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THE EFFECT OF DROUGHT ON WHEAT PLANTS AT DIFFERENT GROWTH STAGES

Modern publications on the impact of drought on winter wheat plants at different growth stages were analysed. The data on the climate conditions of Odesa region during the last 20 years (2000-2019) were summarized and correspondence of the phenological phases of winter wheat to different periods of weather conditions during the growth in the South Steppe zone of Ukraine was analysed. It was concluded that the most negative impact of drought takes place during seed germination and early growth, at flowering and grain filling and is due to the inhibition of growth, photosynthesis, and reproductive processes.

Key words: *Triticum aestivum* L.; phenology; water stress; climate; cultivars.

Climate change has negative consequences for agriculture, associated with increased temperatures, redistribution of precipitation, excessive evaporation, which lead to droughts and thus negatively affect crop yields and grain quality. According to the recent report of the Intergovernmental Panel on Climate Change, in many mid-latitude dry regions precipitation is likely to decrease [12]. The Steppe zone of Ukraine is one of such vulnerable regions where the hot and dry climate can reduce yields of crop plants, particularly of winter wheat which is sensitive to droughts and high temperature [18; 16]. According to the recent data, during the last few decades, the quantity of precipitation in Ukraine did not decrease significantly but its pattern changed: rains became less frequent but more abundant. A large amount of water cannot be absorbed by the upper soil layer within a short time and flows down [44]. Such circumstances require investigation of the impact of drought stress on important crops, further amelioration of cultivars and optimization of agricultural activities.

Wheat plants vary in their susceptibility to water stress depending on cultivar, duration and intensity of drought, and phenological phase. The most drought-sensitive periods are inflorescence development, anthesis and fertilization, grain formation, and, according to some authors, tillering and shoot elongation [25]. According to the data of academician M.A. Litvinenko from Plant Breeding and Genetics Institute [40], the most vulnerable to extreme factors ontogenetic phases are the spring renewal of vegetation, gametogenesis, anthesis, and the most critical phase – the passage from milk to dough ripeness on the 20-22nd day after anthesis. In the initial phase, water stress affects germination, thus decreasing plant density. Drought during tillering and stem elongation stages leads to a decreased tiller number and plant height. Water deficiency at anthesis and post-anthesis stages affect fertilization, yield formation and grain composition and quality [25; 29]. According to a recent meta-analysis [33], drought can reduce wheat biomass by 25% and yield by 27.5% due to the decrease in spike quantity per plant, spike length and grain content, and in grain weight. The effects of severe water stress are more pronounced comparing to mild stress and not entirely reversible.

Climatic conditions of Odesa region

The temperate continental climate of Odesa region is characterized by mild winter with little precipitation, cool spring, hot and dry summer with occasional heavy rains, and long warm autumn. The average annual temperature changes from 8ºC in the north to 11ºC in the south of the region. The annual rainfall is around 450 mm but can vary significantly (from 356 mm in 2013 to 735 in 2010 in the series of years from 2000 to 2019). On average, 57.1% of the precipitation falls during the period of wheat growth and development (from October to the end of vegetation in November or early December, and from March to July). Hydrothermal coefficient of Selianinov (HTC) is a conditional index for the estimation of the aridity of a region, which considers total precipitation and the sum of the temperatures. HTC<0.7 indicates severe drought, 0.71-1.0 – moderate drought, 1.01-1.2 – moderate humidity, >1.21 – sufficient humidity [34]. HTC of Odesa region is 0.7 on average; it mostly fluctuates from 0.6 and lower to 0.7, but can rarely reach values over 1.0. Drought can also be determined by the comparison of total monthly rainfall with the climatic norm: less than 50 % indicates extreme drought, 50-70 % – severe drought, 71-80 % – moderate drought [34]. In 2000-2019, 104 of 240 months had the subnormal total rainfall. 58.7 % of drought events during this period could be characterized as extreme, 26.9 % as severe, and 14.4% as moderate. Apart from the rainfall insufficiency, a problem of precipitation irregularity also takes place. During 2000-2019, 26.4 % of the total rainfall was provided by ineffective precipitation, when 100 % of climatic norm and more fall within 1-3 days. During such incidents, the amount of water is excessive and cannot be absorbed by soil which leads to floods and waterlogging. The gas exchange between the soil and the atmosphere stops, O_2 level decreases and the respiration of plant roots and microorganisms becomes restricted. Flooding inhibits growth and metabolism, decreases final grain yield in wheat [9]. The data about the climatic conditions of Odesa are summarized in Table 1.

The impact of the climate on the productivity formation of grain yield reaches 20-40 %, up to 60-70 % in the years with extreme weather conditions [37]. There

Table 1

The climate characteristics of Odesa region at the period 2000-2019 years

Year	R*, mm	R_{veg}, mm (% of annual rainfall)	R_{ineff}, mm	T_{av}, °C	HTC	Productivity, t/ha
2000	480	226 (47.1 %)	100	11.3	0.86	1.80
2001	475	247 (52.0 %)	153	11.1	0.71	3.09
2002	507	277 (54.6 %)	229	11.5	0.90	2.87
2003	497	255 (51.3 %)	129	10.1	0.66	1.57
2004	596	349 (58.6 %)	46	11.0	0.98	3.24
2005	469	251 (53.5 %)	42	11.3	0.61	2.34
2006	512	362 (70.7 %)	124	10.6	0.95	2.36
2007	425	124 (29.2 %)	92	12.5	0.48	1.50
2008	399	344 (86.2 %)	109	11.7	0.73	3.04
2009	402	151 (37.6 %)	82	11.9	0.44	2.40
2010	735	356 (48.4 %)	167	11.8	1.07	2.55
2011	395	309 (78.2 %)	150	11.0	0.64	2.92
2012	559	254 (45.4 %)	178	12.0	0.77	1.71
2013	356	261 (73.3 %)	35	11.8	0.57	3.12
2014	489	196 (40.1 %)	263	11.8	0.62	3.13
2015	463	368 (79.5 %)	165	12.1	0.56	2.92
2016	754	311 (41.3 %)	452	11.5	1.36	3.68
2017	444	434 (97.8 %)	33	11.7	0.70	3.59
2018	491	285 (58.0 %)	59	11.9	0.45	3.63
2019	440	172 (39.1 %)	0	12.8	0.57	no data
Average	494.4	277 (57.1 %)	130.4	11.57	0.73	2.71

* R – total annual rainfall; R_{veg} – total rainfall of a vegetative season (October-November + March-July); R_{ineff} – total inefficient precipitation; T_{av} – average temperature; HTC – hydrothermal coefficient. The source of the data on wheat productivity is the State statistic service of Ukraine.

is a positive correlation (r=0.42) between wheat productivity and the total rainfall during the vegetative season. Some positive correlations are also found between winter wheat productivity and the moisture reserve in 20 cm soil layer before sowing (r=0.62); total rainfall during winter (r=0.56), spring vegetation period (r=0.75), and summer vegetation period (r=0.42); average winter temperature (r=0.64), average temperature before heading (r=0.29) and after heading (r=-0.58) [40]. In the study [36], it was calculated that due to water insufficiency during different phenological phases of wheat, wheat productivity in the Southern Steppe zone cannot reach possible maximum (Table 2).

Table 2

The agroclimatic conditions in the South Steppe Region - zone of winter wheat cultivation in the period 1981-2010 according to [36]

Months	Phenological phase	R*, mm	W, %	Productivity, % of maximum
VII-VIII	Before sowing	102	52	81
IX-X	Sowing and germination	84	74	85
XI	Tillering	45	110	63
XII-II	End of vegetation	119	128	82
III-V	Stem extension and booting	122	113	93
VI	Heading and anthesis	69	54	52
VII	Ripening	59	52	59

* R – precipitation, W – relative soil moisture content.

Weather conditions, which correspond to each phenological stage of wheat, are considered further in this study.

Physiological and biochemical effects of drought stress

Drought stress changes a range of physiological and biochemical properties. Soil drying induces abscisic acid (ABA) biosynthesis in plant roots. ABA helps to maintain root growth and increase its hydraulic conductivity, thus increasing the plant's water uptake [4; 24]. In the mechanism of root hydraulic conductivity enhancement aquaporins (water channels) are involved [8; 24]. These membrane-bound proteins facilitate symplastic water flow in roots; this water transport pathway takes precedence over the apoplastic pathway in wheat. Aquaporin activity can be modulated by ABA [24]. Altered leaf water relations such as decreased water potential and relative water content affect photosynthesis, as decreased turgor pressure (along with ABA and its glucose ester [6; 17; 24]) results in the closure of stomata and reduced gas exchange. ABA is not a single signal which takes part in stomatal regulation. It was presumed that the increase in xylem sap pH may amplify the root signal and facilitate the redistribution of leaf ABA [24; 32]. Non-stomatal factors, such as inhibition of Calvin cycle enzymes and photosynthetic electron transport, decreased carboxylation efficiency and suppressed capacity for ribulose bisphosphate carboxylase regeneration might also take place as a result of water stress [14]. An imbalance between electron excitation and utilization emerges, and it leads to the production of reactive oxygen species (primarily superoxide and H_2O_2) which accumulate in mitochondria, chloroplasts and peroxisomes and damage cell membranes and macromolecules. As a result, the loss of mitochondrial internal structure, the irregular shape of chloroplasts, disorganisation of granal stacks and accumulation of plastoglobules in chloroplasts can be observed in the tissues of drought-exposed plants [6]. A complex of enzymes and non-enzymatic antioxidants detoxify ROS: superoxide dismutase transforms $O_2^{\cdot-}$ to H_2O_2, and then catalase, peroxidase and ascorbate peroxidase decompose it to water and oxygen [1; 27]. An effective system of H_2O_2 detoxification exists in plant cells – the ascorbate-glutathione cycle [27]. As a result of water stress, proline and soluble carbohydrates content increase, which can contribute to turgor and stomatal conductance sustainment [1; 5; 15]. According to A. Blum [5], such osmotic adjustment can enhance root growth and can be associated with higher yield in wheat.

There are two main pathways of plant response to osmotic stress – ABA-dependent and independent [15]. Under drought and salt stresses, ABA biosynthesis is activated in apical root cells and, to a lesser extent, in leaf mesophyll and stem parenchyma [24]. ABA up-regulates the expression of germin-like proteins (defence against various biotic and abiotic stresses, [11]), tonoplast intrinsic proteins (such as aquaporins), MAPK4 (mitogen-activated protein kinases-4; they take part in stomatal development and distribution), acetyl-CoA carboxylase (takes part in transpiration minimization) [13], down-regulates the genes involved in auxin signal transduction (thus inhibiting plant growth) and the enzymes involved in proline degradation (proline dehydrogenase and prolyl 4-hydroxylase) [15]. Along with other factors, ABA also up-regulates the expression of genes coding the enzymes for glutathione-glutathione disulphide cycle, thus contributing to antioxidant defence; up-regulates ethylene and jasmonic acid signal transduction pathways [15]. ABA induces the synthesis of LEA-proteins (late embryogenesis abundant), particularly dehydrins (DHN) and heat shock proteins (HSP) [6]. Dehydrins have chaperone-like functions: they inhibit coagulation of macromolecules thus maintaining cell structural integrity. HSPs are chaperones involved in protein interactions, folding, assembly, intracellular organisation. Their functions are prevention of protein aggregation and degradation, reactivation of damaged proteins, thus they play a major role in maintaining cellular homeostasis. Chaperone-like proteins are found in chloroplast stroma, such as ClpP which degrades abnormal proteins, Rubisco activase which regulates the activity of ribulose-1,5-bisphosphate carboxylase, RBP (Rubisco binding protein) which maintains the appropriate content of this enzyme [6]. The ABA-independent pathway is involved in down-regulation of the cytokinin signal pathway, up-regulation of proline and soluble sugars biosynthesis [15]. Calcium ions act as a secondary messenger and are involved in the modulation of ABA biosynthesis [32]. They also regulate stomatal closure through activation of nitric oxide synthase and subsequent accumulation of NO in guard cells, which leads to their closure [15; 32]. The signalling pathways induced by osmotic stress are very complex and understanding of them requires further investigations.

Drought negatively affects germination and initial growth of wheat seedlings

Drought stress lowers germination energy and germination rate of wheat seeds [7]. Water deficiency on the stage of seedling development affects seedlings' growth, which is associated with decreased seed reserve utilization. The growth retardation is more expressed in the aboveground parts of plants which results in lower shading of the soil surface and higher loss of soil water, lesser light intercepting photosynthetically active surface and therefore lower yield potential [30]. Drought restricts transpiration, thus reducing the root absorbing power which leads to decreased nutrient uptake. Another factor which affects plant mineral nutrition is lack of soil moisture as a solvent and a medium for diffusion [10]. Under drought stress, anatomical changes also occur, such as disorganisation and degradation of palisade tissue and decrease of the thickness of spongy tissue in leaves, reduction of the volume of endo- and exodermal cells in roots, the diameter of main xylem vessels in roots can also decrease [7]. Water stress leads to the decrease of plant height, shoot fresh and dry weight, length of leaf blades [10].

The optimum temperature for wheat germination is +15...+20ºC, and the optimum soil reserve of productive moisture is 30-60 mm [37]. In Odesa region, the wheat sowing time is the second half of September [35]. The average temperature in September is 18ºC and the normal rainfall is 42 mm. During 2000-2019, rainfall was less than normal in 55 % of years, and inefficient precipitation took place in 35% of years. In August, frequently occurring negative deviation of precipitation from normal (60 % of years), heavy rains (25 % of years), and high temperatures which increase evapotranspiration can prevent sufficient moisture accumulation in the soil. Under the appropriate conditions, germination of wheat takes place in 5-9 days after sowing, and if the moisture is deficient, germination can last for up to three weeks [37]. Seedlings emerge at the end of September – the beginning of October. August and September rainfall in 2000-2019 is displayed on the chart (Fig. 1).

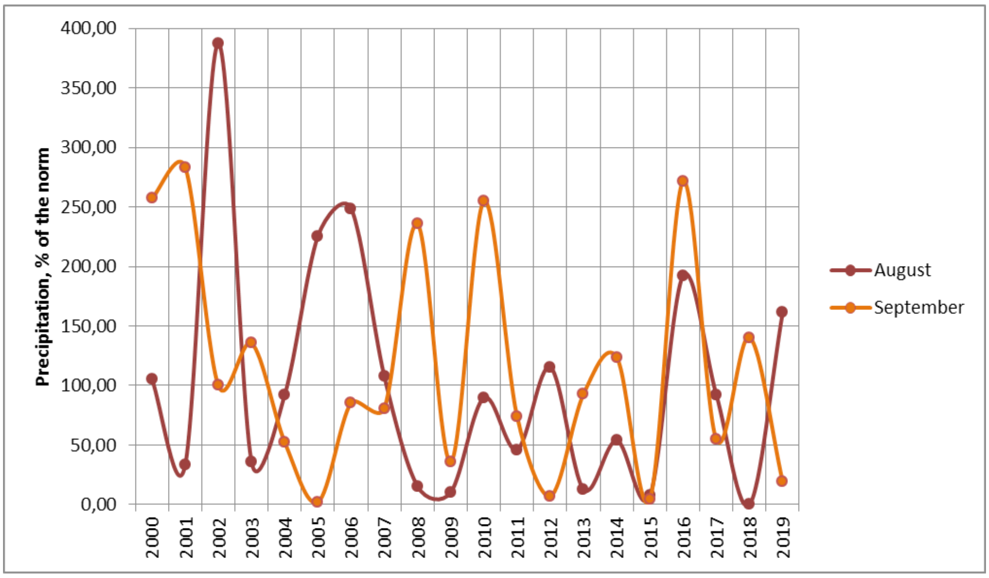

Fig. 1. Precipitation in August and September 2000-2019 in Odesa region

Drought-induced oxidative stress and inhibition of photosynthesis during vegetative stage affect biomass production and yield formation

Effects of water stress on wheat during tillering and jointing were investigated by M. Abid et al. [1] in Nanjing Agricultural University (China). It was found that the increase in ROS content and membrane injury were more pronounced during water stress at the jointing stage. Oxidative stress leads to the increase of enzymatic activity of catalase, superoxide dismutase and ascorbate peroxidase which detoxify ROS, rapid increase with the subsequent decline of glutathione content and decrease of carotenoid content (non-enzymatic antioxidants).

One of the mechanisms of drought tolerance is osmotic adjustment provided by free amino acids, especially proline, and soluble sugars, levels of which increase as a result of water stress. This effect was more pronounced at the tillering stage. Stressful conditions limit the development of the root system, and it results in a decrease of leaf growth and longevity [2; 33]. Water stress during the tillering stage affects the generation of the tillers thus reducing the dry weight of shoots and number of spikes per plant, and during stem elongation phase it prevents some tillers from producing spikes [25]. Comparing to other growth stages, a drought at tillering stage leads to the most significant decrease in wheat biomass [33]. Inhibition of carbon assimilation and stem growth leads to the decrease of stem reserve storage capacity, which subsequently affects grain development [4]. Drought stress with a resulting depression of photosynthesis leads to alteration of phenological phases of wheat and affects grain yield. Severe drought stress accelerates the onset of anthesis and shortens the grain filling duration, reduces the formation of spikes and decreases grain yield traits, including the number of grains per spike and per plant and 1000-grain weight. These reductions are more pronounced in case of drought stress during the jointing stage [1]. Despite the negative effects of water stress on wheat plants, it was shown that mild stress at tillering might generate resistance to severe water deficiency at the later growth stages by maintaining favourable water relations and antioxidant defence in leaves. Comparing to non-acclimated, acclimated plants show higher RWC, increased redox status and lower levels of H_2O_2 and lipid peroxidation [26; 27].

Tillering begins in 10-30 days after germination (depending on the soil moisture and temperature) and lasts till the stop of the vegetation in November or December when the temperature reaches +1...+3ºC. The duration of the autumn vegetation of wheat is 50-70 days [47]. The most favourable temperature for wheat tillering is +9...+18ºC; the optimum soil moisture level is 20 mm. Under favourable conditions, wheat plants form 3-5 tillers during autumn [37]. In Odesa region, the average October and November rainfall is 42.4 mm and 37.5 mm, respectively. In 50% of years between 2000 and 2019, precipitation in October was corresponding to or exceeding the climate norm (Fig. 2), but 31.6% of it was inefficient. Over the last 12 years, only in 2014, the total rainfall in November was higher than 41 mm (the climate norm). In contrast, total winter precipitation corresponded to the norm in 70 % of years during the considered period (Fig. 3), but irregular snowfall combined with the incidents of low negative temperatures can lead to the freezing of wheat plants, inhibition of their growth, reduced pest resistance [37; 40]. Autumn and winter weather conditions allow sufficient accumulation of soil moisture. The satisfactory spring productive moisture reserve is 120-150 mm in the 1 m layer of soil, and the reserve of 150-200 mm is favourable for wheat development [37].

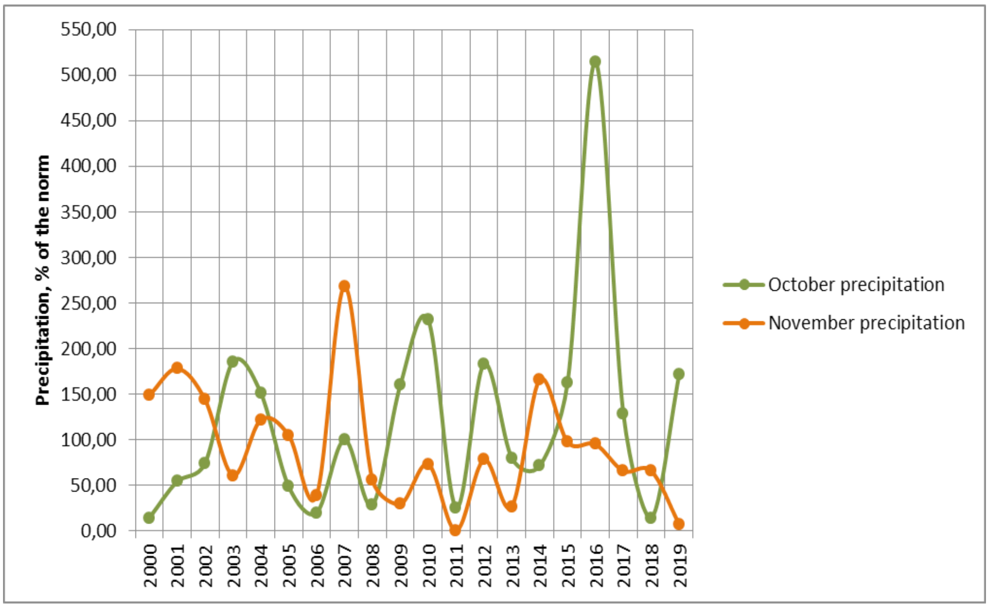

Fig. 2. Precipitation in October and November 2000-2019 in Odesa region

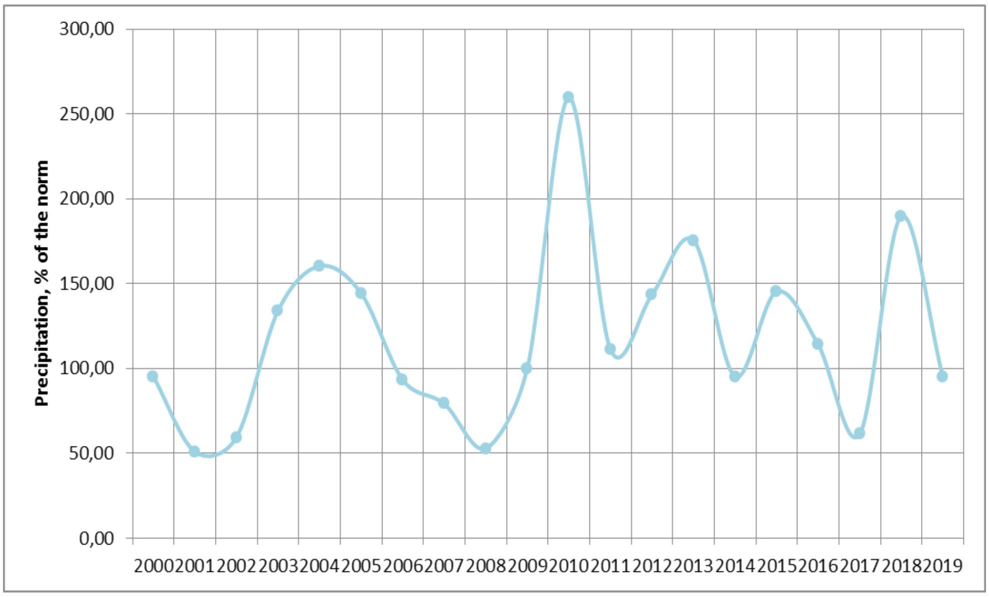

Fig. 3. Total winter precipitation in 2000-2019 in Odesa region

According to the data [46], the average winter precipitation of 137.6 mm and the average water absorption by the soil of 39% led to the accumulation of 130-152 mm of productive moisture (depending on the predecessor). The average winter rainfall in Odesa region is lower (125.1 mm), but the correct selection of a predecessor for wheat cultivation can provide sufficient accumulation of water in the soil.

Vegetation resumes in March and lasts from 70 days in early-maturing varieties to 105 days in late-maturing ones [41]. Spring tillering continues under the temperatures +3...+15ºC and leads to the formation of 1-3 side shoots. Higher temperatures and inefficient soil moisture (less than 100 mm) inhibit this process [37]. Spring tillering and stem extension take from 24-26 days in early cultivars to 33-40 days in late ones [41; 43], so the next phenological phase starts in the second or the third decade of April. The average temperature in March is 4.7ºC (from 1.1ºC to 7.3ºC within 2000 and 2019) which is favourable for wheat tillering. The average total rainfall is 36.2; the amount of precipitation did not reach the climate norm (32 mm) in 60% of years (Fig. 4). The incidents of inefficient precipitation are quite rare in March (3 times over the last 20 years).

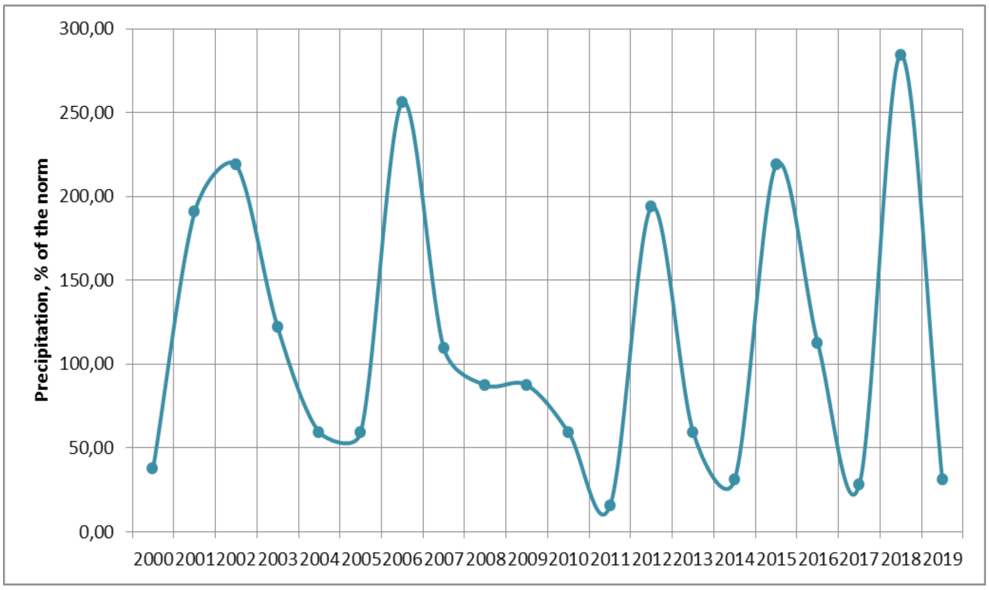

Fig. 4. Precipitation in March 2000-2019 in Odesa region

The number of studies on the effect of water deficiency during booting and heading time is limited. The early heading is reportedly a stage very sensitive to water stress [19; 25]. It results in lowered biomass production due to decreased photosynthetic activity and a decrease in grain number. Yield losses as a result of drought during heading and flowering are comparable to those resulting from the constant water insufficiency during the full growth cycle [19].

Wheat goes through the booting stage during 25-32 days in the second half of April – the beginning of May [41; 43]. The soil moisture reserve of 100-125 mm in 1 m layer provides the highest productivity [37]. The average April temperature in Odesa region is 10.2ºC, and the average rainfall is 28.8 mm (55 % of years within 2000-2019 period had a lower amount of precipitation, and in 25 % of years inefficient precipitation took place; Fig. 5). Wheat heading and anthesis start in the first

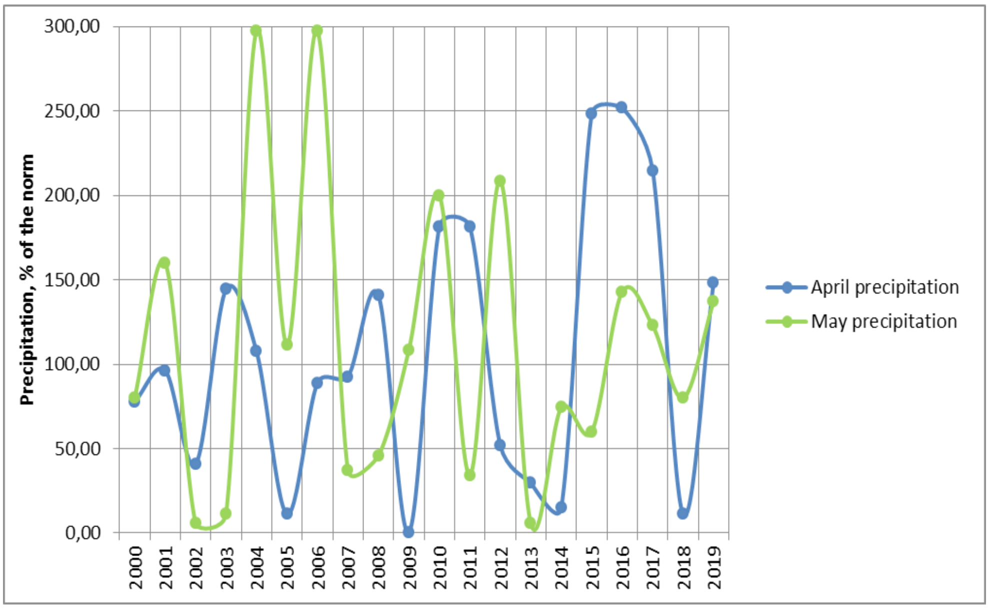

Fig. 5. Precipitation in April and May 2000-2019 in Odesa region

half of May (08-25/05 depending on the sowing date and the features of a cultivar) and last till the beginning of June [42]. The optimal temperature during this period is +15...+20ºC, and precipitation 40-80 mm [37]. The average temperature in May is 16.7ºC; both hot and cold days occur sometimes, but the temperature values usually are not extreme (the average temperature at night is 12.1ºC, and 19.5ºC at the daytime). The average rainfall is 38.9 mm, but in half of the years between 2000 and 2019 this value was under normal (Fig. 5). In the second half of May – the first decade of June, moisture deficit and the temperature fluctuations cause a negative influence on yield formation [47].

Water deficiency during anthesis prevents normal gamete formation

Water stress during reproductive stage has a more deleterious effect on grain yield than the same condition during the vegetative stage [23]. The adverse effect of water insufficiency at anthesis is most pronounced during meiosis. It leads to the production of sterile gametes, loss of gamete viability, and as a result, reduced grain number [21; 33]. Water stress restricts photosynthesis at anthesis to a greater extent than at vegetative stage, due to the reduction of mesophyll conductance and a significant decrease in chlorophyll concentration as a result of photoinhibition and photodestruction of pigments and destabilization of the photosynthetic membrane [24; 28]. Decrease of photosynthetic activity also leads to the shortage of soluble carbohydrates in vegetative tissues and anthers. In the absence of sugars, intine cannot develop properly, which subsequently prevents adhesion of pollen grains to the surface of the stigma. Starch accumulation in the cytoplasm of vegetative cells in pollen grains is also affected so that there is not enough energy for pollen tube growth [4].

The harmful effect of post-anthesis drought on grain yield and quality

The consumption of water by a plant is the highest during the grain formation stage [25]. Prolonged drought during flowering and grain filling can reduce grain yield up to 92 % [33]. Drought shortens the grain-filling period, inhibits the division of endosperm cells, especially in basal and distal parts of spikelets, thus decreasing grain weight [20; 22]. ABA synthesized in the shoot and transported to the reproductive organs can affect cell division in developing seeds [4]. Grain development depends on the quantity of assimilates, accumulated during the vegetative stage, as after anthesis they are redistributed and utilized, especially under environmental stress conditions [31], and this process can be regulated by ABA in developing grains [4; 24]. This may explain the large extent of tiller senescence and mortality during the reproductive phase. Grain size in secondary tillers is lower due to the reduced number of endosperm cells and lower quantity of accumulated starch [31]. Flag leaf photosynthesis also serves a substantial source of assimilates for grain filling. Breakdown of chlorophyll, the decline of photosynthetic activity and inhibition of CO_2 fixation occurring after anthesis can diminish grain filling, which results in lower grain weight [23]. Composition and quality of grains change under drought stress. The ratio of large (A-type) starch granules to middle and small (B- and C-types) increases significantly [3; 20; 29]. A-type granules have a lower amylose content, which can influence grain quality. As a result of drought during grain filling, starch content decreases and the proportion of proteins changes. The decrease of glutenin-to-gliadin ratio and reduction of unextractable polymeric protein fraction affect grain quality [3].

Wheat reproductive processes from the ear formation to the ripening take 24-33 days, up to 42 days in different cultivars [37; 41; 43]. Kernel formation and ripening take place in June and July (from the first half of June to the middle of July). This is the time of high temperatures and droughts, the effect of which is especially harmful if combined with water deficiency during spring vegetation [40]. The average rainfall in June within 2000-2019 reached 44.7 mm which is 4.3 mm lower than the climate norm. 65 % of years during this period had precipitation lower than the norm. Ineffective precipitation is quite rare in June – 2 incidents over the last 20 years. The average temperature is 21.1ºC (24.0ºC at the daytime), but it can reach the values over 30ºC. The total rainfall in July is around 48.1 mm, in 50 % of years it does not reach the climate norm. The average temperature is 23.6ºC (27.0ºC at the daytime). The comparison of the amount of precipitation during these months with the norm is shown on the graph (Fig. 6).

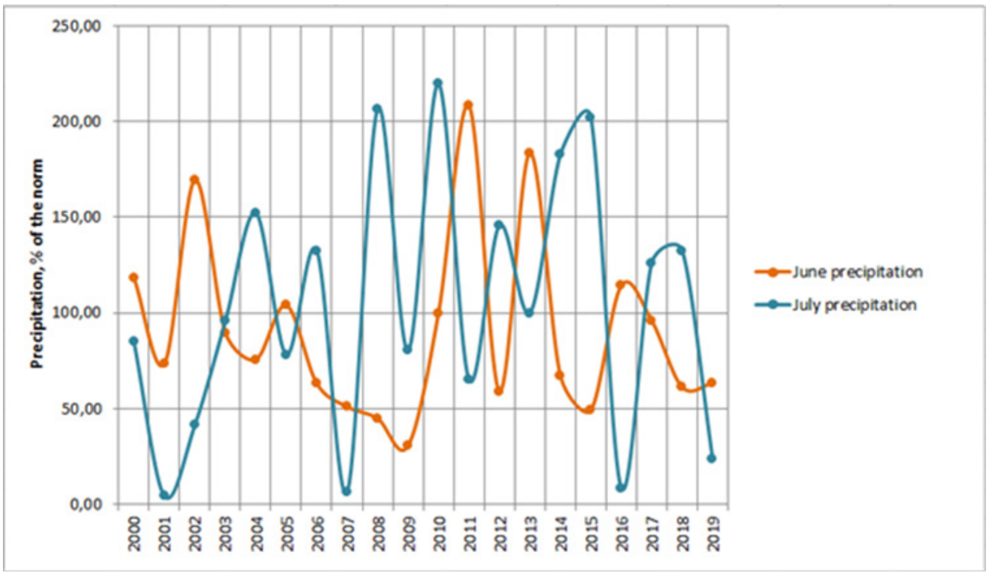

Fig. 6. Precipitation in June and July 2000-2019 in Odesa region

Drought-resistant wheat cultivars of Ukrainian selection

Although changing climate conditions of the Southern Steppe zone, characterized by frequent droughts, unstable precipitation and extreme temperatures, can pose a threat to wheat production, a range of highly productive, drought-resistant wheat cultivars were bred. High germination energy, moderate extent and reversibility of the damage caused by water stress, short recovery time, and stable yield are criteria for the crop drought tolerance [39; 45; 48]. The high rate of germination (above 70 %) under modelled osmotic stress was shown by the cultivars Valensiia, Turunchuk, Kniazhna, Misiia odeska, Blahodarka odeska, Albatros odeskyi, Hratsiia myronivska, Vyshyvanka, Balada myronivska [45]. Drought resistance was estimated by the investigators as advanced in the cultivars Antonivka, Bilosnizhka, Zolotokolosa, Kiriia, Kosovytsia, Povaha, Trypilska, Favorytka [48], Znakhidka odeska [39], Kuialnyk, Pysanka, Podolianka, Poshana, Suputnytsia, Smuhlianka, Khersonska bezosta [39; 48]. Above-average drought resistance was characteristic of the cultivars Bohdana, Vesnianka, Volodarka, Demetra, Zastava odeska, Znakhidka odeska, Lybid, Odeska 51, Prima odeska, Sirena odeska, Stolychna [48], Kiriia [39], Albatros odeskyi, Apohei luhanskyi, Donetska 48, Driada 1, Zemliachka odeska, Zira, Zustrich, Nikoniia, Selianka [39; 48]. On the contrary, low tolerance to water deficit under field conditions was inherent to wheat cultivars Bilosnizhka, Vdala, Dalnytska, Liona [39; 48]. Deterioration of growth, development and productivity was also observed in Vesta, Hlibovchanka, Dolia, Kharkivska 105, Myronivska 67, Panna, Snizhana, Spivanka [48]. Plant resistance assessment in the studies [39; 48] was carried out after the observations under the field conditions during the periods of soil moisture deficiency, high temperatures and dry winds. In the investigation [49], several highly productive and adaptive wheat varieties were pointed out: Podolianka, Smuhlianka, Natalka, Pereiaslavka, Khurtovyna, Kyivska ostysta, Zbruch, Malynivka, Snihurka, Darynka Kyivska, Lymarivna, Ladyzhynka. In the same study, 136 Ukrainian and foreign winter wheat cultivars were ranged based on their drought and high-temperature resistance. It was found that 28.6 % of the cultivars bred in the institutions of Southern Ukraine had high and above-average drought resistance, comparing to 10.6% of the cultivars from the Kyiv region and 1.6% of the foreign cultivars [49].

In the study [40], the results of the previous work of wheat breeding in Odesa region were summarized, and the direction of the future efforts was established. The most suitable varieties for cultivation are those of the universal type, which are characterized by frost, drought, heat, and pest resistance along with high potential productivity. The features which contribute significantly to drought resistance are the intensity of nodal roots growth, roots soil penetration depth, early maturity, the high regeneration capacity of seedlings and tillers, leaf water retention during the grain formation, high assimilate reutilization capacity under high temperatures. A range of corresponding varieties was created, such as Blahodarka odeska, Misiia odeska, Sluzhnytsia odeska, Hoduvalnytsia odeska, Zahrava odeska, Epokha odeska, Istyna odeska, Zhuravka odeska, Holubka odeska, Lebidka odeska, Kniahynia Olha, Lastivka odeska, Zadumka odeska, Vykhovanka odeska, Lira odeska, Nyva odeska, Shchedrist odeska, Era odeska, Melodiia odeska etc. These varieties are characterized by high productivity (78-104 c/ha), elevated drought, frost and pest resistance, and high grain quality.

Conclusion

In the present study, the impact of drought on winter wheat growth and productivity was investigated, and the climate conditions of Odesa region at each wheat phenological phase were reviewed. Drought lowers seed germination rate, affects mineral nutrition and growth of seedlings, restricts the production of tillers and inhibits the photosynthetic activity of plants. Drought and inefficient precipitation often take place during autumn vegetation of wheat. Moisture supply in winter usually corresponds to the climatic norm, which allows sufficient soil moisture accumulation. In March, wheat vegetation resumes. Water insufficiency in March and April, when wheat tillering, jointing and booting take place, affects growth and development of the plants, leads to the alteration of phenological phases, and decreases potential yield. Drought during anthesis and grain filling is especially harmful because of the negative effect on gametogenesis, insufficient accumulation of assimilates due to the inhibited photosynthesis, reduction of grain number and weight and deterioration of its quality. Reproductive processes in wheat take place in May, June and partly July. In Odesa region, it is the time of the establishment of high temperatures and drought. Although such climate conditions negatively affect wheat production, a range of resistant and productive universal cultivars were bred. The effects of drought and the plant response to them have not been studied completely and need further investigation.

Стаття надійшла до редакції 26.03 2020

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ВПЛИВ ПОСУХИ НА ПШЕНИЦЮ НА РІЗНИХ СТАДІЯХ РОСТУ

Резюме
Кліматичні умови України та Одеської області зокрема поступово змінюються: середні температури зростають, розподіл опадів стає нерівномірним, частішають випадки екстремальних погодних умов, таких як посухи, зливи, значні коливання температури. Це призводить до необхідності проведення детальних досліджень впливу кліматичних факторів на економічно важливі рослини та механізмів формування ними посухостійкості. Така інформація сприятиме процесу створення універсальних сортів та покращенню систем агротехнічних заходів. Метою даної роботи була систематизація інформації про вплив дефіциту вологи на біохімічні процеси, ріст, розвиток та продуктивність пшениці м’якої озимої (*Triticum aestivum* L.), залежно від фази розвитку, під час якої трапляється посуха у Південному степу України, зокрема в Одеському регіоні. Для цього було проаналізовано сучасні публікації на тему впливу посухи на пшеницю під час різних фенологічних фаз, а також простежено агрометеорологічні умови за останні двадцять років у Одеському регіоні, відзначено сучасні сорти пшениці, пристосовані до умов вирощування у посушливому південному регіоні України. Відмічено, що посуха впродовж вегетативної стадії чинить негативний вплив на накопичення біомаси та формування продуктивних пагонів, а під час цвітіння та дозрівання зерна зменшує врожай та погіршує його якість. На стадії проростання посуха спричиняє нерівномірну появу сходів, погіршує мінеральне живлення, пригнічує ріст надземних частин. На стадії кущіння формується менше продуктивних пагонів, знижується інтенсивність фотосинтезу, фенологічні фази зсуваються у бік прискорення. Посуха під час колосіння призводить до зменшення кількості зерен у колоссі. Під час цвітіння нестача вологи негативно впливає на фертильність та життєздатність гамет, а під час дозрівання зерна, пригнічує поділ клітин ендосперму та погіршує якість зерна. В цілому, не всі аспекти впливу посухи на біохімічні та фізіологічні процеси розвитку пшениці м’якої озимої відомі, тому необхідні подальші дослідження.

Ключові слова: *Triticum aestivum* L.; фенологія; водний дефіцит; клімат; сорти.

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