamogetonaceae, near which numerous Cyperaceae, *Typha* sp., and *Sparganium* sp. grew. The herbaceous groups of flat interfluvies consisted of the representatives of Poaceae and Chenopodiaceae families. In the composition of mixed forests the main role belonged to *Pinus* spp. and *Betula* spp. Single *Juglans regia* only grew in valley forests.

In the Early Lubny period, a forest type of vegetation prevailed within the northern part of the Prydniprovskia Upland. In the mixed and birch-pine forests, broad-leaved species were represented by *Tilia cordata* and *Quercus robur*, and the undergrowth consisted of *Corylus* sp. and *Elaeagnus* sp. On lowered relief elements arboreal groups consisted of individual *Juglans cinerea* and *J. nigra*. The grass cover of forests included Polypodiaceae and *Bryales*. A few grassy groups consisted of Chenopodiaceae, *Artemisia* spp., miscellaneous herbs and coastal aquatic plants.

In the middle Lubny period, the role of *Alnus* spp. and *Betula* spp. decreased in the composition of forests, whereas a number of *Tilia cordata* increased, and *Juglans nigra* was absent. In the composition of herbaceous groups, a number of miscellaneous herbs and coastal aquatic plants appreciably decreased due to the increased part of Asteraceae and *Artemisia* sp.

A forest type of vegetation was also typical for the territory of the Podil'ska Upland in the Early Lubny period. In the composition of forests, besides various *Pinus* species (with the participation of heat-loving *Haploxylon* species), *Picea* sp. sect. *Eupicea*, *Tilia*

cordata, *T. platyphyllos*, *Tilia* sp., *Quercus robur*, *Q. pubescens*, *Quercus* sp., and *Carpinus betulus* were presented. *Juglans regia* and *J. cinerea* thermophilic species also entered into the composition of forests, but in smaller quantities in comparison with the Martonosha period as well as *Tilia dasystyla*. A few herbaceous groups mainly consisted of miscellaneous herbs with a small part of Poaceae and Asteraceae.

In the Middle Lubny period the areas occupied by herbaceous groups with various Asteraceae increased. *Tilia* spp dominates in the deciduous component of coniferous–broad-leaved and mixed forests, whereas a number of plants of the temperate zone decreased. The forests included a small amount of *Picea* sp. sect. *Omorica*, *Carpinus orientalis*, *Fagus* sp., *Rhamnus* sp., *Corylus* sp. The thermophilic species were presented by *Juglans regia* and *J. cinerea*.

In the Late Lubny period the areas occupied by mixed forests increased. In comparison with the Middle Lubny period, a number of *Pinus* sp. subg *Diploxylon* increased in their composition but Tiliaceae family representatives decreased. Herbaceous groups grew mainly in forest glades.

Thus, in spite of the regional distinctions of the composition of Lubny vegetation, general tendencies of its changes associated with climatic fluctuations was clearly observed during the Lubny period. The most significant part of arboreal groups including coniferous (including dark coniferous) species as well as hygrophilous plants (*Carpinus betulus*) and an insignificant number of thermophilic elements was typical for the composition of Early Lubny vegetation in most regions of the platform Ukraine. In the Middle Lubny period the area occupied by herbaceous cenoses expanded in the structure of vegetation of all regions of Ukraine. The dominant components of deciduous forest were *Quercus* spp. and *Tilia* spp. In the Late Lubny period, the areas occupied by the forests expanded again in the structure of vegetation cover, but a significant part of them belonged to *Pinus* sp. subg. *Diploxylon* and *Betula* spp.

The Tiligul period was characterized by considerable aridization and a decrease in the temperature regime of climate (Figure 2), which resulted in impoverishment of both arboreal and herbaceous groups.

Within the Prydonetska Plain a steppe type of vegetation predominated. Significant areas were occupied by mugwort-orach coenoses with a small part of miscellaneous herbs and Poaceae. Few birch-pine forests including single *Quercus robur* and *Corylus* sp. occupied lowered relief elements.

A forest-steppe type of vegetation was inherent

in the Prydniprovsk Lowland. The composition of arboreal groups was close to the forests of the Prydonetska Plain. Herbaceous cenoses were mainly represented by plants of Asteraceae family, whereas Chenopodiaceae have a subordinate value.

In the Tiligul period, as compared with the Lubny period, in the central part of the Prydniprovsk Upland the area occupied by forests decreased, and broad-leaved and thermophilic species almost completely disappeared from their composition.

In the Early Tiligul period gramineous-herb, mugwort and orach cenoses dominated. Pine and birch-pine forests had a subordinate value, but in comparison with the Late Tiligul period they occupied larger areas. Within the region of the research there were a large number of freshwater reservoirs, around which *Typha* sp., *Potamogeton* sp., *Sparganium* sp., *Betula humilis*, and *Alnus* sp. grew.

During inter-stage warming the area of forests increased, and a few *Tilia cordata*, *Quercus robur*, and *Corylus avellana* appeared in their composition again. A part of meadow grasses increased in herbaceous cenoses.

In the Late Tiligul period aridization significantly increased, which led to domination of herbaceous cenoses consisting of Chenopodiaceae and Asteraceae in the composition of vegetation cover. Compared to the Early Tiligul period, a part of helophyte cenoses decreased. Few arboreal groups with *Pinus sylvestris* and *Betula pendula* sometimes included single *Quercus robur*.

Conclusions The analysis of the results of the palynological studies showed that regardless of the established regional differences, the general features of vegetation development due to changes in climatic conditions associated with global climate changes were retraced in the territory of plain Ukraine in the range of 1.8–0.43 million years.

The climatic conditions of each stage of nature development of the Pleistocene of Ukraine differed by the temperature regime and the degree of aridization or climate humidization, which affected the composition of vegetation cover. Temperature and humidity fluctuations occurred during each stage, which indicates the existence of not only macro- but also micro-rhythmicity in the development of Pleistocene vegetation in Ukraine.

During the formation of sediments that correspond to Calabrian according to ISS, the warmest climatic conditions were typical for the Early and Late Shyrokyne periods, and the dampest climatic conditions were in the Middle Kryzhanivka and Early Shyrokyne periods.

Among more recent Pleistocene stages of nature development in Ukraine (in the range of 0.8-0.43 million years), the warmest and dampest conditions existed in the Early and Middle Martonosha periods, while the coldest ones were in the Tiligul period (Figure 2).

Climatic conditions of the Sula period were less severe than in the subsequent stages of fall of temperature. The existence of refugia (mainly near ponds) with thermophilic and broad-leaved species was established within the western, northwestern and partly central regions of Ukraine in the Sula period. It was determined that the vegetative cover of the cold stages of the Early Neopleistocene (especially the Sula period) was characterized by the differentiation of vegetation cover in different regions of Ukraine. In the Sula period steppes dominated within the Near Black Sea Lowland (Sirenko, Turlo, 1986) and the Prydonetska Plain, forest-steppes in the Prydniprovskaya Lowland and the Prydniprovskaya Upland, and forests in the northern part of the Prydniprovskaya Upland and the Podil'ska Upland.

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