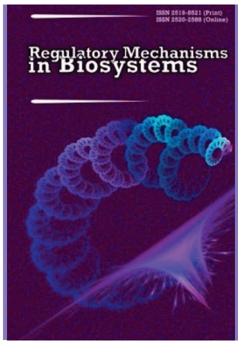

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Photosynthetic potential of *Malus domestica* columnar group

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Productivity is one of the primary economic and biological characteristics of an apple tree variety; it is this characteristic that determines the value and economic feasibility of the variety. The photosynthetic activity of the leaf surface of plants plays a leading role in forming the potential productivity of the apple tree. By "potential productivity," we mean the productivity of plants under conditions of ideal agroenvironment, optimal nutrition, and absence of diseases. To diagnose the potential productivity of cultivars we used an indicator of chlorophyll fluorescence induction–induction coefficient (K_i). According to our data, the K_i of leaves of columnar cultivars ranged from 0.720 to 0.740, indicating a high level of efficiency of photophysical processes near the photosystem II (PS II) reaction centers. For plants of columnar cultivars, the viability index ranged from 1.78 to 2.19. It has been established that individual age sections of tree trunks form different productivity potentials. Thus, based on the chlorophyll *a* (Chl *a*) fluorescence induction index, a higher intensity of photosynthesis was observed in the leaves of the cultivars ‘Valuta’, ‘Favoryt’, and ‘Bilosnizhka’ on seven to nine-year-old trunks. In contrast, for ‘Tantsivnytsia’, the highest intensity was observed on the oldest spur formation (14–19 years old). In traditional apple cultivars, the intensity of photosynthesis, as indicated by K_i, decreased with the age of spur formation; however, such a decline was not observed in columnar cultivars. The leaves of plants from the traditional cultivar ‘Idared’, situated on a homogeneous shoot, exhibited the highest photosynthetic intensity based on the $F_{680\gamma t}$ / $F_{680\beta t}$ light intensity. Conversely, in the leaves of three-year-old spur formations, a 25.3% decrease in photosynthetic intensity was observed, falling to a 45.7% decrease in six-year-olds. With the optimal combination of agroecological factors for columnar cultivars, stability in the photosynthetic potential across various complex spur formations is observed. In typical apple cultivars, the age of spur formation leads to a suppression of photosynthetic intensity. The cultivar ‘Bilosnizhka’ is characterized by the highest Chl *a*/ Chl *b* content, indicating lower adaptability. In the leaves of this cultivar, the amount of Chl *a* exceeded Chl *b* by three times; in contrast, in the cultivars ‘Sparta’ and ‘Tantsivnytsia’, the difference was 2.5 times higher. This value (2.5x) correlates with increased adaptability to the conditions in which they were studied. The highest level of leaf net productivity of photosynthesis (NPP) is observed in plants of the ‘Valuta’ cultivar (13.9 g/m² for day); in the cultivars ‘Bilosnizhka’, ‘Favoryt’, ‘Bolero’, ‘Sparta’, ‘Tantsivnytsia’, and ‘Papirovka’, the accumulation of dry matter is lowered by 32.6–40.6%.

Keywords: leaf photosynthesis; chlorophyll fluorescence; cultivar; induction coefficient; chlorophyll; adaptability.

Introduction

Entirely new perspectives in the evolution of the apple orchard have opened up with the discovery of a spontaneous mutant ‘Wijcik’ (‘Mcintosh Wijcik’), which has become the basis for the selection of columnar cultivars around the world (Tobutt, 1984, 1994; Jacob, 2007). The mutation is characterized by an unusual type of crown and plant habit, as well as the enhanced establishment of generative organs (Blažek, 1990; Blažek & Křelinová, 2011; Wada et al., 2018; Sun et al., 2020, 2021). The identification of the columnar gene (*Co*) in ‘Wijcik’ has opened up fundamentally new opportunities in the breeding of apple trees, specifically in terms of plant structure and an increased potential yield of more than 200 t/ha (Okada et al., 2020), which has been observed in cultivars with a columnar-type of growth. According to International Code of Nomenclature for Cultivated Plants, these cultivars belong to *Malus domestica* Columnar Group (Mezhenskyj, 2008). The biological feature of these columns is the almost complete absence of lateral branching, crop formation on both simple and complex spur formations located on the trunk of the tree, dwarf-type growth, early fruiting, and high yields. Ukrainian breeders have created over 20 columnar apple cultivars (Havryliuk & Kondratenko, 2019, 2020). Some of them have successfully passed the primary and state cultivar studies and are consequently undergoing technical evaluation in small industrial plantations of various types at present. These studies show the ability of “columns” to form high yields of one-dimensional fruits, consistent in shape and size. These yields are located on complex spur formations, ranging in age from 2–20 years, which is atypical in conventional apple cultivars (Havryliuk et al., 2022a, 2022b). We investigated the unique features of some of these columnar apple cultivars by assessing the functional state of their photosynthetic apparatus, utilizing the fluorescence induction method.

Currently, there are a large number of methods for diagnosing the functional state and potential productivity of plants (Vasylenko et al., 2021). Scientists point to the high susceptibility of photosynthesis to oxidative damage (Melis, 1991; Hsu, 1992). It has been proposed that the work of the photosynthetic apparatus is an indicator of a plant's response to the ecological pressures of growth conditions specifically (Allen, 1992).

Modern biophysical methods of diagnosing the state of photosynthetic systems make it possible to assess not only the result of plant reactions to stress but also to obtain data on the processes occurring during the direct action of a factor (Shikhov et al., 2011; Ptushenkom et al., 2013). The diagnostic analysis is possible due to the ability of chlorophyll to change its optical properties. This ability is related to functional rearrangements in photosynthetic membranes caused by one or another factor. It is accompanied by changes in the fluorescence intensity of leaves in the red part of the spectrum during the light and dark phases of photosynthesis. The informative possibilities of fluorescence measurements are further expanded by utilizing the thermal induction of chlorophyll fluorescence modifications methodology (Schechter et al., 1991; Pavlichenko et al., 2023).

Fluorescence emissions, including their photo- and thermo-induced changes, are recorded using modern research devices and presented in graphical form. Analysis of the obtained induction curve allows diagnosis of the functional state of the plastid complex of fruit plant leaves, particularly apple trees, which is directly influenced by the variable levels of certain environmental factors. According to Kytaiev & Pelekhatyi (1981), with increased levels of potential productivity observed in apple trees, there is a decrease in the thermal stability of the leaves. This weakening allows for the testing of plants to assess the efficiency of the photosynthetic apparatus and potential productivity.

The study of fluorescence emission values can be used to assess both the potential productivity and the adaptability of plants to the conditions of the growing zone. However, the abundance of values (several dozen) and the need to link the physiological meaning of each of them with the practical tasks of varietal study significantly complicates the use of science-intensive fluorescence research methods, which includes thermal induction of native chlorophyll fluorescence (Kryvoshapka & Kytaiev, 2019).

The need to narrow the spectrum of fluorescence parameters, especially those characterizing slow photosynthetic reactions, to two or three of the most informative is emphasized by Trokhymchuk & Makarova (2012). This will allow a more accurate assessment of both the stability and efficiency of the photosynthetic apparatus, as well as the associated adaptability and potential productivity of fruit crops, including apple trees.

The chlorophyll fluorescence induction method is increasingly used to analyze photosynthetic processes in leaves, as there is a direct relationship between native chlorophyll fluorescence intensity and photosynthetic reactions (Maxwell & Jonson, 2000). Therefore, this method is used to diagnose the functional state of plants and entire ecosystems (Vasylenko et al., 2021). CFI also notes the sensitivity of photosynthesis to various stressors, such as temperature, heavy metals, light intensity, air pollution, toxins, and changes in vertical zonation. Studies explicitly concerned with the photosynthetic apparatus efficiency of columnar apple cultivars, in our opinion, will establish not only the potential of plant productivity but also reveal the source of the longevity of these complex spur formations. It will also further substantiate the prospects for using specific species in certain models of intensive gardening. Therefore, the study aimed to determine the functional state and photosynthetic potential of plants of columnar apple cultivars by analyzing the fluorescent parameters relating to the photosynthetic activity of leaves.

Material and methods

The research was carried out in 2017–2021 at the Prof. V. L. Symyrenko Department of Horticulture, at the National University of Life and Environmental Sciences of Ukraine. The experimental basis for the research was the planting of apple trees, of the cultivar test specimens, at the Institute of Horticulture of the National Academy of Agrarian Sciences of Ukraine. Experimental studies to determine the functional state of the leaves of columnar apple cultivars were conducted in the Laboratory of Plant Physiology and Microbiology of the Institute of Horticulture of the NAAS.

The subjects of the study were seven cultivars of columnar type apples of three ripening periods (summer apple ‘President’, autumn apple ‘Bolero’, ‘Favoryt’, and winter apple ‘Valuta’, ‘Sparta’, ‘Bilosnizhka’ and ‘Tantsivnytsia’) and three "traditional" ‘Papirovka’, ‘Idared’, ‘Teremok’, respectively summer, autumn and winter cultivars in apple orchards of the primary varietal study of NAAS.

Plantings (not irrigated) were laid in 2002 and 2010, which was done in accordance with the primary cultivar testing method. Trees on rootstock ‘54-118’ were planted according to an arrangement of 4 × 1 m for columnar cultivars and 3 × 4 m for traditional ones.

Assessing the functional state of the photosynthetic apparatus using a portable chronofluorometer. Express diagnostics of plant condition were performed using a portable chronofluorometer “Floratest”, which allowed control of the operation of photosystem II (PS II) (Kytaiev et al., 2008). The device was developed by the V. M. Glushkov Institute of Cybernetics of the National Academy of Sciences of Ukraine.

This instrument registers the “Kautsky curve” (induction fluorescence changes), the shape of which fully reflects the course of photosynthesis in leaf chloroplasts (Table 1) (Havryliuk et al., 2019). Plant samples were analyzed in the third decade of July for a 5 year period (2017–2021), in twenty replicates in the timeframe when the leaf blades were fully formed; the cycle duration of one measurement was 3 minutes (a total of 740 measurements). Preparation of the sample for analysis: leaves were collected from different aged spur formations, in the morning from 8 to 10 o'clock. They were selected, based on their location: on one consistent side of the row, well lit and not shaded by other leaves. They were placed in dark bags, without light penetration (dark adaptation) and after 20 minutes were analyzed in the laboratory using a chronofluorimeter (Floratest). When assessing the functional state of the photosynthetic apparatus, by inductive changes in chlorophyll fluorescence, a consistent set of parameters was used, which allowed changes in photosynthetic processes in the leaves to be analyzed, namely:

F_0 – “Background” level of fluorescence; depends on the loss of excitation energy during migration by the pigment matrix, as well as on the content of chlorophyll molecules that do not have a functional connection with the reaction centers (RC);

F_{pL} – (I) – (“Plateau”) – the level of fluorescence at the time of achieving a temporary slowdown in its signal, due to the rapid energy saturation of PS II reaction centers, which do not restore the primary Q_a acceptor, ie do not transfer energy to the electron transport chain (biochemical reactions, ATP production – the main “fuel” cells required for its operation);

F_p – (P) – maximum fluorescence value;

F_t – (T) – stationary level, which is characterized by a dynamic balance between the processes that cause an increase in fluorescence and the processes that lead to its decrease.

The following indicators were calculated by the analytical method: K_{pl} – plateau coefficient for saturating photosynthesis of the intensity of exciting light (above 400 W/m^2), characterizes the share of primary acceptors of PS II – Q_a electrons that do not restore the reaction centers:

$$K_{pL} = \Delta F_{pL} / F_v,\ \Delta F_{pL} = F_{pL} - F_0,\ F_v = F_p - F_0.$$

K_i – chlorophyll fluorescence induction coefficient shows the proportion of chlorophylls involved in photosynthesis in terms of their total number and determines the efficiency of the light phase of photosynthesis: F_v / F_p; Rfd – the coefficient of efficiency of dark photochemical processes or the coefficient of fluorescence decline, which characterizes the quantum efficiency of photosynthesis (viability index): $(F_p - F_t) / F_t$.

Luminescent method of analysis photo- and thermal-induction of chlorophyll fluorescence. The functional state of the photosynthetic apparatus was diagnosed using luminescent methods of analysis, in particular, photo- and thermal-induction of chlorophyll fluorescence (Kytaiev et al., 2008).

Light induction and thermal induction of chlorophyll fluorescence of the leaf blade were excited (provoked) in a continuous mode with blue-violet light (λ_{max} = 435.8 nm). Excitation light of different intensities (from 5 to 300–600 W/m^2) was used in the experiments. This made it possible to achieve saturation of the light stages of the photosynthetic process responsible for the formation of light and thermal induction changes in chlorophyll fluorescence. Prior to analysis, the leaves were kept in the dark (dark adaptation) for 30 minutes.

The intensity of chlorophyll fluorescence was determined directly on the graph at the following points: $F_{max(680)}$, $F_{st(680)}$, $F_{st(740)}$, $F_{st(530)}$, $F_{t\alpha(680)}$, $F_{t\beta(680)}$, $F_{t\gamma(680)}$, $F_{t\beta\gamma(680)}$, $F_{t(680)}$, $F_{t(740)}$, $F_{t(530)}$. The coefficient of chloroplasts structural organization efficiency was calculated as the ratio of temperature waves intensity: $F_{680\gamma t} / F_{680\beta t}$, where $F_{680\gamma t}$ – is the amplitude of the chlorophyll temperature induction γ-wave; $F_{680\beta t}$ – is the amplitude of the chlorophyll temperature induction β-wave.

The study was performed using a spectral microfluorimeter SMF-2. The device excited and recorded fluorescence spectra in a certain area of the leaf surface; individual changes in fluorescence, which are the result of light or heat. Fluorescence emission was recorded in the spectrum region of 500–800 nm. Temperature-induced changes in fluorescence were recorded for a stationary level of light induction of fluorescence by heating the leaves from 20 to 80 ºС.

Chlorophyll concentrations were determined in late July when the leaves had formed but had not yet begun to age. Leaves were selected in eight replicates from complex spur formation located in different age areas of the trunk, but with the same level of illumination. Research was conducted in the time period encompassing 2017 through 2019 inclusive. Alcohol was used to extract pigments, specifically a 96% ethanol solution. The optical density of the alcohol extract was determined using a photoelectric photometer KFK3-01-ZOM3. The content in the leaves Chl a and Chl b (wavelengths 649 and 665 nm) (Pochinok, 1976).

Table 1
The intensity of chlorophyll fluorescence in areas of the curve

Section of CFI Curve	Appearance (signs) plots	Time interval	Stages of the photosynthetic process, information about which gives this area
Point O	Starting area	0 to 5 ms incl.	The efficiency of light collection and reaction centers of chlorophyll II
O–I–D–P	Reaching the main maximum	0.1 till 10 s (0.1 till 1 s)	Electronic transport link (from H_2O to F_d and NADPH) – the so-called "light stage" of photosynthesis
P–S–M	Recession and exit to another maximum	3 till 50 s (0.5 till 10 s)	Activation (via F_d) of Calvin cycle enzyme proteins, the establishment of pH gradient in membranes, restoration of competing acceptors (O_2, NO_2^- etc.)
M–T	Decline and return to stationary mode	10 till 300 s (10 till 2000 s)	Adjusting the reactions of the Calvin cycle and the flow of substances through the vessels of the leaf
M–S_1, S_1–M_1–T	Exit tointermediate minimum Access to stationary mode	10 till 100 s 50 till 300 s (100 till 2000 s)	Debugging Calvin cycle reactions. Establishing the transport of substances through the membranes and vessels of the leaf

These physiological studies also included the determination of net productivity of photosynthesis (NPP) utilizing the Koshelev & Ursulenko method (1977). Indicators of photosynthetic activity were calculated according to the formulas proposed by Ovsyannikov (1973). The increase in dry matter of leaves for a per day was determined by sampling leaves, using a plant punch; 20 repetitions per one section of the trunk, a total of 80 samples per cultivar.

The research site zone is located in the Western Forest-Steppe of Ukraine. The region's climate is temperate continental and is characterized by mild winters and warm summers. The average annual air temperature, recorded during the research timespan, was 10.1 °C. The coldest month was January, with an average monthly temperature of minus 3.2 °C, while the warmest was August (21.8 °C). The first autumn frosts were generally observed in the second decade (a set of 10 days) of October, while winter commences in the second decade of November. Permanent snow cover is laid in December and the spring melt begins in the second decade of March. There are also thaw cycles in the winter, occurring between December and February, which last an average of 40 days in total (cycles are repeated 6 to 10 times, each lasting several days). Spring frosts are likely until mid-May. The growing season for fruit crops, according to the five-year data set, begins in the first decade of April. Active growth and development of fruit plants is observed in the third decade of April. The sum of active temperatures of 10 °C and above (Σactt ≥ 10 °C) is 3450.0 °C, and the number of days with temperatures of 10 °C and above is generally around 180. The average annual rainfall is calculated as 380 mm, with the wettest month being July (68 mm). The average number of days with precipitation is 150. The soil of the experimental area is dark gray, podzolic, medium loamy, which is typical for the right-bank part of the Western Forest-Steppe (Litvinova et al., 2023a, 2023b; Voitovyk et al., 2023). The humus content in the arable soil layer (0–40 cm) is 1.00–1.90%, and the pH of the aqueous extract is 6.22–8.33.

Statistical analysis of the study data was performed using Statistica 13.1 software (StatSoft, Inc., USA). Results are expressed as means ± standard deviation of three analytical replicates in each year. Data were analyzed using two-way or one-way ANOVA, and significant differences ($P < 0.05$) between the mean values were determined by Duncan's multiple-range test.

Results

Productivity is one of the main economic and biological properties of the cultivar, and it characterizes the value and economic feasibility of the same. A comprehensive evaluation of apple cultivars with different ecological and geographical origins has made it possible to determine the production potential of cultivars and identify annual fruiting and productivity trends. All components of productivity were characterized by specific quantitative and qualitative parameters, which varied depending both on the biological characteristics of the cultivar and conditions of the year.

The leading role in the potential productivity formation of apple trees is played by the photosynthetic activity of the leaf surface of plants. The main pigment of a plant cell that has the ability to fluoresce is chlorophyll (Maxwell & Johnson, 2000). The basis for the widespread use of the method of "chlorophyll fluorescence induction" in the study of photosynthesis was a sufficient sensitivity to changes in CFI (Kytaiev & Pelekhatyi 1981), which occur in the photosynthetic apparatus during adaptation to different environmental conditions (Kasampalis et al., 2021). The theory of the method of fluorescence induction has been presented in numerous reviews and monographs (Krause & Weis, 1991; Dau, 1994; Schreiber et al., 1995). The fluorescence intensity of chlorophyll varies depending on the state of the photosynthetic apparatus. In his research, Korneev (2002) found an association between native chlorophyll fluorescence intensity and photosynthetic reactions, which makes it possible to use this method to determine the potential productivity of plants.

Absorbed by the pigment complex in primary photophysiological processes, the radiation is converted mainly into chemical energy, while the rest of it is dissipated in the form of heat, and is also emitted in the form of fluorescence. The more efficient the photosynthetic apparatus, the lower the fluorescence intensity (Lazár, 1999; Roháček & Barták, 1999).

Assessing the functional state of the photosynthetic apparatus using a portable chronofluorometer. In the columnar apple cultivars 'Valuta' and 'Bilosnizhka' the background fluorescence level (F_0) of the leaves was lower than in the control cultivar 'Bolero'; in other cultivars – at the level of control, which indicates an increase in the amount of chlorophyll in their leaves (Table 2).

At the level of conditional control ('Idared') F_0 is marked in the cultivar 'Sparta'. Fewer chlorophylls that do not participate in the photosynthetic process were found in the leaves of 'Valuta', 'Tantsivnytsia', and 'Bilosnizhka'. The 'Favoryt' cultivar did not differ significantly from the 'Teremok' cultivar in terms of leaf fluorescence. No difference was found within the summer cultivars.

F_p characterizes the highest level of chlorophyll *a* fluorescence (Chl *a*) and is represented as a maximum on the induction curve. Adaptive changes in the structure of the pigment complex to the lighting conditions are due to the fact that this indicator is the most variable. The values of the maximum value of fluorescence depend on the intensity of the exciting radiation. They are proportional to the total number of chlorophylls and inversely proportional to the density of the reaction centers. The indicator F_0 / F_p more fully characterizes the use of energy for useful activities (synthesis of organic matter). According to long-term research conducted by the Laboratory of Plant Physiology of NAAS, the optimal level of background fluorescence for apple leaves is not more than 20–25% of the maximum value of fluorescence (F_p). In all studied cultivars of columnar apple trees, the pigment complex of leaves is active, although the indicator (F_0 / F_p) is slightly increased – 26–28%. The reason for this may be the effect of drought on plants (non-irrigated plantings).

To diagnose the potential productivity of cultivars, we used the information indicator of chlorophyll fluorescence induction – induction coefficient (K_i), which characterizes the functional activity of leaves and is a barometer of the impact on the plant of exogenous factors. It was found that the greater the K_i, the better the absorption of CO_2 and the higher the intensity of photosynthesis. The decrease in the values of Ki is due to the suppression of PS II and a decrease in the proportion of reaction centers in this system that are unable to recover (Mamonova et al., 2018). According to our data, the K_i of leaves of columnar cultivars in the third decade of July ranged from 0.720 to 0.740, which indicates a high level of efficiency of photophysical processes near the PS II reaction centers.

The potential productivity was observed to be at a high level in all cultivars. At the same time, the highest level of potential productivity at the end of July in terms of Ki was observed in plants of the 'Bilosnizhka' cultivar. There was no significant difference in the efficiency of the light phase of photosynthesis in the leaves of the studied cultivars compared to the control ('Bolero'). The coefficient of adaptability or "viability index" (Rfd) characterizes the efficiency of photosynthetic processes (Mamonova et al., 2018), so we used it to assess the impact of growing conditions on plant conditions. A decrease in the estimated Rfd to 1.47–1.91 indicates a negative effect of growth conditions or a possible effect of a stress factor on the efficiency of the Calvin cycle. For plants of columnar cultivars in the third decade of July, the viability index was in the range of 1.78–2.19 (Table 3). The efficiency of photosynthetic processes in terms of adaptability in 'Valuta' plants in the third decade of July should be considered low. Using a detailed analysis of the results of this study, it was found that individual age areas of tree trunks form different productivity potentials.

Thus, according to the fluorescence induction index of chlorophyll (K_i), higher intensity of photosynthesis over the years of study compared to control ('Bolero') was observed in the leaves of cultivars 'Valuta', 'Favoryt' and 'Bilosnizhka' on a seven- to the nine-year-old trunk, in 'Tantsivnytsia' – on 19-year-olds, ie on the oldest spur formation. For the cultivars 'President' and 'Sparta', the most intensive CO_2 uptake is characteristic for the leaves which are located on annual spur formation. A comparison of winter columnar cultivars with conditional control ('Idared') revealed a markedly higher chlorophyll fluorescence induction coefficient calculated for fruiting leaves in the older parts of the column trunk (except 'Sparta'). For the cultivar 'Idared' higher intensity of photosynthesis is characteristic of the leaves of annual shoots (Table 4).

Table 2
Indicators of functional activity of the pigment complex of apple leaves, Institute of Horticulture of the NAAS 2017–2021 (x ± SD, n = 100)

Cultivars	Indicators of the functional state of the leaf surface (mean by years)				
	F_0, relative units	F_p, relative units	F_0 / F_p, %	K_i	Rfd
Bolero	311.2 ± 18.4^{ab}	$1\,159{,}9 \pm 104.0^{ab}$	27.3 ± 5.3	0.721 ± 0.007^{a}	1.945 ± 0.089^{bc}
Bilosnizhka	267.1 ± 16.2^{c}	1044.3 ± 42.3^{bc}	25.7 ± 3.7	0.740 ± 0.025^{a}	1.973 ± 0.144^{b}
Favoryt	311.0 ± 14.1^{ab}	1208.9 ± 139.5^{a}	26.5 ± 3.8	0.730 ± 0.038^{a}	2.051 ± 0.194^{ab}
President	307.8 ± 18.4^{ab}	1128.3 ± 53.1^{abc}	27.7 ± 3.6	0.720 ± 0.008^{a}	2.105 ± 0.151^{ab}
Sparta	320.7 ± 9.0^{a}	1222.1 ± 37.3^{a}	26.5 ± 3.2	0.733 ± 0.011^{a}	2.188 ± 0.150^{a}
Tantsivnytsia	292.1 ± 16.4^{b}	1076.3 ± 12.0^{bc}	27.1 ± 3.2	0.727 ± 0.010^{a}	1.905 ± 0.043^{bc}
Valuta	278.7 ± 19.1^{bc}	1035.4 ± 71.4^{cb}	27.3 ± 4.4	0.723 ± 0.017^{a}	1.784 ± 0.063^{c}
Idared	316.2 ± 21.4^{a}	1218.2 ± 107.5^{a}	26.8 ± 6.3	0.731 ± 0.021^{a}	2.128 ± 0.112^{ab}
Papirovka	307.4 ± 14.5^{ab}	1165.7 ± 66.1^{ab}	26.4 ± 2.7	0.732 ± 0.010^{a}	1.982 ± 0.094^{b}
Teremok	322.7 ± 17.8^{a}	1204.3 ± 130.1^{a}	26.8 ± 1.6	0.728 ± 0.008^{a}	2.112 ± 0.235^{ab}

Note: for tables 2–6, different letters indicate values that are significantly different within one column according to results of the Tukey' test ($P < 0.05$).

Table 3
Indicators of functional activity of the pigment complex of apple leaves of different trunk ages, mean by 2017–2021,
Institute of Horticulture of the NAAS (x ± SD, n = 20)

Cultivars	Age of the trunk section	F_0, relative units	F_p, relative units	F_0 / F_p, %	K_i, index	Rfd, index
Bolero	one–year-old area of the trunk	311 ± 17.2^{b}	$1\,122 \pm 165.1^{c}$	27.9 ± 5.9	0.716 ± 0.064^{cd}	2.00 ± 0.24^{bc}
	five years old	285.3 ± 19.9^{c}	$1\,037.4 \pm 74.6^{cde}$	27.6 ± 4.9	0.717 ± 0.059^{cd}	1.95 ± 0.31^{bc}
	10 years old	326.4 ± 18.5^{ab}	$1\,279.6 \pm 312.1^{b}$	25.9 ± 3.7	0.731 ± 0.045^{bc}	2.01 ± 0.30^{bc}
	19 years old	322.1 ± 18.7^{ab}	$1\,200.6 \pm 232.4^{bc}$	27.7 ± 6.8	0.717 ± 0.073^{cd}	1.82 ± 0.25^{cd}
Bilosnizhka	one–year-old area of the trunk	270.9 ± 16.6^{cd}	989.5 ± 173.4^{de}	27.8 ± 5.8	0.720 ± 0.059^{bcd}	2.06 ± 0.30^{bc}
	three years	282.7 ± 17.8^{c}	$1\,056.4 \pm 34.8^{cd}$	26.7 ± 4.2	0.729 ± 0.041^{bc}	1.90 ± 0.13^{cd}
	five-year	270.6 ± 16.1^{cd}	$1\,040.0 \pm 197.3^{cde}$	25.8 ± 3.2	0.736 ± 0.036^{bc}	1.81 ± 0.25^{cd}
	nine-year-old	244.3 ± 11.1^{cd}	$1\,091.2 \pm 27.2^{cd}$	22.5 ± 1.4	0.776 ± 0.014^{a}	2.12 ± 0.25^{b}
Valuta	one–year-old area of the trunk	292.1 ± 12.2^{bc}	$1\,098.8 \pm 194.0^{cd}$	27.3 ± 6.0	0.726 ± 0.060^{bc}	1.71 ± 0.10^{dc}
	three years	269.9 ± 14.5^{cd}	936.5 ± 115.6^{cd}	28.8 ± 3.9	0.707 ± 0.040^{cd}	1.75 ± 0.26^{cd}
	five-year	296.7 ± 14.2^{bc}	$1\,074.1 \pm 216.2^{cd}$	28.4 ± 6.4	0.714 ± 0.064^{cd}	1.82 ± 0.39^{cd}
	nine-year-old	256.0 ± 12.6^{de}	$1\,032.0 \pm 33.9^{cde}$	24.8 ± 1.4	0.746 ± 0.016^{bc}	1.85 ± 0.13^{cd}
President	one–year-old area of the trunk	289.7 ± 19.9^{bc}	$1\,120.5 \pm 273.1^{c}$	26.3 ± 3.8	0.731 ± 0.041^{bc}	1.88 ± 0.29^{cd}
	three years	309.0 ± 13.6^{b}	$1\,120.0 \pm 201.1^{c}$	27.9 ± 2.4	0.718 ± 0.027^{cd}	2.20 ± 0.19^{ab}
	five-year	332.8 ± 15.0^{ab}	$1\,200.4 \pm 233.3^{bc}$	28.5 ± 5.7	0.713 ± 0.059^{cd}	2.20 ± 0.34^{ab}
	nine-year-old	299.7 ± 11.1^{bc}	$1\,072.3 \pm 15.5^{cd}$	28.0 ± 2.4	0.717 ± 0.029^{cd}	2.14 ± 0.13^{ab}
Sparta	one–year-old area of the trunk	315.0 ± 12.1^{a}	$1\,267.6 \pm 158.3^{b}$	24.9 ± 1.1	0.748 ± 0.013^{b}	2.31 ± 0.47^{a}
	five years old	313.9 ± 19.7^{ab}	$1\,177.1 \pm 196.8^{bc}$	26.9 ± 2.8	0.731 ± 0.028^{bc}	2.27 ± 0.11^{ab}
	10 years old	333.4 ± 15.7^{a}	$1\,228.6 \pm 247.7^{bc}$	27.7 ± 5.0	0.722 ± 0.049^{bcd}	1.98 ± 0.26^{bc}
	19 years old	320.4 ± 13.3^{ab}	$1\,215.2 \pm 46.8^{bc}$	26.4 ± 3.7	0.733 ± 0.039^{b}	2.19 ± 0.23^{ab}
Tantsivnytsia	one–year-old area of the trunk	285.3 ± 14.1^{c}	$1\,092.9 \pm 157.9^{cd}$	26.2 ± 3.2	0.734 ± 0.035^{bc}	1.91 ± 0.23^{c}
	five years old	297.3 ± 16.7^{bc}	$1\,066.9 \pm 76.6^{cd}$	27.8 ± 2.3	0.719 ± 0.035^{c}	1.96 ± 0.27^{b}
	10 years old	302.7 ± 18.3^{bc}	$1\,068.0 \pm 220.2^{cd}$	28.0 ± 4.0	0.718 ± 0.041^{cd}	1.86 ± 0.33^{cd}
	19 years old	283.2 ± 18.0^{c}	$1\,077.3 \pm 179.4^{cd}$	26.2 ± 3.1	0.737 ± 0.032^{bc}	1.89 ± 0.36^{cd}
Favoryt	one–year-old area of the trunk	322.8 ± 14.2^{ab}	$1\,107.6 \pm 355.6^{c}$	30.1 ± 5.1	0.694 ± 0.057^{dc}	1.78 ± 0.34^{cd}
	three years	309.3 ± 11.2^{b}	$1\,098.7 \pm 168.4^{cd}$	28.5 ± 3.9	0.711 ± 0.046^{cd}	2.07 ± 0.48^{bc}
	five-year	310.8 ± 14.2^{b}	$1\,232.4 \pm 141.8^{b}$	25.5 ± 4.3	0.740 ± 0.048^{bc}	2.10 ± 0.21^{b}
	nine-year-old	301.0 ± 19.5^{bc}	$1\,397.0 \pm 355.0^{a}$	21.8 ± 2.0	0.780 ± 0.020^{a}	2.25 ± 0.57^{ab}

In the autumn group of cultivars, the induction coefficient was higher in the 'Favoryt' leaves, located on seven- to nine-year sections of the trunk, and in the 'Teremok' cultivar, on three-year increments. In the summer cultivar 'President', a high level of CO_2 absorption was observed in the leaves, which are located on one-year sections of the trunk, and in 'Papirovka' – on five-year increments. Thus, in plants of most columnar cultivars of winter maturity, older complex spur formations are able to form a higher productivity potential. It should be noted that the leaves of 19-year-old spur formations of 'Bolero', 'Tantsivnytsia' and 'Sparta' cultivars retain a high level of photosynthesis: the potential productivity of complex spur formation located in the oldest parts of the trunk is also high.

Luminescent method of analysis photo- and thermal-induction of chlorophyll fluorescence. Highly productive trees are characterized by an intensive course of metabolic processes, accompanied by the accumulation of peroxide compounds, which activate the cellular processes of pinocetosis and extrusion. The accumulation of peroxides reduces the stability of the membranes of the photosynthetic apparatus, which are controlled by the time range between the appearance of temperature-induced β- and γ-fluorescence waves. According to Kytaiev & Pelekhatyi (1981), a shorter time interval between the appearance of these fluorescent changes may indicate higher potential productivity of apple plants under optimal growing conditions. The intensity of membrane transport processes is lower in less productive plants. The level of peroxide compounds in them is also lower, which may cause high stability of green plastid membranes in such plants and is reflected in inflated values of temperature-time index γ-β (Sovakova et al., 2014).

Table 4
Indicators of pigment complex functional activity of "traditional" apple tree leaves of different trunk ages, mean by 2017–2021, Institute of Horticulture of the NAAS (x ± SD, n = 20)

Cultivars	Age of the trunk section	F$_0$, relative units	F$_p$, relative units	F$_0$/ F$_p$, %	K$_i$, index	Rfd, index
Idared	one–year age area of the trunk	334.9 ± 18.7^{b}	$1\,338.7 \pm 150.8^{a}$	25.3 ± 5.0	0.746 ± 0.052^{a}	2.22 ± 0.36^{a}
	three years	292.8 ± 15.8^{c}	$1\,184.0 \pm 384.7^{bd}$	25.9 ± 7.1	0.740 ± 0.073^{a}	2.00 ± 0.19^{b}
	five years	320.8 ± 10.2^{bc}	$1\,132.0 \pm 299.8^{bd}$	29.2 ± 6.8	0.707 ± 0.067^{b}	2.16 ± 0.28^{ab}
Teremok	one–year age area of the trunk	291.7 ± 18.1^{c}	$1\,078.9 \pm 107.9^{d}$	26.9 ± 2.7	0.730 ± 0.028^{ab}	1.84 ± 0.32^{b}
	three years	311.5 ± 13.0^{c}	$1\,195.2 \pm 142.6^{b}$	26.3 ± 3.4	0.735 ± 0.037^{a}	2.24 ± 0.26^{a}
	five years	364.8 ± 15.1^{a}	$1\,338.7 \pm 37.7^{a}$	27.3 ± 2.1	0.719 ± 0.027^{ab}	2.25 ± 0.27^{a}
Papirovka	one–year age area of the trunk	302.3 ± 17.4^{c}	$1\,089.6 \pm 20.4^{bd}$	27.7 ± 1.1	0.721 ± 0.010^{ab}	2.09 ± 0.07^{ab}
	three years	310.9 ± 10.3^{c}	$1\,198.9 \pm 107.1^{b}$	26.0 ± 1.9	0.736 ± 0.023^{ab}	1.95 ± 0.27^{b}
	five years	308.8 ± 16.8^{c}	$1\,208.5 \pm 110.1^{b}$	25.6 ± 1.8	0.740 ± 0.021^{a}	1.91 ± 0.08^{b}

The constancy of the photosynthetic apparatus and the efficiency of its work are the basis of research to determine the potential for productivity. The efficiency of the potential of the photosynthetic apparatus realization of the columnar apple tree depends on the level of agrotechnics and adaptability of plants to the conditions of the cultivation microzone. Under favorable agroecological factors (especially illuminance), the ratio of the maximum amplitude of the γ-wave to β (F680γt / F680βt) in cultivars of common apple should be more than 2.0 (Makarova & Kytaiev, 2008). This relationship shows the level of tension of membrane transport links during photosynthetic reactions. In plants with openwork and correspondingly better-illuminated crown, this figure is usually higher than in plants with dense leaf cover.

Our studies showed that the highest intensity of photosynthesis (IPS) according to the F680γt / F680βt; ratio was observed in the leaves of plants of the common cultivar 'Idared', which were on the shoot; in the leaves of three-year-old spur formations there was a decrease in the intensity of photosynthesis by 25.4%, in six-year – up to 46.0% (Table 5).

Leaves of complex spur formation of all ages of 'Tantsivnytsia' apple trees have almost the same ratio of amplitudes of thermo-induced waves. In the leaves of 16-year-old formations, IPS was 17% higher than on the elongation shoots. In 'Bolero' apple trees, a decrease in the F680γt / F680βt ratio was observed in leaves placed on four- to eight-year-old complex spur formation; this occurred under the influence of very thick foliage of the crown in this area of the trunk. For the 'Sparta' cultivar, the highest level of tension of membrane transport processes is inherent in the leaves, which are located on the four-year-old section of the trunk, in other areas it is 20.0% lower. The analysis of the diagram shows that with the optimal combination of agroecological factors, columnar cultivars are characterized by the stability of photosynthetic potential in complex spur formation of different ages. In ordinary apple cultivars with the age of spur formation, there is a suppression of the intensity of photosynthesis.

Table 5
Pigment complex photosynthetic productivity of apple cultivars on different age spur formation by the ratio of the amplitudes of thermo-induced waves (F680γt / F680βt), mean by 2017–2019, Institute of Horticulture of the NAAS (n = 15)

Cultivars	Age of fruit formations	The ratio of the amplitudes of thermo-induced waves (F680γt / F680βt)
Idared	one-year age area of the trunk	2.441 ± 0.179^{ab}
	3-year-old	1.821 ± 0.307^{bc}
	6-year-old	1.318 ± 0.194^{dc}
Bolero	one-year age area of the trunk	2.101 ± 0.155^{b}
	4-year-old	1.505 ± 0.147^{cd}
	10-year-old	1.392 ± 0.102^{cd}
	16-19-year-old	1.951 ± 0.151^{bc}
Tantsivnytsia	one-year age area of the trunk	2.182 ± 0.086^{ab}
	4-year-old	2.114 ± 0.251^{b}
	10-year-old	2.433 ± 0.187^{ab}
	16-19-year-old	2.646 ± 0.155^{a}
Sparta	one-year age area of the trunk	1.641 ± 0.187^{bcd}
	4-year-old	2.100 ± 0.214^{b}
	10-year-old	1.680 ± 0.142^{bcd}
	16-19-year-old	1.685 ± 0.095^{bcd}

Determination of chlorophyll concentration in leaves. The efficiency of photosynthesis depends on the quantitative content of green pigments in the leaves and the ratio of their forms (Tanaka et al., 1998). This relationship determines the structural organization of chloroplasts and the potential of plant adaptation to changes in environmental conditions, especially light.

In the studied apple cultivars there was a variation in the content of Chl *a* in the leaves from 5.04 to 8.03 mg/g of raw weight (Table 6).

Table 6
The content of green pigments in apple leaves, mean by 2017–2019, Institute of Horticulture of the NAAS (x ± SD, n = 15)

Cultivars	Chlorophyll content (Chl), mg/g of raw mass			Chl *a* / Chl *b*
	a	*b*	*Σa+b*	
Bolero	6.81 ± 0.90^{bcd}	2.45 ± 0.39^{c}	9.12 ± 1.26^{bc}	2.79 ± 0.11^{ab}
Bilosnizhka	6.42 ± 0.69^{c}	2.12 ± 0.27^{cd}	8.41 ± 0.92^{c}	3.03 ± 0.17^{a}
Favoryt	5.05 ± 0.78^{ed}	1.74 ± 0.25^{d}	6.69 ± 0.99^{d}	2.90 ± 0.19^{ab}
President	5.60 ± 0.74^{de}	2.14 ± 0.31^{c}	7.62 ± 0.98^{cd}	2.63 ± 0.24^{bc}
Sparta	8.09 ± 0.68^{a}	3.27 ± 0.35^{a}	11.17 ± 1.00^{a}	2.48 ± 0.09^{cb}
Tantsivnytsia	7.30 ± 0.98^{b}	2.87 ± 0.41^{b}	10.01 ± 1.35^{b}	2.55 ± 0.10^{bc}
Valuta	6.17 ± 0.60^{cd}	2.29 ± 0.31^{c}	8.32 ± 0.88^{c}	2.71 ± 0.16^{bc}
Idared	5.92 ± 0.62^{cd}	2.46 ± 0.74^{c}	8.24 ± 0.95^{c}	2.56 ± 0.62^{bc}
Papirovka	5.62 ± 0.84^{de}	2.08 ± 0.42^{cd}	7.58 ± 1.21^{cd}	2.74 ± 0.28^{bc}
Teremok	6.06 ± 0.60^{cd}	2.38 ± 0.25^{c}	8.31 ± 0.60^{c}	2.57 ± 0.38^{bc}

'Idared', 'Papirovka', 'Favoryt', and 'President' were characterized by significantly lower content in Chl *a* leaves compared to the control; the highest amount of this pigment is determined in the leaves of 'Sparta'.

The content of Chl *b* in the leaves of the studied apple cultivars varies from 1.63 to 3.22 mg/g of raw weight. The lowest content of this pigment is the cultivar 'Favoryt', the highest – 'Tantsivnytsia' and 'Sparta'.

The total amount of Chl *a* + *b* pigments, depending on the cultivar, ranges from 6.63 to 11.16 mg/g of raw weight. 'Sparta' plants were characterized by much higher values of this indicator, 'Papirovka', 'President' and 'Favoryt' plants were the lowest.

The leaves of most higher plants contain twice as much Chl *a* as Chl *b*. The higher the content of Chl *b* in the leaves of plants, the higher their adaptive potential and more stable pigment system. 'Bilosnizhka' is characterized by the highest content of Chl *a* / Chl *b* and, accordingly, the lowest adaptability; in the leaves of this cultivar the amount of Chl *a* exceeded Chl *b* by three times; in 'Sparta', 'Tantsivnytsia' – 2.5 times, which indicates better adaptability of the cultivars to the conditions in which they were studied. Significantly lower levels of Chl *a* / Chl *b* relative to control were recorded in 'Sparta'.

Determination of the net productivity of photosynthesis. One of the most important biological indicators of the photosynthetic apparatus of a plant is the level of net productivity of photosynthesis (Havryliuk & Kondratenko, 2019). The highest level of net productivity of photosynthesis leaves was observed in plants of 'Valuta' (13.9 g/m^2 for a day); 'Bilosnizhka', 'Favoryt', 'Bolero', 'Sparta', 'Tantsivnytsia' and 'Papirovka' have 32–40% lower dry matter accumulation.

Comparing the obtained data with those in the scientific literature that the net photosynthesis productivity of some apple cultivars reaches 10–12 g of dry matter per 1 m^2 of leaf surface per day, and on average during the growing season real NPP does not exceed 40–50% of potential (4–6 g/m^2 for a day), we note that the level of NPP leaves in columnar cultivars is high. 'Bilosnizhka' and 'Favoryt', although they have a large leaf surface and leaves with a thick layer of palisade parenchyma, inefficiently use the biological potential in the process of fruit formation. It should also be noted that the rate of NPP for all columnar cultivars was highest in the leaves, placed on three-four-year spur formation. In 20-year-old 'Bolero' and 'Sparta' trees, the intensity of photosynthesis of leaves, which were located on the oldest part of the trunk, was higher than those on the youngest part, by 8–25%, respectively. However, a significant difference between the age areas of the trunk of the studied cultivars on the level of NPP has not been established.

Based on the results of diagnosing the potential productivity of traditional and columnar apple cultivars using the chlorophyll fluorescence induction index, it was found that in traditional apple cultivars, the intensity of photosynthesis in terms of K_i decreased with the age of spur formation; in columnar varieties, such a decline was not noted. Columnar varieties are distinguished by the stability of the photosynthetic potential on complex spur formation of different ages and the absence of photosynthesis intensity inhibition. The obtained results indicate the potential for a longer period of growing columnar apple trees compared to the traditional cultivars.

According to the results attained, we recommend the methods used in our study. We believe that with further expanded research, new methods of studying plant productivity will allow more accurate control of overall productivity, not only in apple trees, but other plants as well.

Conclusion

To diagnose the potential productivity of cultivars, we used the information indicator of chlorophyll fluorescence induction – induction coefficient (K_i). Decreasing K_i value is caused by suppression of PS II and decreasing proportion of reaction centers in this system that are unable to recover. The K_i of columnar cultivars leaves fluctuated in the range of 0.720–0.740, which indicates a high level of efficiency of photophysical processes near PS II reaction centers.

The highest level of potential productivity in terms of K_i was observed in plants of 'Bilosnizhka'. There was no significant difference in the efficiency of the light phase of photosynthesis in the leaves of the studied cultivars compared to the control ('Bolero'). The viability index of the plants of the columnar cultivars ranged from 1.78 to 2.19. A detailed analysis of the results of this study showed that different age zones of the trunk have different productivity potentials. Thus, according to the fluorescence induction index of chlorophyll (K_i), higher intensity of photosynthesis was observed in the leaves of cultivars 'Valuta', 'Favoryt' and 'Bilosnizhka' on the seven-nine-year-old stem, in 'Tantsivnytsia' – on the 19-year-old stem, ie the oldest spur formation. A comparison of winter columnar cultivars with conditional control ('Idared') revealed a markedly higher chlorophyll fluorescence induction coefficient calculated for fruiting leaves in the older parts of the 'column' trunk (except 'Sparta'). In 'Idared', the higher intensity of photosynthesis is characteristic of the leaves of annual shoots. In general, the intensity of photosynthesis in terms of K_i decreased with the age of spur formation in traditional apple cultivars, and no such decrease was observed in columnar cultivars. It should be noted that the leaves of 19-year-old spur formations of the cultivars 'Bolero', 'Tantsivnytsia', and 'Sparta' retain a high level of photosynthesis.

The highest level of net productivity of photosynthesis of leaves was observed in plants of 'Valuta' (13.9 g/m^2 for day); 'Bilosnizhka', 'Favoryt', 'Bolero', 'Sparta', 'Tantsivnytsia', and 'Papirovka' have 32–40% lower dry matter accumulation.

The authors declare no conflict of interest.

References

Allen, J. F. (1992). Protein phosphorylation in regulation of photosynthesis. Biochimica et Biophysica Acta - Bioenergetics, 1098(3), 275–335.

Blažek, J. (1990). Segregation and general evaluation of spur type or compact growth habits in apples. Fruit Breeding and Genetics, 317, 71–80.

Blažek, J., & Křelinová, J. (2011). Tree growth and some other characteristics of new columnar apple cultivars bred in Holovousy, Czech Republic. Horticultural Science, 38(1), 11–20.

Dau, H. (1994). Molecular mechanisms and quantitative models of variable photosystem II fluorescence. Photochemistry and Photobiology, 60(1), 1–23.

Havryliuk, O. S., & Kondratenko, T. Y. (2020). Strukturno-funktsionalnyi stan lystkiv kolonopodibnykh sortiv yabluni v umovakh Kyivshchyny [The intensity of photosynthesis of leaves of columnar apple-tree in the conditions of Kyiv]. Scientific reports of NULES of Ukraine, 2, 84 (in Ukrainian).

Havryliuk, O. S., Kondratenko, Y., & Kytaiev, O. I. (2019). Diahnostyka funktsional'noho stanu roslyn kolonopodibnykh sortiv yabluni [Diagnosis of the functional state of plants of columnar apple varieties]. Plant and Soil Science, 10(2), 70–80 (in Ukrainian).

Havryliuk, O., & Kondratenko, T. (2019). Specific of the assimilation surface of columnar apple-tree. Agrobiodiversity for Improving Nutrition, Health and Life Quality, (3), 57–65.

Havryliuk, O., Kondratenko, T., Mazur, B., Kutovenko, V., Mazurenko, B., Voitsekhivska, O., & Dmytrenko, Y. (2022a). Morphophysiological peculiarities of productivity formation in columnar apple cultivars. Agronomy Research, 20(1), 148–160.

Havryliuk, O., Kondratenko, T., Mazur, B., Tonkha, O., Andrusyk, Y., Kutovenko, V., Yakovlev, R., Kryvoshapka, V., Trokhymchuk, A., & Dmytrenko, Y. (2022b). Efficiency of productivity potential realization of different-age sites of a trunk of grades of columnar type apple-trees. Agronomy Research, 20(2), 241–260.

Hsu, B. D. (1992). A theoretical study on the fluorescence induction curve of spinach thylakoids in the absence of DCMU. Biochimica et Biophysica Acta - Bioenergetics, 1140(1), 30–36.

Ivanova, I., Serdyuk, M., Malkina, V., Tonkha, O., Tsyz, O., Mazur, B., Shkinder-Barmina, A., Gerasko, T., & Havryliuk, O. (2022). Cultivar features of polyphenolic compounds and ascorbic acid accumulation in the cherry fruits (*Prunus cerasus* L.) in the Southern Steppe of Ukraine. Agronomy Research, 20(3), 588–602.

Jacob, H. B. (2010). Breeding experiments of apple varieties with columnar growth and low chilling requirements. Acta Horticulturae, 872, 159–164.

Kasampalis, D. S., Tsouvaltzis, P., Ntouros, K., Gertsis, A., Gitas, I., & Siomos, A. S. (2021). The use of digital imaging, chlorophyll fluorescence and Vis/NIR spectroscopy in assessing the ripening stage and freshness status of bell pepper fruit. Computers and Electronics in Agriculture, 187, 106265.

Korneev, D., & Kochubej, S. (2000). Izucheniye Q-vosstanavlivayushchikh kompleksov fotosistemy 2 s pomoshchyu induktsii fluorestsentsii khlorofila [Study of QB-reducing complexes of photosystem 2 using the induction of chlorophyll fluorescence]. Fiziologiya i Biokhimiya Kul'turnikh Rastenii, 32(1), 20–24 (in Russian).

Koshelev, V. K., & Ursulenko, P. K. (1977). Opredelenie produktivnosti fotosinteza listev yabloni putem koltsevaniya chereshka [Determination of the productivity of photosynthesis of apple leaves by banding the petiole]. Sbornik Nauchnikh Rabot, Michurinsk, 25, 66–70 (in Russian).

Krause, G. H., & Weis, E. (1991). Chlorophyll fluorescence and photosynthesis: The basics. Annual Review of Plant Biology, 42(1), 313–349.

Kryvoshapka, V., & Kytaev, O. (2019). Fluorestsentnie-spektralnie issledovaniya funktsionalnogo sostoyaniya rastenii v svyazi s ikh ustoichivostyu k zasukhe i visokoi temperature [Fluorescence-spectral investigations of functional state of plants in relation to their resistance to drought and high temperature]. Stiinta Agricola, 2, 31–34 (in Russian).

Kytaiev, O., & Pelekhatyi, V. M. (1981). Liuministsentni spektralni doslidzhennia pidhotovky roslyn yabluni do zymy [Luminescent spectral studies of preparation of apple plants for winter]. Sadivnytstvo, 29, 60–68 (in Ukrainian).

Lazár, D. (1999). Chlorophyll *a* fluorescence induction. Biochimica et Biophysica Acta - Bioenergetics, 1412(1), 1–28.

Litvinova, O., Dehodiuk, S., Litvinov, D., Havryliuk, O., Kyrychenko, A., Borys, N., & Dmytrenko, O. (2023a). Efficiency of technology elements for growing winter wheat on typical chernozem. Agronomy Research, 21(3), 1199–1212.

Litvinova, O., Tonkha, O., Havryliuk, O., Litvinov, D., Symochko, L., Dehodiuk, S., & Zhyla, R. (2023b). Fertilizers and pesticides impact on surface-active substances accumulation in the dark gray podzolic soils. Journal of Ecological Engineering, 24(7), 119–127.

Makarova, D., & Kytaiev, O. (2008). Potentsiina produktyvnist' ta sumisnist' sortiv yabluni na klonovykh pidshchepakh selektsii UAAN [Potential productivity and compatibility of apple cultivars on clonal rootstocks of UAAS selection]. Journal of Lviv National Agrarian University, Agronomy, 12(2), 97–101 (in Ukrainian).

Mamonova, R. Y., Kytaiev, O. I., Shykhalieieva, H. M., Slyusar, S. I., & Kolesnyk, Y. S. (2018). Funktsionalna diahnostyka adaptyvnosti introdukovanykh vydiv rodu snizhnoiahidnyk (*Symphoricarpos* Duhamel) v umovakh Kyieva [Functional diagnostics of adaptability of introduced species of the genus snowberry (*Symphoricarpos* Duhamel) in Kiev city conditions]. Scientific Reports of NULES of Ukraine, 1, 71 (in Ukrainian).

Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence – a practical guide. Journal of Experimental Botany, 51(345), 659–668.

Melis, A. (1991). Dynamics of photosynthetic membrane composition and function. Biochimica et Biophysica Acta - Bioenergetics, 1058(2), 87–106.

Mezhenskyj, V. M. (2008). Groups of ornamental cultivars and forms of species of the genus *Malus* Mill. Scientific Bulletin of the Bila Tserkva National Agrarian University, 54, 98–101 (in Ukrainian).

Okada, K., Wada, M., Takebayashi, Y., Kojima, M., Sakakibara, H., Nakayasu, M., Mizutani, M., Nakajima, M., Moriya, S., Shimizu, T., & Abe, K. (2020). Columnar growth phenotype in apple results from gibberellin deficiency by ectopic expression of a dioxygenase gene. Tree Physiology, 40(9), 1205–1216.

Pavlichenko, A., Dmytrenko, O., Litvinova, O., Kovalova, S., Litvinov, D., & Havryliuk, O. (2023). Changes in gray forest soil organic matter pools under anthropogenic load in agrocenoses. Agronomy Research, 21(3), 1266–1277.

Pochinok, H. N. (1976). Metody biokhimicheskogo analiza rasteniy [Methods of biochemical analysis of plants]. Naukova Dumka, Kyiv (in Ukrainian).

Ptushenkom, V. V., Karavaev, V. A., Solntsev, M. K., & Tikhonov, A. N. (2013). Biophysical methods of ecological monitoring. photosynthetic characteristics of tree plants growing in Moscow city. Biophysics, 58, 228–233.

Roháček, K., & Barták, M. (1999). Technique of the modulated chlorophyll fluorescence: Basic concepts, useful parameters, and some applications. Photosynthetica, 36(13), 339.

Schreiber, U., Bilger, W., & Neubauer, C. (1995). Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment of in vivo photosynthesis. In: Schulze, E. D., & Caldwell, M. M. (Eds.). Ecophysiology of photosynthesis. Springer Study Edition. Vol. 100. Springer, Berlin, Heidelberg.

Shikhov, V. N., Velichko, V. V., Nesterenko, T. V., & Tikhomirov, A. A. (2011). Ontogenetic approach to assessment of chufa response to culture conditions by the method of chlorophyll fluorescence induction. Russ Journal of Plant Physiology, 58, 359–363.

Sovakova, M., Sovakov, O., & Kytaiev, O. (2014). Ecological tolerance of linden species (*Tilia* L.) by photo- and thermo-induced changes in chlorophyll fluorescence of leaves. Ukrainian Journal of Forest and Wood Science, 1982, 285–293.

Sun, X., Wen, C., Hou, H., Huo, H., Zhu, J., Dai, H., & Zhang, Y. (2020). Genes involved in strigolactone biosyntheses and their expression analyses in columnar apple and standard apple. Biologia Plantarum, 64, 68–76.

Sun, X., Wen, C., Zhu, J., Dai, H., & Zhang, Y. (2021). Apple columnar gene *MdDMR6* increases the salt stress tolerance in transgenic tobacco seedling and apple calli. Journal of Plant Growth Regulation, 40(1), 187–196.

Tanaka, A., Ito, H., Tanaka, R., Tanaka, N. K., Yoshida, K., & Okada, K. (1998). Chlorophyll *a* oxygenase (CAO) is involved in chlorophyll *b* formation from chlorophyll *a*. Proceedings of the National Academy of Sciences, 95(21), 12719–12723.

Tobutt, K. R. (1984). Breeding columnar apples varieties at East Malling. Scientific Horticulture, 35, 72–77.

Tobutt, K. R. (1994). Combining apetalous parthenocarpy with columnar growth habit in apple. Euphytica, 77, 51–54.

Trokhymchuk, A. I., & Makarova, D. H. (2012). Physiological drought resistance of promising apple cultivars (*Malus domestica* Borkh.) in the right-bank subzone of the Western Forest-Steppe of Ukraine. Horticulture, (66), 230–234.

Vasylenko, O., Kondratenko, T., Havryliuk, O., Andrusyk, Y., Kutovenko, V., Dmytrenko, Y., Grevtseva, N., & Marchyshyna, Y. (2021). The study of the productivity potential of grape cultivars according to the indicators of functional activity of leaves. Potravinarstvo, 15, 639–647.

Voitovyk, M., Butenko, A., Prymak, I., Mishchenko, Y., Tkachenko, M., Tsiuk, O., Panchenko, O., Slieptsov, Y., Kopylova, T., & Havryliuk, O. (2023). Influence of fertilizing and tillage systems on humus content of typical chernozem. Agraarteadus 34(1), 44–50.

Wada, M., Iwanami, H., Moriya, S., Hanada, T., Moriya-Tanaka, Y., Honda, C., Taku, S., Kazuyuki, A., & Okada, K. (2018). A root-localized gene in normal apples is ectopically expressed in aerial parts of columnar apples. Plant Growth Regulation, 85(3), 389–398.