

Original Research Paper

Modeling Winter Hardiness Formation in Winter Wheat Plants

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Abstract: A dynamic model, which describes the growth processes, plant development and the passing of the two phases of the autumn hardening under the influence of agrometeorological conditions in autumn, was developed. The model illustrates effects of intensity of Photosynthetically Active Radiation (PAR), sunlight levels, air temperature and soil moisture on the increment of reserves of photosynthesis products and soluble carbohydrates in winter wheat plants. The results of numerical experiments showed a significant influence of intensity of sunlight levels and air temperature on the passing of two phases of hardening during autumnal period of vegetation of winter wheat plants.

Keywords: Winter Wheat, Photosynthesis, Respiration, Soluble Carbohydrates, Biomass, Cold Hardening, Winter Hardiness, Mathematical Model

Introduction

A steady increasing demand for food products in a global scale leads to necessary intensifying the crop production. In conditions that exacerbates by global climate change, the usage of mathematical modeling is an effective tool for solving issues of optimizing the system of land use. At the same time, the range and scale of the simulated processes is extremely huge. It can vary from global ecology to prognostication of the dynamics of each component of agroecosystems (Stepanenko *et al.*, 2011).

There are several problems in using dynamic models for crop phenology prediction. Firstly, most existing models do not sufficiently imitate the physiological processes underlying the plant phenology. Secondly, the models focus on the varieties and agrometeorological conditions of the particular region and cannot provide satisfactory results when applying the same models to new territories (Zalud *et al.*, 2003). Unfortunately, most of the available models have not found practical use because of the difficulties to obtain the parameters of physiological processes that are used for modelling.

Over the past 20 years, more than 70 models for winter wheat crops has been developed, that simulate changes in crop productivity in response to environmental factors (Hunt and Pararajasingham, 1995; Porter and Semenov, 2005; Ritchie *et al.*, 1985).

However, there are less than 20 models that focus on modeling physiological processes in a plant organism (Leonardis *et al.*, 2003; Martin and Seginer, 2012).

One of the main processes that set conditions to the future harvest of winter wheat is the hardening of the plants to unfavorable winter conditions. Despite significant achievements in winter frost resistance studies, only a few models devoted to genetic and environmental factors that affect wintering of plants. (Antonenko, 2002; Bergjord *et al.*, 2008; Lecomte *et al.*, 2003; Fowler *et al.*, 1999; Ritchie *et al.*, 1985). Furthermore, models that associated with the very high complexity of physiological processes in the plant organism and/or a set of environmental factors involved into the process of plants ability to acclimatize to low temperatures (Andrews *et al.*, 1986; Gusta and Fowler, 1977).

In the 1980s, the realization of genetic potential was at the level of 50% of the potential yield of winter wheat. Over the last decade, the level of realization of its genetic potential in production conditions ranges from 25 to 35% (MENRU, 2013). One of the reasons for this situation is a significant increase in the level of potential productivity of modern varieties against the background of the lack of increase in the level of resistance of winter wheat plants to unfavorable winter conditions.

Assessment of winter crops during winter and forecasting the potential of plants to withstand the unfavorable agrometeorological factors in winter is an

important part of economic planning in the agricultural sector. In Ukraine, about 1.5 million hectares of winter crops have recently been reseeded due to unfavorable wintering conditions (Netis, 2011).

The aim of the study is to consider approaches and methods for modeling winter hardiness formation in winter wheat plants as well as the structure of developed model and the results of numerical experiments described.

Materials and methods

The study involved five varieties of soft winter wheat, which vary in frost and winter hardiness levels: Odessa 16, Odessa 267, Albatros Odesskiy, Antonivka and Strumok.

Seeds were sown in the fields of the Odessa Plant Breeding and Genetics Institute – National Center of Seed and Cultivar Investigation on September 25 and October 2, 2013. In each treatment, there were three repetitions. The area of the sown plot is 2 m². A Dunaevsky seeder, which based on a T-16 tractor, was used for sowing. During the growing season, the plants were nourished with nitroamophos at recommended doses of N40P40K40 (Netis, 2011).

After the appearance of the first leaf, samples of 50 plants of each winter wheat variety were selected once a day to determine the soluble sugars content in the over ground parts of plants and tillering nodes, the water content of plant tissues, the presence of free and bound water. Sugar content was determined by anthron method (Dolgopolova *et al.*, 2015). Determination of total water content and the presence of bound and free water was

carried out by the gravimetric method (Ermakov *et al.*, 1972). The article presents average results research on five varieties of winter wheat of the first term of sowing.

Description of the Model of Winter Hardiness Formation of Winter Wheat Plants

The concept of modeling of winter hardiness formation by winter wheat plants is based on the existing concept of two hardening stages of winter crops under agrometeorological conditions of the autumn period that influence.

The first stage occurs under conditions of high level of sunlight, while the air temperature decreases appreciably at night. The second stage takes place at air temperatures -2...-5°C.

Thus, the model describes following physiological and biochemical processes caused by the genotype and occurring in the plant under the influence of agrometeorological conditions:

- i. Processes of photosynthesis, respiration, growth and development of plants
- ii. Formation of overground and underground parts of plants
- iii. Formation of tillering shoots
- iv. Photosynthesis reserves formed and the sugars accumulated in the overground parts and tillering nodes
- v. The amount of free and bound water in plant cells.

The block diagram of the model is shown in Fig. 1

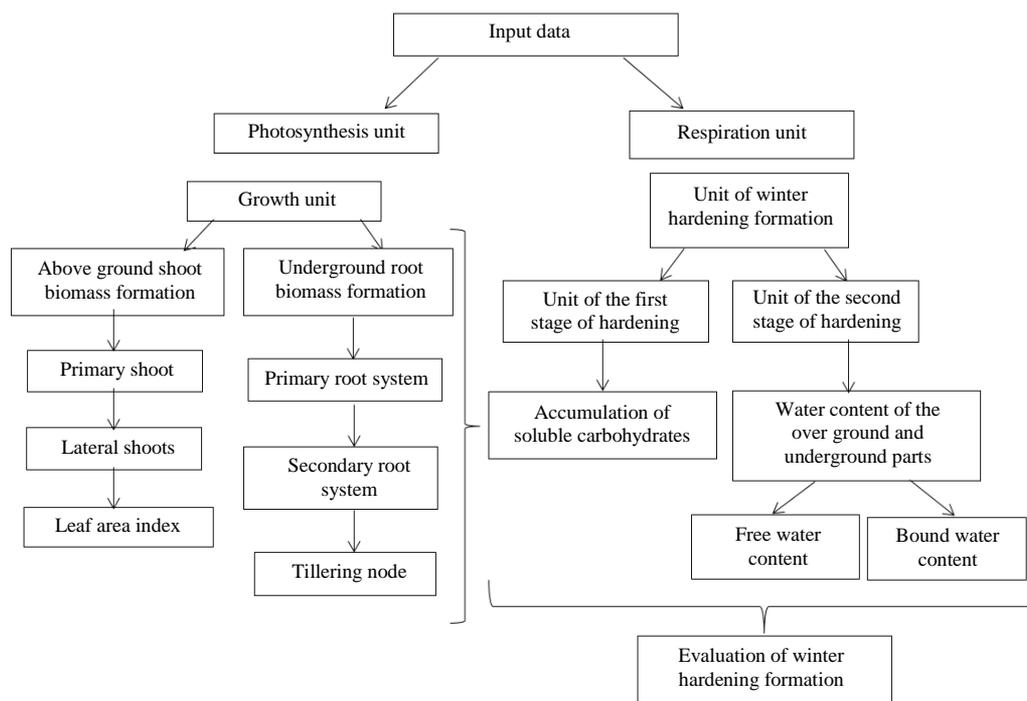


Fig. 1: The block diagram of the dynamic model of the winter hardiness formation by winter wheat plants during autumn-winter period

At the first stage, the model describes the processes of photosynthesis and respiration during the transitional stage of winter wheat plants to independent autotrophic nutrition after germination. Next, the formation of the overground and underground parts of plants is illustrated. When the average daily air temperature passes over +5°C downwards, the processes of soluble carbohydrates accumulation in the leaves and tillering nodes of winter wheat plants are described. The bound and free water content in plant cells is modeled when the average daily air temperature passes through 0°C. The hardening level is estimated by the number of accumulated sugars in tillering nodes and leaves and the ratio of bound and free water. Primarily, simulation of winter wheat autumn vegetation includes a quantitative description of the processes of photosynthesis, respiration and growth.

Photosynthesis is the main process of formation of organic substances in plant cells. The process of photosynthesis is described by a semi-empirical equation. In this equation in addition to such environmental factors as photosynthetically active radiation and CO₂ concentration in the atmosphere also takes into consideration the influence of the level of mineral nutrition, the phase of plant development, temperature regime and moisture supply of plants (Polevoy, 2013):

$$P = \frac{1}{1/P_{pot}K_p(N_{str}^L) + 1/(a_c C_0) + 1/(a_p PAR)} \min \left\{ a_p, \psi_p, \frac{ET}{ET_{pot}} \right\} \quad (1)$$

Where:

- P_{pot} = The intensity of potential photosynthesis (mg CO₂*dm⁻²*h⁻¹)
- a_c = The photosynthesis 'light response curve' (relative units)
- C_0 = Concentration of CO in the atmosphere
- a_p = Slope of the photosynthesis 'light response curve' (mg CO₂*dm⁻²*h⁻¹/(W*m⁻²))
- PAR = Absorbed PAR by vegetation (W*m⁻²)
- a_p = Ontogenetic curve of photosynthesis (relative units)
- ψ_p = Temperature response of photosynthesis (relative units)
- $K_p(N_{str}^L)$ = Mineral supply ratio of plants (relative units)
- ET = Evapotranspiration (mm*dm⁻¹)
- EP_{pot} = Evaporation (mm*dm⁻¹)

Part of the carbon that is assimilated during photosynthesis spends on plant respiration. This process includes respiration for growth and respiration for supporting structures. The changes in respiration intensity in ontogenesis and the influence of air temperature are taking into consideration (Polevoy, 2012):

$$\frac{dR}{dt} = \alpha_R \left[C_G \frac{dm}{dt} + C_m m \varphi_R \right] \quad (2)$$

Where:

- α_R = The ontogenetic curve of respiration (relative units)
- C_G = A coefficient of expenditure on respiration for growth (relative units)
- C_m = A coefficient of expenditure on maintenance respiration (g of dry matter*g⁻¹*day⁻¹)
- m = A mass of plants (g/m²)
- φ_R = The temperature curve of respiration (relative units)

After the first green leaf appeared, the second and third embryonic leaves develop. The growth of the first and second pairs of germinal roots continues, coleoptile roots appear, i.e., the primary root system forms under conditions of enough moisture level. Simultaneously, a part of the stem of the former embryonic shoot transforms into the tillering node of the main (maternal) shoot. The phase of a sprout formation and tillering of the main shoot of winter wheat begins when the first lateral shoot appears above the soil surface. The process of shoot formation and tillering occurs almost coextensive. Side shoots of the first-order form shoots of the second one and shoots of the second-order form shoots of the third, etc. The beginning of the tillering phase occurs when secondary (nodal) root develop from the tillering nodes first of the main and then lateral shoots (Orlyuk and Goncharova, 2002).

A certain sum of effective air temperatures and total solar radiation is necessary for each successive lateral tillering shoot to appear. Therefore, the equation for the rate of formation of lateral tillers is next:

$$\frac{dN_{ts}}{dt} = \left\{ \begin{array}{l} \frac{2.3b_{ts} (10^{a_{ts}-b_{ts}/T}) \times N_{ts}^{\max}}{(1+10^{a_{ts}-b_{ts}/T})^2} \\ \min \{ k_{ts}(Q), k_{ts}(\sum T_{ef}) \} \text{ if } W_{0-20} > W_{0-20}^{crit} \\ 0, \text{ if } W_{0-20} \leq W_{0-20}^{crit}, \sum T_{ef} \leq \sum T_{ef}^{til} \end{array} \right\} \quad (3)$$

Where:

- $\frac{dN_{ts}}{dt}$ = Rate of lateral tillering shoots formation (g/m²*day)
- N_{ts}^{\max} = A maximum possible number of tillering shoots under specified conditions (piece/plant)
- $k_{ts}(Q)$ = A function of availability of required amount of solar radiation (relative units)
- $k_{ts}(\sum T_{ef})$ = A function of availability of required amount of warmth (relative units)
- W_{0-20}^{crit} = A critical moisture content in the arable soil layer at which tillering does not occur (mm)
- T_{ef}^{til} = A necessary sum of effective temperatures for the beginning of tillering process (°C)
- a_{ts}, b_{ts} = Parameters

The next equation determines the possible largest amount of shoots under specified conditions, which assimilates will provide:

$$N_{ts}^{\max} = \frac{dm_{ts}^{res} / dt}{G_{ts}^{\max}} \quad (4)$$

Where:

N_{ts}^{\max} = The maximum possible number of shoots under specified conditions (piece/plant)

dm_{ts}^{res} = A reserve of assimilates, remaining after supplying the main shoot ($g/m^2 \cdot day$)

The reserve of assimilates is determined as the difference between the number of assimilates that moves to the over ground shoot system and the number of assimilates moves to the main shoot:

$$\frac{dm_{ts}^{res}}{dt} = \frac{dm_{ov.gr}}{dt} - \frac{dm_{m.sh}}{dt} \quad (5)$$

Where:

$\frac{dm_{ov.gr}}{dt}$ = The biomass increment of the over ground shoot system ($g/m^2 \cdot day$)

$\frac{dm_{m.sh}}{dt}$ = The biomass increment of the main shoot ($g/m^2 \cdot day$)

G_{ts}^{\max} = The largest possible biomass increment of lateral shoots under specified conditions, defined as:

$$G_{ts}^{\max} = (m_{ts} \times G_{ts}^{abs}) \min \{k_{ts}(T_{air}), k_{ts}(W)\} \quad (6)$$

Where:

m_{ts} = A biomass of lateral shoots ($g/m^2 \cdot day$)

G_{ts}^{abs} = Absolute relative biomass increment of lateral shoots ($g/m^2 \cdot day$)

$k_{ts}(T_{air})$ = The function of the influence of the air temperature on the growth of lateral shoots

$k_{ts}(W)$ = The function of the influence of the soil moisture on the growth of lateral shoots

The dynamics of the biomass of the overground shoot system and underground root system of winter wheat plants are described by equations (Antonenko, 2002):

$$\frac{dm_{ov.gr}}{dt} = \left(\frac{dP}{dt} - \frac{dR}{dt} \right) \times \gamma_{ov.gr} \quad (7)$$

$$\frac{dm_{und.gr}}{dt} = \left(\frac{dP}{dt} - \frac{dR}{dt} \right) \times (1 - \gamma_{ov.gr}) \quad (8)$$

Where:

$\frac{dm_{ov.gr}}{dt}, \frac{dm_{und.gr}}{dt}$ = The biomass increment of the over ground shoot system and underground root system, respectively ($g/m^2 \cdot day$)

$\gamma_{ov.gr}$ = A growth function of the over ground shoot system of plants

The increment in the overground mass distributes initially to the main shoot, then to lateral shoots of the 1st, 2nd and next orders:

$$\frac{dm_{m.sh}}{dt} = \gamma_{m.sh} \times \frac{dm_{ov.gr}}{dt} \quad (9)$$

$$\frac{dm_{ts1}}{dt} = \gamma_{ts1} \times \left(\frac{dm_{ov.gr}}{dt} - \frac{dm_{m.sh}}{dt} \right) \quad (10)$$

$$\frac{dm_{tsn}}{dt} = \gamma_{tsn} \times \left(\frac{dm_{ov.gr}}{dt} - \frac{dm_{m.sh}}{dt} - \sum_i^n \frac{dm_{tsi}}{dt} \right) \quad (11)$$

Where:

$\frac{dm_{m.sh}}{dt}, \frac{dm_{ts1}}{dt}, \frac{dm_{tsn}}{dt}$ = An increment of biomass of lateral shoots of the 1st, i -th, n -th orders ($g/m^2 \cdot day$)

$\gamma_{m.sh}, \gamma_{ts1}, \gamma_{tsn}$ = Distribution functions of assimilates for the main and lateral shoots

The area of the assimilating surface is described by an equation:

$$L^{j+1} = L^j + \frac{\Delta m_i^j}{\sigma} \quad (12)$$

Where:

L^{j+1} = The relative leaf area index (m^2/m^2)

Δm_i^j = An increment of the dry biomass of leaves ($g/m^2 \cdot day$)

σ = A specific canopy leaf area density (g/m^2)

The flow of essential nutrients to the underground root system of plants goes to form the primary, secondary root system and the tillering node:

$$\frac{dm_{r1}}{dt} = \gamma_{r1} \times \frac{dm_{und.gr}}{dt} \quad (13)$$

$$\frac{dm_{r2}}{dt} = \gamma_{r2} \times \frac{dm_{und.gr}}{dt} \quad (14)$$

$$\frac{dm_m}{dt} = \gamma_m \times \frac{dm_{und.gr}}{dt} \quad (15)$$

Where:

$\frac{dm_{r1}}{dt}, \frac{dm_{r2}}{dt}, \frac{dm_m}{dt}$ = The biomass increment of the primary and secondary root system and the tillering node, respectively ($\text{g/m}^2 \cdot \text{day}$)
 $\gamma_{r1}, \gamma_{r2}, \gamma_m$ = Growth functions of the primary and secondary root system and tillering node, respectively.

During the second half of autumn, decreasing in the average daily air temperature causes inhibition of growth processes. Because of lack of warmth, plants grow poorly and the excess of photosynthetic products, which is not used for growth processes, leads to carbohydrates formation in the overground shoot system and tillering nodes. These photosynthetic products play a protective role and ensuring that plants preparing for wintering, i.e., the process of plant hardening.

The change in the mechanism of distribution of assimilates between the continued slow growth of plant organs and assimilates reserve formation that is turning into sugars is simulated after a stable transition of air temperature through $+5^\circ\text{C}$. The number of products of photosynthesis is compared with the largest possible increment in the overground shoot biomass and underground root biomass of plants, which are defined similarly to Equation 6. The increment in the mass of the overground shoot biomass and underground root biomass of plants is determined as:

$$\frac{dm_{ov.gr}}{dt} = \left\{ \begin{array}{l} G_{ov.gr}^{max} \text{ if } \frac{dP}{dt} > G_{ov.gr}^{max} + G_{und.gr}^{max} \\ \left(\frac{G_{ov.gr}^{max}}{G_{ov.gr}^{max} + G_{und.gr}^{max}} \times \frac{dP}{dt} - \frac{dR_{ov.gr}}{dt} \right) \text{ if } \frac{dP}{dt} < G_{ov.gr}^{max} + G_{und.gr}^{max} \end{array} \right\} \quad (16)$$

$$\frac{dm_{und.gr}}{dt} = \left\{ \begin{array}{l} G_{und.gr}^{max} \text{ if } \frac{dP}{dt} > G_{ov.gr}^{max} + G_{und.gr}^{max} \\ \left(\frac{G_{und.gr}^{max}}{G_{ov.gr}^{max} + G_{und.gr}^{max}} \times \frac{dP}{dt} - \frac{dR_{ov.gr}}{dt} \right) \text{ if } \frac{dP}{dt} < G_{ov.gr}^{max} + G_{und.gr}^{max} \end{array} \right\} \quad (17)$$

The excess of photosynthesis products is defined as the difference:

$$\frac{dm_{res}}{dt} = \frac{dP}{dt} - (G_{ov.gr}^{max} + G_{und.gr}^{max}) \quad (18)$$

where, $\frac{dm_{res}}{dt}$ is the reserve of photosynthesis products, formed after meeting the needs of the underground and over ground parts of plants in assimilates ($\text{g/m}^2 \cdot \text{day}$)

The concentration of the reserve products of photosynthesis is defined as the ratio:

$$mc_{res} = \frac{m_{res}}{M} \quad (19)$$

Where:

mc_{res} = The concentration of excess photosynthetic products in plants ($\text{mg/g} \cdot \text{day}$)
 M = The mass of the plant ($\text{g/m}^2 \cdot \text{day}$)

The process of formation of soluble carbohydrates in the overground shoot system and tillering nodes is determined by the Michaelis–Menten kinetics equations type:

$$\frac{dCS_{ov.gr}^{pot}}{dt} = \frac{\frac{dCS_{ov.gr}^{pot}}{dt} \times mc_{res} \times K_{ov.gr}^{M-M}}{\frac{dCS_{ov.gr}^{pot}}{dt} + (mc_{res} \times K_{ov.gr}^{M-M})} \quad (20)$$

$$\frac{dCS_m^{pot}}{dt} = \frac{\frac{dCS_m^{pot}}{dt} \times mc_{res} \times K_m^{M-M}}{\frac{dCS_m^{pot}}{dt} + (mc_{res} \times K_m^{M-M})} \quad (21)$$

Where:

$\frac{dCS_{ov.gr}^{pot}}{dt}, \frac{dCS_m^{pot}}{dt}$ = The rates of formation of sugars in the over ground shoot system and the tillering node, respectively (mg/day)

$\frac{dCS_{ov.gr}^{pot}}{dt}, \frac{dCS_m^{pot}}{dt}$ = The potential rates of sugars formation in the over ground shoot system and the tillering node, respectively (mg/day)

$K_{ov.gr}^{M-M}, K_m^{M-M}$ = Michaelis-Menten constants for the over ground shoot system and the tillering node, respectively (mg/g)

Plant tissue dehydration and the transition from free to bound water occur at the second hardening stage. The different physiological value determines the feature difference between free and bound water. The free water content determines physiological processes intensity and the bound water content determines how plants resist to unfavorable environmental conditions.

The increased content of free water in plant cells leads to an increase in the processes of growth, metabolism and respiration and thereby contributes to an increase in plant productivity under ideal conditions of existence.

However, under unfavorable conditions, plants that have an increased content of bound water have an advantage that contributing to the preservation of a larger amount of non-freezing water at temperatures below zero, which is one of the factors that increase cold resistance of plants (McMaster and Wilhelm, 2003).

The water content of the underground part of plants is calculated as:

$$W_{w.c.und.gr} = (0.89 - 0.038 \times k_{w.c}(\Sigma T_{ef}) + 65) \times k_{w.c}(W) \quad (22)$$

where, $k_{w.c}(\Sigma T_{ef})$, $k_{w.c}(W)$ are functions of the influence of warmth and moisture.

The amount of bound water in the underground part of plants is determined by the equation:

$$S_{b.w.und.gr} = S_{b.w.und.gr} \times k_{b.w}(T_{air}) \quad (23)$$

where, $k_{b.w}(T_{air})$ is the functions of the influence of air temperature.

The amount of free water in the underground part of plants described as:

$$S_{f.w.und.gr} = W_{w.c.und.gr} - S_{b.w.und.gr} \quad (24)$$

Identification of the parameters was carried out based on laboratory-field experimental studies, materials of mass agrometeorological observations on winter wheat culture, agrometeorological features of its cultivation and literature review.

Results and Discussion

The model has a daily time step. Maximum, average and minimum air temperature, daily intake of solar radiation, reserves of productive moisture in the soil layer of 0-20 cm and the amount of precipitation is used as an input meteorological information in the model.

Verification of the adequacy of the model was carried out by comparing the modeling results with the

obtained results of laboratory-field experimental studies on the following indicators: Dynamics of accumulation of overground biomass, dynamics of the soluble carbohydrates content in the overground part and tillering nodes, the free and bound water content in the tillering nodes. Based on the model and real values obtained, the average calculation error defines as:

$$\text{AverageError} = \left[\frac{(\text{simulatedvalue} - \text{actualvalue})}{\text{actualvalue}} \right] * 100\%$$

To test the adequacy of the model as the initial values of dry biomass of the overground parts of winter wheat plants, the first experimental value of this measure was taken. The value of dry biomass of the overground part of winter wheat plants was 0.138 g of dry matter. Comparison of the values of the overground part of plant biomass calculated with the model with the real data showed good agreement of dynamics and absolute values of biomass (Fig. 2).

The initial model value of the sugar content in the overground parts of plants is 12% (Fig. 3) and for tillering nodes is 16% dry matter mass (Fig. 4).

The calculated value of the dynamics of soluble carbohydrate content in the overground part of plants and tillering nodes agrees well with the data of the field experiment.

The first model value of the free and bound water content in the tillering nodes of plants is 87% and 2.6% from dry matter mass, respectively. Comparison of the calculated free water and bound water content in the tillering nodes with the real data showed good alignment of the dynamics and absolute values (Figs. 5 and 6).

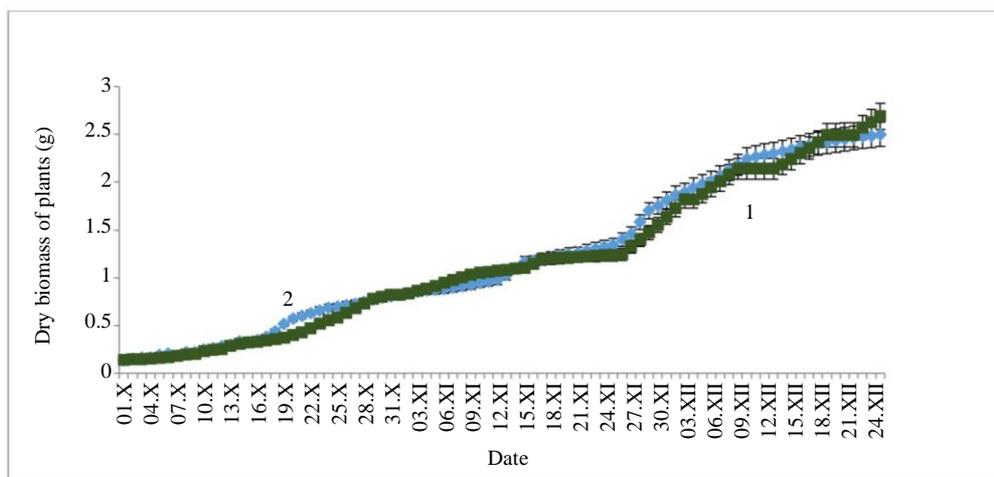


Fig. 2: Modeled (1) and observed (2) dynamics of the overground dry biomass of winter wheat plants parts, ($P < 0.05$)

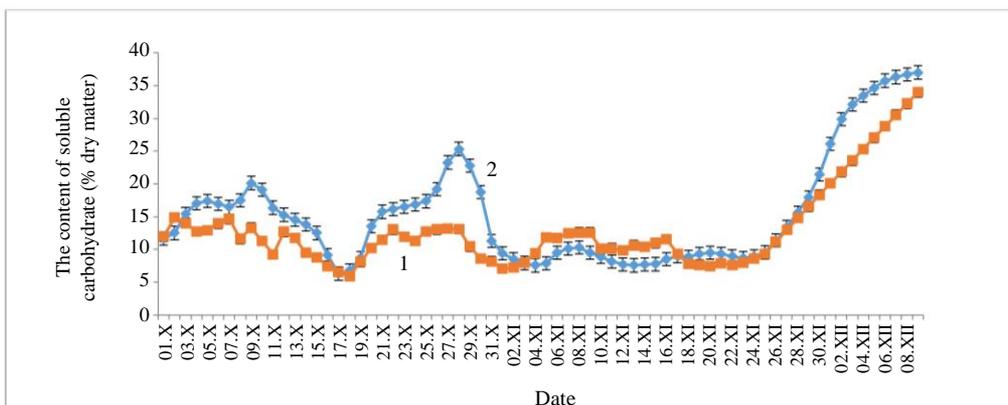


Fig. 3: Modeled (1) and observed (2) dynamics of soluble carbohydrate content in the overground part of winter wheat plants, ($P < 0.05$)

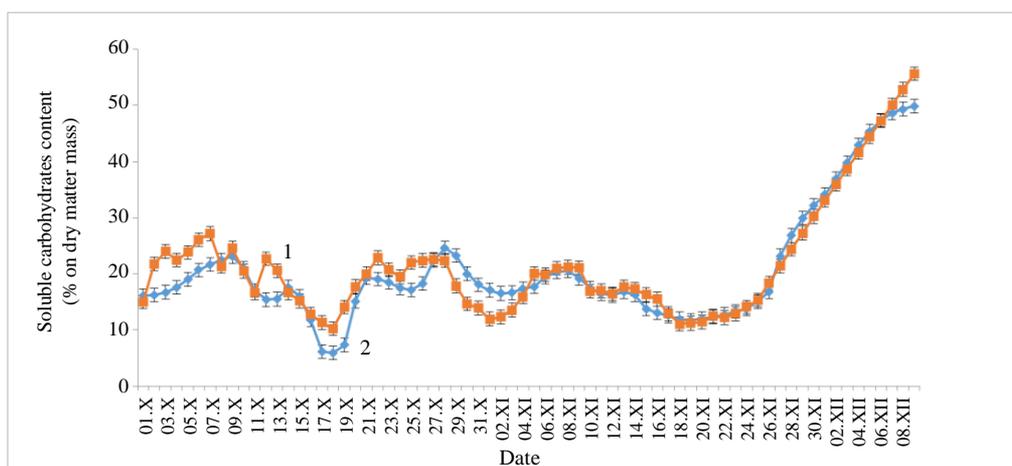


Fig. 4: Modeled (1) and observed (2) dynamics of the soluble carbohydrates content in the tillering nodes of winter wheat plants, ($P < 0.05$)

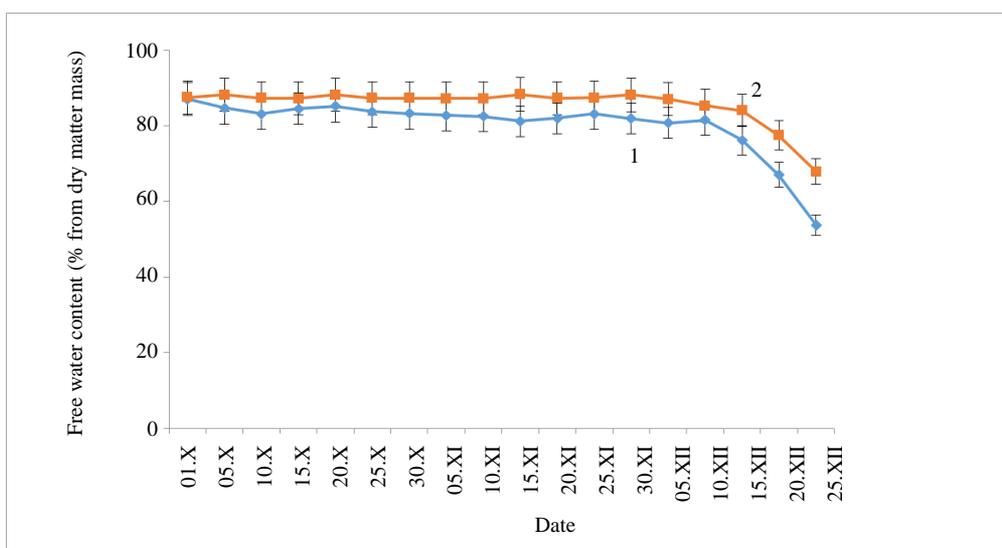


Fig. 5: Modeled (1) and observed (2) dynamics of free water content in the tillering nodes of winter wheat plants

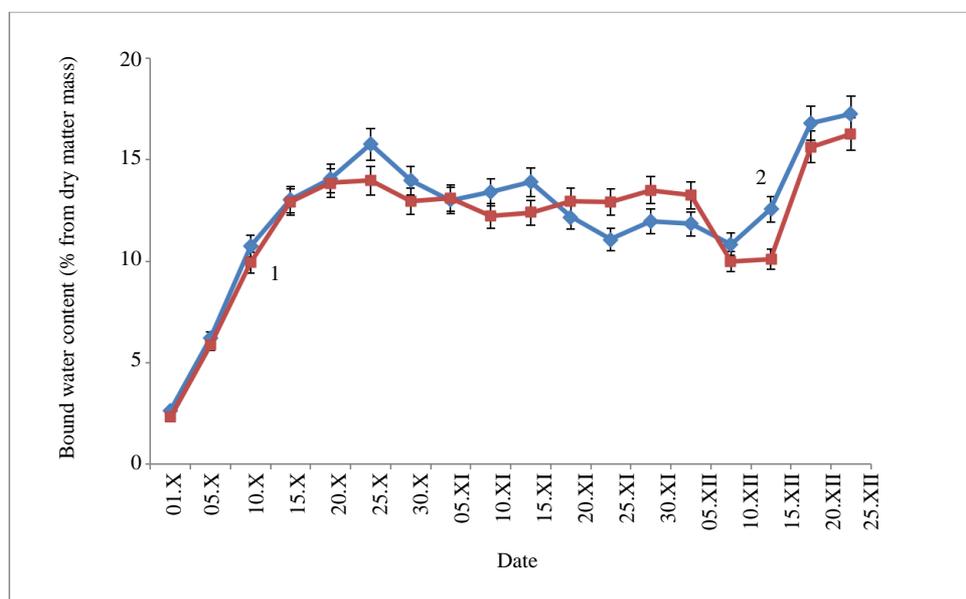


Fig. 6: Modeled (1) and observed (2) dynamics of bound water content in the tillering nodes of winter wheat plants

The model adequacy estimation showed that the average error of model values calculation is 8% for the dynamics of dry biomass accumulation in the overground part of winter wheat plants during the first sowing period. The average error of model values calculation in sugar accumulation in the overground part of plants and tillering nodes is 22% and 15%, respectively. The average error of calculated model values of free water and bound water content in the tillering nodes is 10% and 14%, respectively. The obtained results are acceptable for using the model in application calculations.

The model that adequately describes winter hardiness formation made it possible to conduct a series of numerical experiments to assess agrometeorological conditions that affect photosynthesis products reserves formation, soluble carbohydrates increment in the first hardening stage and the dynamics of free and bound water in plant cells in the second hardening stage.

The greatest increase in reserves of photosynthesis products is observed at $PAR = 0.9 \text{ cal/cm}^2 \cdot \text{min}$ and air temperature 15°C , the least increment is at $PAR = 0.1 \text{ cal/cm}^2 \cdot \text{min}$ and air temperature 5°C , while the increase in photosynthesis products reserves halved from 0.5 to 0.28 mg/day (Fig. 7).

If the moisture reserves in the 0-20 cm layer are close to the least moisture-holding capacity and an increase in PAR intensity up to $0.9 \text{ cal/cm}^2 \cdot \text{min}$, the increment in reserves of photosynthesis products increases to 0.5 mg per day. The increment in reserves of photosynthesis products decreases threefold and equal 0.15 mg per day if there is a gradual decrease in

soil moisture up to 0.3 relative units from the least moisture-holding capacity (Fig.8).

Further, in the course of a numerical experiment, the effect of the light intensity and air temperature on the growth dynamics of soluble carbohydrates in tillering nodes of winter wheat plants were studied. When the air temperature is above $+5^\circ\text{C}$ and in fair weather, there is the greatest increment in soluble carbohydrates from 3 to 5 mg per day in the tillering nodes of the plants. When the weather is cloudy or overcast, the increment in soluble carbohydrates is significantly reduced up to 2 mg per day in the tillering nodes (Fig. 9).

As mentioned before, in the second half of autumn the course of air temperature decreasing, especially at night, leads to inhibition of growth processes and those products of photosynthesis that are not used for overground and underground biomass increment go to soluble carbohydrates formation in plant tissues. With an increase in the amplitude of air temperature, an increase in the soluble carbohydrates in the plant tissues are observed. If an air temperature amplitude is 3°C , the increase in soluble carbohydrates is 0.7-1.25 mg per day in tillering nodes. If an increase in the amplitude of air temperature is 15°C , the increase in carbohydrates is up to 3-5 mg per day in the tillering nodes of plants (Fig. 10).

The results obtained are consistent with the data (Antonenko, 2002), according to which, the soluble carbohydrates accumulation in the autumn can occur at variable air temperatures, especially on sunny days, when in the daytime the air temperature rises to $+10\dots+15^\circ\text{C}$ and at night can fall to 0°C .

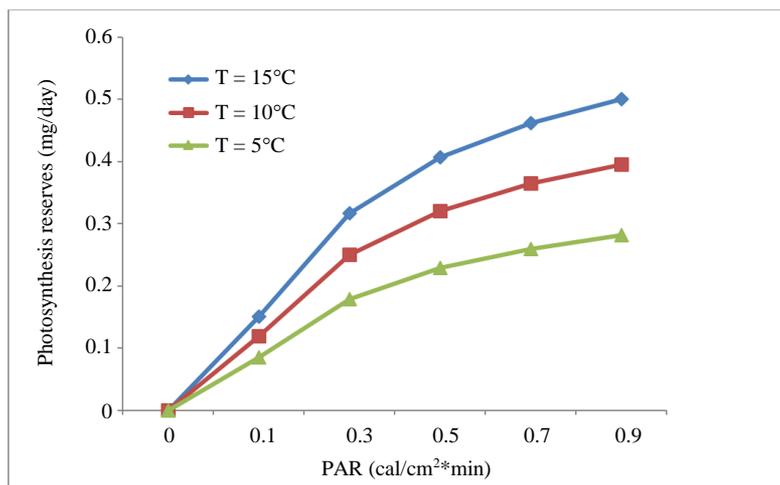


Fig. 7: The photosynthesis reserves of winter wheat plants increment response depending on the PAR intensity at different air temperatures

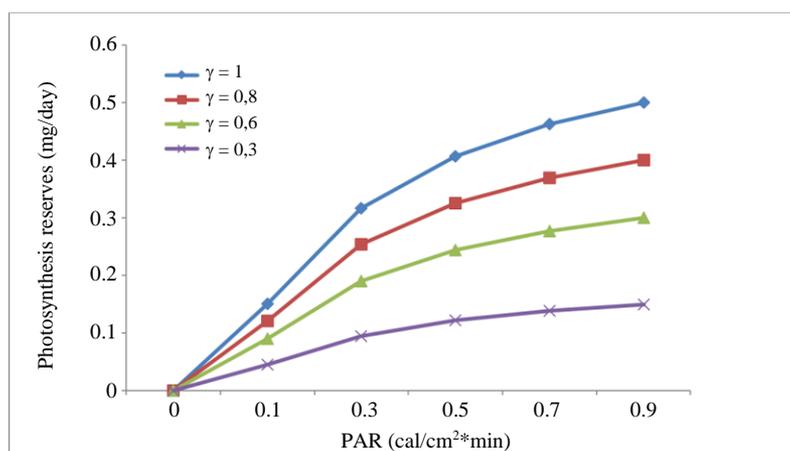


Fig. 8: The photosynthesis reserves increment response depending on the soil moisture level

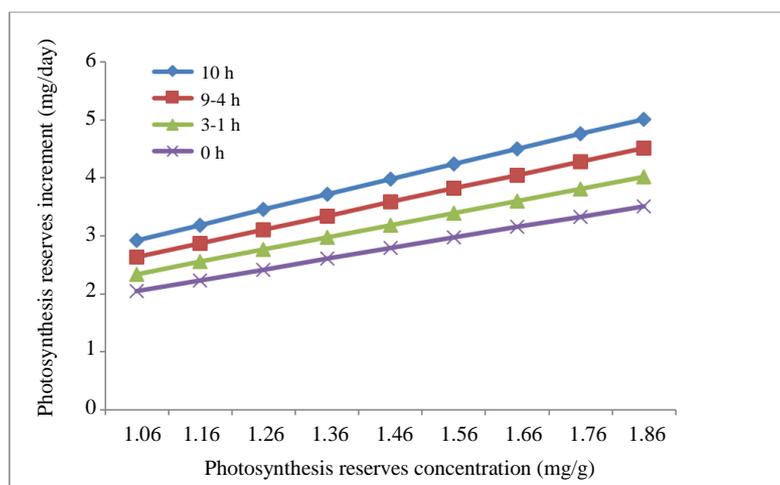


Fig. 9: The photosynthesis reserves increment response depending on the duration of the sunshine, at $T_{\text{average}} = +5^{\circ}\text{C}$ in the tillering nodes of winter wheat plants

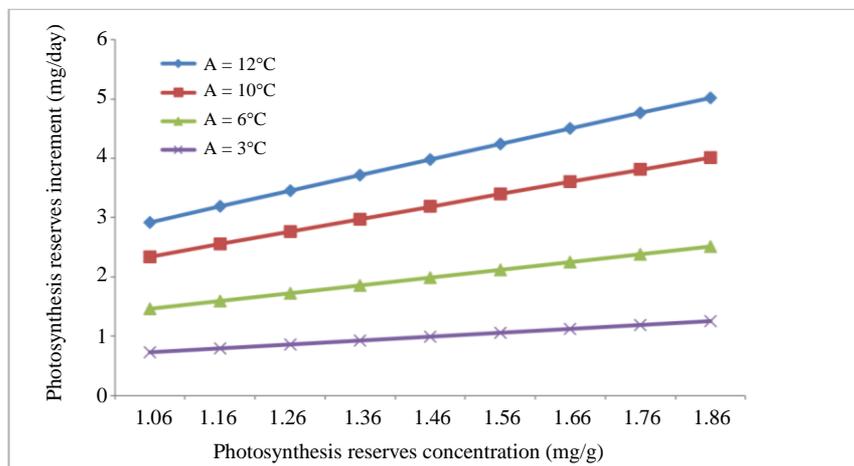


Fig. 10: The photosynthesis reserves increment response depending on the air temperature amplitude

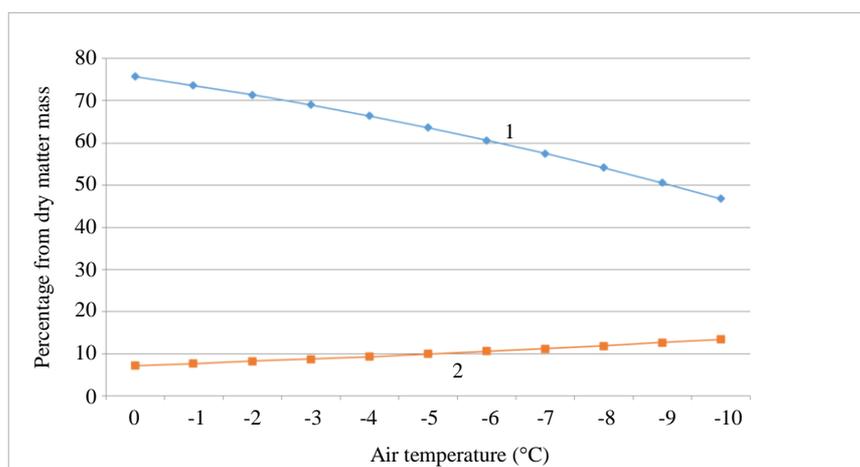


Fig. 11: Dynamics of free (1) and bound (2) water content in plant tissues at air temperatures below 0°C

During the second hardening stage, there is a close connection between the amount of bound and free water in plant cells and the air temperature below 0°C (Fig. 11). At a temperature 0°C, the ratio of bound to free water is 0.095 and at a temperature -10°C, the ratio increases up to 0.29. Thus, when there is a decrease in air temperature, the fractional composition of water changes due to the partial transition of free water into bound water, which significantly increases the winter hardiness of plants.

The results obtained are consistent with studies (Kovtun *et al.*, 1990), according to which the bound water content in winter wheat leaves is also increasing as winter approaches.

Conclusion

A dynamic model of the winter hardiness formation of winter wheat plants has been developed. The model

describes the processes of growth and development of plants, as well as the passage of two stages of autumn hardening under the agrometeorological conditions that affect during the autumn growing season.

The model adequacy estimation showed that the obtained results are acceptable for using the model in application calculations.

The numerical experiments showed that an increase in photosynthesis products reserves depends on the light intensity and air temperature: The greatest increase is observed when high light intensity (0.9 cal/cm²*min) and air temperature +15°C combined. The largest increase in soluble carbohydrates is at a high level of light intensity and a high value of the amplitude of air temperature (A = 10-12°C). During the plant's hardening period, when the air temperature passes through 0°C towards negative temperatures, the ratio of bound water to free water increases due to the transferring of free water to bound water.

The developed dynamic model of winter hardiness formation by winter wheat plants has been implemented into the working practice of agrometeorological support of agriculture of the Ukrainian Hydrometeorological Center.

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Author's Contributions

Blyshchyk Daria: Conducted all laboratory and field experiments, contributed to the writing of the manuscript and coordinated the mouse work.

Polevoy Anatoliy: Coordinated model development process, conducted numerical experiments, coordinated the data-analysis.

Feoktistov Pavel: Designed the research plan and organized the study, coordinated the data-analysis.

Ethics

This article is original and contains unpublished material. The corresponding author confirms that all of the other authors have read and approved the manuscript and no ethical issues involved.

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