proceedings

MDPI

Proceedings

Interaction between Soil Drouhgt and Allelipathic Factor on Wheat Seedlings Performance †

Nataliya P. Didyk *, Nadia V. Rosits`ka, Bogdana O. Ivanytska and Nataliya V. Zaimenko

National Botanical Garden of the National Academy of Sciences of Ukraine, Str. Timiryazyevska 1, 01014 Kyiv, Ukraine
* Correspondence: nataliya_didyk@ukr.net; Tel.: +380-44-285-5453
† Presented at the 1st International Electronic Conference on Plant Science, 1–15 December 2020; Available online: https://iecps2020.sciforum.net/.

Published: 1 December 2020

Abstract: The interaction between pre-sowing seed priming and soil drought on wheat physiological performance and allelopathic potential was studied in the laboratory pot experiment. The mixture of cinnamic, salicylic and ascorbic acids (0.01, 0.1 and 1 mM) was used as a priming agent. The soil moisture was regulated by watering pots to 20%, 40% and 60% of field capacity. The macronutrient content in the rhizosphere soil was also measured. The results obtained indicated that a mild allelopathic stress applied to seeds made seedlings more resistant to subsequent drought stress and contributed to the increase of their allelopathic potential. Intensification of drought stress resulted in the decrease of production of allelopathic inhibitors in wheat plants and increase allelopathic stimulants and organic carbon in the rhizosphere soil. Changes in allelopathic activity of the rhizosphere soil closely correlated with the changes in organic carbon, nitrates, iron and phosphorus. While soil reaction, concentration of ammonia, manganese, potassium, sulfur displayed no correlation with soil allelopathic activity. The phenomena of cross-synergism and cross-antagonism between the interacting factors have been discussed.

Keywords: allelochemicals; soil drought; seed priming; cross-adaptation; wheat

1. Introduction

Drought is the most challenging abiotic stress causing annual yield losses worldwide about 17% [**Error! Reference source not found.**]. In Ukraine for the last 40 years the notable increase in the drought frequencies, especially during the spring, occurred leading to an enhanced risk of death of susceptible plants in the early stages of ontogenesis. During the last two decades the frequency of droughts has nearly doubled. It is expected that further warming in Ukraine will lead to a sharp increase in the deficit of water in the soil in the spring and summer months. Besides, recently appeared a dangerous tendency of extending of droughts to the areas used to belong to zones of sufficient humidity, such as Polissie and Northern Forest-Steppe [**Error! Reference source not found.**].

Although selection and breeding is the ultimate way to produce stress tolerant crops, exogenous application of phytoprotectans boosting natural plant defense strategies has been considered a shot-term solution to alleviate the adverse effects of different stresses on plants during the last decade. Phytoprotectants are various non-toxic substances mostly of natural origin that benefit plant potential to adapt to various abiotic or biotic stress-factors by interacting with plant-signaling cascades thereby reducing negative plant reactions to stress [3–5]. Among the latter plant secondary metabolites with antioxidant potential such as ascorbic acid, salicylic acid and some phenolics are promising. Being natural substances, they are safe for the environment and agricultural products [4,6].

Ascorbic acid (AA) is a unique multifunctional compound. It is involved in the most important energy processes of plant cells such as photosynthesis and respiration. It is a potent antioxidant. Endogenic AA affects growth processes, flowering, and water balance, regulates activity of some enzymes associated with the metabolism of nucleic acid and protein synthesis, and participates in adaptive responses to various types of biotic and abiotic stresses [**Error! Reference source not found.**]. Seed priming with exogenous ascorbic acids was shown to improve seedling`s growth and performance under various abiotic stresses including soil drought [**Error! Reference source not found.**].

Salicylic acid (SA) is an endogenic phenolic acid involved in the signal induction of systemic acquired resistance of plants to infections and abiotic stress factors, has antioxidant and prooxidant properties [**Error! Reference source not found.**]. Endogenous SA affects various physiological processes such as transpiration, stomata movements, photosynthesis, nutrient uptake and transport of ions, plant growth and development [**Error! Reference source not found.**]. Exogenous SA can induce resistance in plants to abiotic and biotic stress factors such as drought, high and low temperature, salt and osmotic stress, toxic metals, phytopathogenes [3,6,9,10].

Though physiological and biochemical mechanisms of protective effect of exogenous AA and SA are not fully elucidated yet, there is an opinion that their antioxidant potential and ability to modulate signaling cascades are the key factors contributing to this phenomenon.

Cinnamic acid (CA) is a phenolic acid occurring naturally in plants that has low toxicity and a broad spectrum of biological activities. It regulates growth and development, have antioxidant, antimutagenic, antimicrobial potentials [**Error! Reference source not found.**]. Phenolic acids are common plant allelochemicals with diverse modes of action. They are universally distributed in plants, especially, in their decomposition products. Recent interest in phenolic compounds stems from their potential to protect against oxidative stress caused by many types of biotic and abiotic stressors. Exogenous phenolic acids enter through the plant cell membrane and change the activity and function of certain enzymes and plant hormones. At low concentrations exogenic phenolic acids may stimulate plant defensive systems. However, in high concentrations they increase lipid peroxidation, inhibit nutrients and water absorption leading to slowing of plant growth [**Error! Reference source not found.**].

Studies of mixtures of phenolic compounds have shown that individual components can be additive when being evaluated for their combined effects [**Error! Reference source not found.**]. Our previous studies showed that combined application of AA, SA and CA display synergistic effect towards plant growth parameters under drought conditions [**Error! Reference source not found.**].

Seed priming is a pre-sowing treatment used to improve the rate and uniformity of germination, as well as seedlings vigor and stress resistance. Numerous studies showed that the effectiveness of a certain priming technique vary significantly depending on a crop species and cultivars. In fact to optimize the priming method for concrete crop variety, one need to take into account not only taxonomical position but also the impact of a particular environmental conditions [**Error! Reference source not found.**].

The objective of the present study was to assess the interaction between pre-sowing seed priming with the mentioned above mixture of organic acids and soil drought intensity on physiological processes and allelopathic potential of wheat seedlings as well as allelopathic and nutritional regime of the rhizosphere soil in the factorial pot experiment.

2. Experiments

2.1. Seed Materials

Factorial experiment was performed using wheat *(Triticum aestivum* L., cv. "Pereyaslavka") as a test-plant. Wheat is considered the first strategic food crop in Ukraine. It is the basic staple food for bread making. Wheat seeds were surface-sterilized with a 5% sodium hypochlorite solution for five minutes and washed thoroughly with sterilized tap water.

2.2. Experimental Setup and Cultivation Conditions

The experiment was conducted in the laboratory conditions at the Department of Allelopathy, M.M. Gryshko National Botanical Garden (Kyiv, Ukraine). Polyethylene containers (10 cm internal diameter) were filled with 0.5 kg of gray podzol soil sterilized in an oven at 100 °C for two hours, air-dried and sieved (through 2 mm sieve). Wheat seeds were presoaked in Petri dishes each containing 5 mL of the aqueous solution of mixture of AA, SA and CA (1:1:1) in one of the following concentrations of 0.01; 0.1; 1 mM or distilled water (control) for three hours and sown in these pots. The experiment included 3 levels of soil moisture: 20%, 40% and 60% of field capacity (FC). The moisture level was maintained by gravimetric method till the end of the experiments. Test-plants were cultivated for 28 days at 22–30 °C temperature, natural sunlight and 60–75% relative humidity. The experimental design was two factorial (3 × 3), arranged in a completely randomized design with five replications.

2.3. Measurements

The number of germinated seeds was counted on 3–7 days after sowing. Root and shoot length and seedling dry biomass were recorded at the end of the experiments. The characteristics of water balance (relative water content (RWC) and water deficit (WD) in the foliar tissues) were measured by gravimetric method [**Error! Reference source not found.**] two weeks after germination and at the end of the experiments. The content of flavonoids and catalase activity were determined before harvesting. Catalase activity (CAT) was determined by the method [**Error! Reference source not found.**]. Flavonoids were extracted with 70% ethanol, their quantitative content was determined using qualitative reaction with $AlCl_3$ spectrophotometrically [**Error! Reference source not found.**]. Allelopathic activity of the rhizosphere soil was assessed by direct bioassay [**Error! Reference source not found.**] on cress (*Lepidium sativum* L.) root growth. The same gray podzol soil on which test-plants were not cultivated was used as a control. Allelochemicals from dried shoots and roots were extracted with distilled water (2 g per 100 mL), their biological activity was assessed using bioassay on cress root growth [**Error! Reference source not found.**]. As the control we used distill water. The contents of macronutrients in the rhizosphere soil were determined by colorimetric method [**Error! Reference source not found.**].

2.4. Statistical Analysis

A two-way general linear model analysis of variance (ANOVA) was used to compare the significant effects of main factors treatment (mixture concentration) and soil moisture level and their interaction (treatment + soil moisture level) on biometrical and physiological parameters of the wheat seedlings, allelopathic activity, and nutrients availability in the rhizosphere soil. The data presented in tables are group weighted means. All the replicates were analyzed together with experimental repeats. Levene’s test was used to check the homogeneity of variances. The individual treatment means were compared using LSD (least significant difference) test, with a significant level at $P \leq 0.05$. The interaction between pre-sowing seed priming and soil drought was assessed using coefficient of interactive effect. The latter was counted as the difference between empirical data on the combined effect of the mentioned above factors with the theoretically calculated sum of the impacts of the isolated factors [**Error! Reference source not found.**]. In the case, the co-efficient of interactive effect (CIE) > 0 we assume a cross-synergism, otherwise (CIE < 0) we assume a cross-antagonism. The reliability of the CIE was estimated by the error of the co-efficient of interactive effect (CIE error) calculated as the root of the sum of the squares of the effects of the factors acting alone and in combination [**Error! Reference source not found.**]. In the case, [CIE] < CIE error we assumed independent effect [**Error! Reference source not found.**].

We also used factor analysis (principal components method) to distinguish the characteristics of the rhizosphere soil which displayed the highest sensitivity to the environmental factors. All statistical tests were performed using Statistica 10.0 and Microsoft Office Excel 2007 software.

3. Results

The results obtained showed that the both studied factors (seed priming and soil moisture) significantly affected test-plants growth and performance ($P < 0.05$). The characteristics of water deficit and flavonoid content in the leaves of wheat seedlings were the most sensitive to the both studied factors (Table 1).

Moderate (40% FC) drought stress inhibited seed germination, growth of shoots but stimulated the development of the root system and accumulation of protective antioxidants (flavonoids, catalase) in wheat seedlings. Under severe drought (20% FC) all registered characteristics of wheat growth and development, as well as biosynthesis of protective substances declined sharply. It could be concluded that wheat seedlings were subjected to physiological stress at 40% FC and displayed significant inhibition of growth and metabolic processes at 20% FC.

Table 1. Analysis of variance of the effects of priming mixture concentration (PM) and soil moisture on wheat seeds germination and seedling performance.

Soil Moist ure, %	PM Concent-Ration, M	Germi-Nation,%	Shoot Height, mm	Leaf Area, cm²	D. w., mg		RWC, %	WD, %	CA, mM H_2O_2/min × g d.w.	Flavo-Noids, % to d.w.
					Roots	Shoots				
20	0	50.1	119.8	2.9	3.4	6	80.1	23.1	7.5	0.51
20	10^{-5}	53.2	148.8	4.5	8.4	7.2	85.4	15.2	9.6	0.67
20	10^{-4}	67.1	153.1	4.7	8.5	7.9	89.2	9.3	9.6	0.78
20	10^{-3}	67.1	152.1	4.8	8.5	7.3	87.3	11.1	8.9	0.86
40	0	60.3	194.2	7.8	7.6	9.3	91.2	7.3	8.3	0.79
40	10^{-5}	73.2	197.6	8.2	7.3	14.6	92.5	3.2	7.2	1.07
40	10^{-4}	75.3	209.4	7.8	8.6	14.9	91.7	4.1	7.8	0.89
40	10^{-3}	72.6	220.3	8.4	7.6	14.5	91.9	1.6	7.5	0.97
60	0	72.5	210.1	7.9	6.3	13.1	91.6	3.1	5.5	0.68
60	10^{-5}	78.4	216.3	8.8	8.4	13.9	91.7	2.1	5.3	0.75
60	10^{-4}	80.1	203.8	7.9	7.4	17.5	91.6	1.9	5.5	0.73
60	10^{-3}	75.1	203.2	7.8	7.3	18.1	91.8	2.8	6.2	0.74
LSD		*1.1*	*4.1*	*0.3*	*5.9*	*6.8*	*1.4*	*6.1*	*0.8*	*0.1*
F_1		*2.47*	*2.36*	*3.23*	*2.42*	*2.24*	*2.70*	*8.50*	*2.70*	*16.95*
P_1		*0.05*	*0.08*	*0.03*	*0.05*	*0.07*	*0.03*	*0.00*	*0.03*	*0.00*
F_2		*2.90*	*4.80*	*5.55*	*2.63*	*4.68*	*5.52*	*17.21*	*3.10*	*20.77*
P_2		*0.07*	*0.01*	*0.01*	*0.08*	*0.01*	*0.01*	*0.00*	*0.06*	*0.00*

1—values of F and P for concentration of priming mixture as a categorical predictor, 2—values of F and P for soil moisture as a categorical predictor, LSD—least significant difference, F—Fisher's test, P—significance level.

Pre-sowing priming of wheat seeds with a mixture of AA, SA and CA significantly stimulated seed germination, biomass accumulation by shoots and roots of wheat seedlings, improved characteristics of water balance in the leaves under moderate and severe soil drought. Among the studied physiological characteristics catalase activity and flavonoid content were the most sensitive to the impact of the pre-sowing seed priming. The size of the protective effect of priming on the studied physiological characteristics of wheat seedlings positively correlated with the intensity of soil drought.

Water soluble allelochemicals extracted from shoots and roots of wheat seedlings displayed inhibitory effect on cress root growth (Table 2). Whereas the rhizosphere soil showed stimulative effect in the same bioassay. As soil moisture increased the inhibitory effect of water extracts from wheat seedlings shoots and roots increased also. The opposite tendency was observed for the stimulative activity of the rhizosphere soil.

Analysis of variance showed that the both soil moisture and seed priming significantly ($P < 0.05$) affected allelopathic activity of water extracts from roots and shoots of wheat seedlings as well as the content of allelochemicals and organic carbon in the rhizosphere soil. Moisture level also significantly affected the content of iron ions and nitrates in the rhizosphere soil (Table. 2).

Table 2. Analysis of variance of the effects of the priming mixture concentration and soil moisture on allelopathic activity of wheat seedlings, rhizosphere soil as well as on some agrochemical characteristics of the latter.

Soil Moisture, %	**PM Concentrati**	**Allelopathic Activity, % to Control**			**Soil pH, Carbon (%) and Macronutrients, mg/L**										
		Water Extracts		**Soil**	**C, %**	**pH**	**Mn**	**S**	**Fe**	**Mg**	**Ca**	**K**	**P**	**NO_3**	**NH_4**
		Roots	**Shoots**												
20	0	93.6	93.6	158	6.2	7.7	100	200	1250	132	6236	214.5	164	23	7.7
20	10^{-5}	88.0	49.6	127	6.2	7.7	100	200	1250	132	6331	205.2	164	15	10
20	10^{-4}	88.7	48.0	122	6.6	7.8	110	200	1150	132	6831	205.2	164	15	7.7
20	10^{-3}	80.7	48.0	128	6.2	7.8	100	200	1150	132	5664	205.2	164	15	10
40	0	64.5	60.1	112	3.9	7.8	100	200	1250	142	5998	223.8	109	18	10
40	10^{-5}	60.8	56.4	117	3.6	7.7	100	200	1250	132	5664	223.8	109	9.5	10
40	10^{-4}	61.2	54.7	113	3.9	7.8	100	200	1150	132	5831	224.5	112	11	10
40	10^{-3}	60.2	51.8	114	4.2	7.7	100	200	1200	122	5998	223.8	109	11	8.2
60	0	64.3	63.1	110	3.2	7.8	100	200	1000	131	5664	186.6	109	18	10
60	10^{-5}	63.2	55.7	97	2.6	7.6	80	200	750	122	5664	214.5	109	8.5	7.9
60	10^{-4}	62.3	49.8	93	2.1	7.7	80	200	750	132	6164	223.8	110	7.5	7.9
60	10^{-3}	58.5	45.8	94	2.6	7.7	120	200	750	131	6831	214.5	109	8.0	10
LSD		*2.2*	*2.3*	*2.6*	*0.1*	*0.1*	*8.9*	*8.3*	*6.9*	*4.4*	*4.4*	*7.2*	*3.8*	*2.2*	*0.8*
F_1		*3.5*	*2.31*	*3.32*	*1.5*	*0.1*	*1.7*	*0.9*	*0.24*	*4.1*	*2.78*	*0.08*	*0.6*	*4.6*	*0.9*
P_1		*0.02*	*0.10*	*0.02*	*0.2*	*1.0*	*0.2*	*0.5*	*0.86*	*0.1*	*0.08*	*0.96*	*0.61*	*0.1*	*0.5*
F_2		*19.8*	*0.38*	*42.7*	*34*	*0.2*	*1.5*	*0.6*	*0.18*	*0.2*	*0.08*	*0.21*	*0.84*	*8.6*	*0.8*
P_2		*0.00*	*0.68*	*0.00*	*0.0*	*0.9*	*0.2*	*0.7*	*0.88*	*0.9*	*0.98*	*0.89*	*0.5*	*0.1*	*0.5*

1—values of F and P for concentration of priming mixture as a categorical predictor, 2—values of F and P for soil moisture as a categorical predictor, LSD—least significant difference, F—Fisher's test, P—significance level.

Analysis of the interactive effect of pre-sowing seed priming and soil drought on allelopathic activity of the rhizosphere soil and water extracts from roots of wheat seedlings showed cross-synergism (C_{IE} = 26.7 and 21.4, respectively). However, the interactive effect of pre-sowing seed priming and soil drought on allelopathic activity of the water extracts from shoots of wheat seedling was negative (C_{IE} = −41.7), so we assumed a cross-antagonism.

The analysis of the distribution of macronutrients in the rhizosphere soil under wheat seedlings showed that the content of organic carbon (C %), iron, phosphorus and nitrates inversely depended on the level of soil moisture (Figure 1). The content of manganese, sulfur, potassium and calcium in the soil under the test plants did not display any significant dependence on the moisture level.

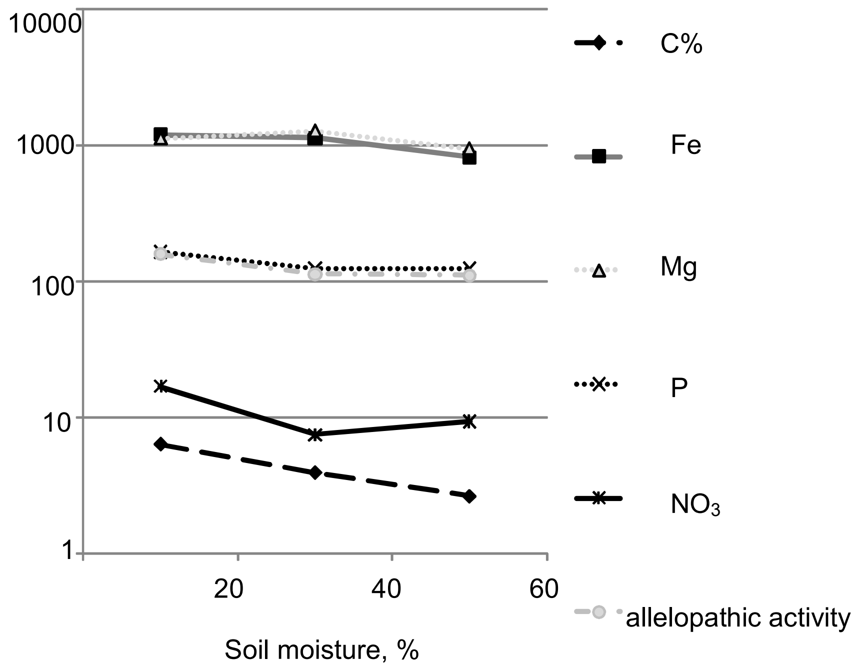

Figure 1. The dependence of content of some macronutrients (mg), organic carbon (C%) as well as allelopathic activity of the rhizosphere soil of wheat seedlings on soil moisture level.

Correlation analysis showed that allelopathic activity of the rhizosphere soil positively correlated with the content of organic carbon (R = 0.87), iron (R = 0.73), phosphorus (R = 0.42), and nitrates (R = 0.74).

Factor analysis (principal components method) of the studied characteristics of the rhizosphere soil showed that the allelopathic activity, concentrations of organic carbon, nitrates and magnium ions are the most sensitive to environmental changes (Figure 2). Changes in allelopathic activity of the rhizosphere soil closely correlated with changes in organic carbon, nitrates, iron and phosphorus. While the rest of the studied macronutrients as well soil reaction showed no such correlation. This conclusion is in good agreement with ANOVA results (see Table 2).

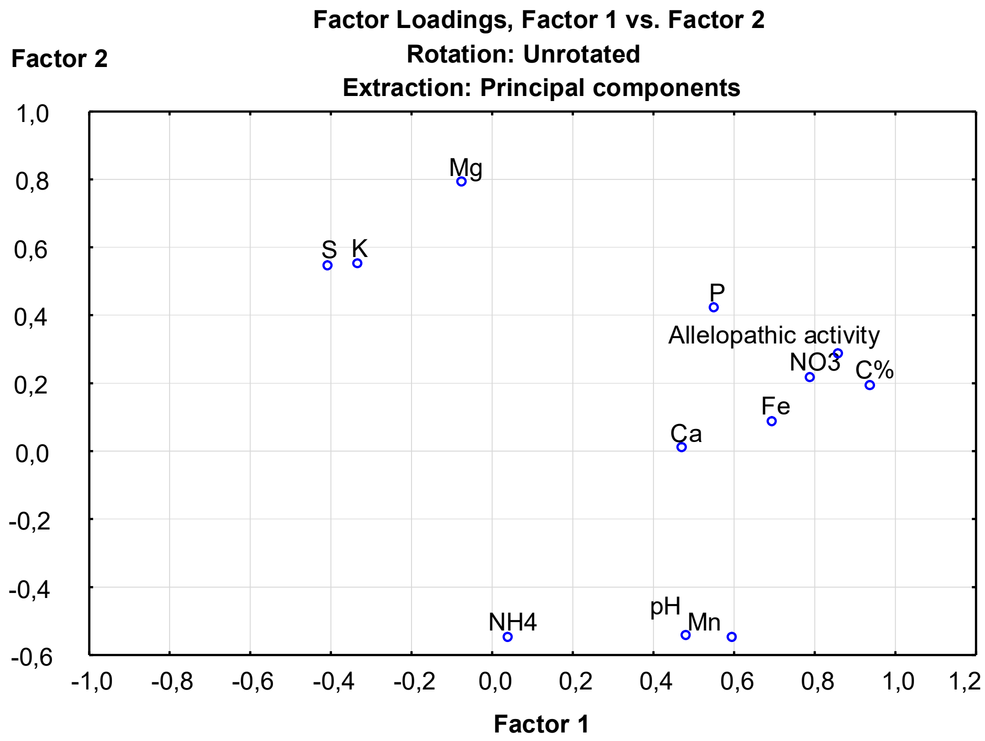

Figure 2. Factor analysis of the rhizosphere soil characteristics.

4. Discussion

Summarizing the data obtained in this study as well as the results of other works [3,4,6] published on the problem of interaction between allelopathy and abiotic stress factors, it can be concluded that a short and mild exposure to allelopathic stress (in our study it was simulated by wheat seeds pre-sowing priming with millimolar concentration of AA, SA and CA) may mitigate the adverse effects of a subsequent abiotic stress (i.e., soil drought). This phenomenon is referred to as a cross-adaptation. Despite the considerable interest of modern phytophysiologists in the phenomena of cross-adaptation, cross-synergism, and cross-antagonism their physiological mechanisms are practically unclear. It is believed that cross-adaptation is based on non-specific adaptive reactions, playing an important role in the induction of protective antioxidant systems [20,21]. It is known, that exogenous phenolic acids can cause the oxidative damage through enhanced generation of ROS leading to the increase in the activities of antioxidant defense systems and induction of signaling cascades [22,23]. In phytotoxic concentrations exogenic phenolic acids could have in test-plants similar effects as a water stress [22,24].

In our study, pre-sowing priming of wheat seeds with millimolar concentration of AA, SA and CA induced nonspecific defense mechanisms (increased catalase activity, flavonoid content, changes in shoot/root ratio) which contributed to the observed increased resistance to the subsequent soil drought. On the other hand, seed priming stimulated accumulation of allelopathic inhibitors in shoots and roots of the wheat seedlings (cross-synergism).

In our experiment the effect size of seed priming positively correlated with the intensity of soil drought. This tendency is in a good agreement with the findings of other authors stating that intensification of stress conditions enhances the physiological activity of phenolic acids to test-plants [**Error! Reference source not found.**]. It is known that climatic and edaphic factors (ultraviolet (UV) radiation, low/high temperature, ozone, heavy metals, drought, availability of nutrient ions etc.) may play a significant role in accumulating allelochemicals or their breakdown products to bioactive levels [3,4,6,25]. Nevertheless till now the issue of the interaction between allelopathic factor and environmental stresses has been given little consideration.

Soil drought stimulated excretion of allelochemicals with stimulative activity into the rhizosphere soil by wheat seedlings. On the other hand drought inhibited accumulation of phytotoxic allelochemicals in living organs (shoots and roots) of wheat seedlings. This led to amelioration of allelopathic conditions of soil surrounding seedling`s roots, which could contribute to enhanced vitality of wheat seedlings under stressful conditions (cross-adaptation).

Winter wheat is known for its high allelopathic potential due to the presence of hydroxamic and phenolic acids in its exudations [**Error! Reference source not found.**]. This trait allows this crop to reduce the seed bank of weeds in the soil and minimize the necessity in herbicides. The results obtained in our study demonstrated that abiotic (drought) and biotic (allelochemicals) factors of the environment could significantly modify both intrapopulation allelopathic interactions between wheat plants as well as their effects on weeds.

Apart from the direct effect of soil moisture on crop physiological processes this factor also alters soil microbial population, mineralization processes, redox reaction and absorptive properties [**Error! Reference source not found.**]. In our studies as soil drought intensified the content of organic carbon, iron, phosphorus and nitrates increased. This tendency correlated well with the stimulative activity of the rhizosphere soil. While the content of ammonia, magnesium, manganese, sulfur, potassium, and calcium in the rhizosphere soil of test plants did not show any significant dependence on the level of soil moisture. Obviously, this is due to the differences in the mobility of the nutrients in the soil, which are more readily up taken by plants with optimal water supply.

Many allelochemicals, particularly, organic acids, phenolics etc. were shown to interact with soil nutrients immobilizing them or increasing their availability to plants. For example, phenolic acids (p-coumaric, ferulic, p-hydroxybenzoic, protocatechuic etc.) were shown to influence the accumulation of soil organic N and inorganic ions such as Al, Fe, Mn, and PO_4 [**Error! Reference source not found.**]. On the other hand nutrient ions such as Mn, Fe, Al could form complexes with phenolic allelochemicals, thus modulating their effect on plants [**Error! Reference source not found.**]. Effect of allelochemicals on nutrient dynamics may ultimately affect the growth of plants in the community. Though such an effect could contribute significantly to the overall allelopathic effects within plant community the interaction between these two mentioned factors is rather poorly studied till now. Further studies are needed to elucidate the relations between abiotic factors and allelochemicals for understanding of the actual modes of action of allelopathic factor in the agricultural and natural ecosystems.

According to the results of our study changes in allelopathic activity of the rhizosphere soil closely correlated with changes in organic carbon, nitrates, iron and phosphorus. While soil reaction, concentration of ammonia, manganese, potassium, sulfur displayed no correlation with soil allelopathic activity. Further studies are needed to elucidate relations between macronutrients and allelopathic regime of the rhizosphere soil.

The results of our studies also demonstrated that wheat seedlings could modify allelopathic and nutritional regime in the soil surrounding their roots in response to pre-sowing seed priming and drought stress suggesting that wheat seedling could directly influence the magnitude of effects of the studied factors through feedback regulation. Such information will open new possibilities for a deliberate and predictable approach for improvement of the adaptation of the current agricultural practices to the predicted global climatic changes and growing food requirements of the world population.

5. Conclusions

In summary, the present study demonstrated complicated interactions between allelopathy and soil drought on physiological and allelopathic characteristics of the target plants. A mild allelopathic stress applied to seeds made seedlings more resistant to subsequent drought stress and contributed to the increase of their allelopathic potential. Intensification of drought stress resulted in the decrease of production of allelopathic inhibitors in the tissues of wheat seedlings and enhancement of concentrations allelopathic stimulants and organic carbon in the rhizosphere soil. Changes in allelopathic activity of the rhizosphere soil closely correlated with the changes in organic carbon, nitrates, iron and phosphorus. While soil reaction, concentration of ammonia, manganese, potassium, sulfur displayed no correlation with soil allelopathic activity.

Thus, wheat seedlings showed their ability to modify allelopathic and nutritional regime in the soil surrounding their roots in response to pre-sowing seed priming and drought stress, which allowed them to change their immediate environment condition to be more favorable for their further growth and development. Our findings give additional evidence that the ecological role of allelochemicals is more versatile than it is commonly believed (i.e., limited to intraspecific or interspecific competition or defense against pests and pathogens). It is a great challenge for the future studies to assess the real role of allelochemicals in adaptation of plant communities to the stressful environmental factors at the ecosystem level.

Author Contributions: N.P.D. conceived and designed the experiments, analysed the data; N.V.R. and B.O.I. performed the experiments; N.P.D. and N.V.Z. X.X. and Y.Y. wrote the paper. All authors have read and agreed to the published version of the manuscript.

Abbreviations

The following abbreviations are used in this manuscript:

AA	Ascorbic acid
CA	Cinnamic acid
SA	Salicylic acid
CAT	Catalase activity
RWC	relative water content
WD	water deficit
d.w.	dry weght
PM	priming mixture
C%	organic carbon
ANOVA	analysis of variance
LSD	least significant difference

References

1. Rehman, S.; Harris, P.J.C.; Ashraf, M. Stress environments and their impact on crop production. In *Abiotic Stresses: Plant Resistance through Breeding and Molecular Approaches*; Ashraf, M., Harris, P.J.C., Eds.; Haworth Press: New York, NY, USA, 2005; pp. 3–18.
2. Vyshnivskiy, P.S. Multiplicity of manifestation of adverse weather conditions in the forest steppe zone in growing oilseeds cabbage. In *Proceedings of the National Scientific Center "Institute of Agriculture NAAS"*; Tvory: Kyiv, Ukraine, 2013; pp. 102–108.
3. Didyk, N.P.; Blum, O.B. Natural antioxidants of plant origin against ozone damage of sensitive crops. *Acta Physiol. Plant.* **2011**, *33*, 25-34, doi:10.1007/s11738-010-0527-5.
4. Didyk, N.P.; Rositska, N.V.; Berebenchuk, L.D. The effect of rutin, ascorbic and salicylic acids on the functional state of wheat plants under drought conditions. *Physiol. Biochem. Cultiv. Plants* **2011**, *43*, 453–458.
5. Didyk, N.P. Seed pre-treatments improve resistance to allelopathic stress. *Fiziol. Rast. Genet.* **2017**, *49*, 339–346.
6. Didyk, N.P.; Zakrasov, O.V.; Rositska, N.V.; Kharitonova, I.P. Acclimation of corn plants to drought stress after a pre-treatment with allelochemicals. *Fiziol. Rast. Genet.* **2014**, *46*, 449–454.
7. Zhang, Y. Biological Role of Ascorbate in Plants. In *Ascorbic Acid in Plants: Biosynthesis, Regulation and Enhancement*; Springer: New York, NY, USA, 2013; pp. 7–33, doi:10.1007/978-1-4614-4127-4.
8. Kolupaev, Y.E.; Yastreb, T.O. Stress-protective effects of salicylic acid and its structural analogues. *Physiol. Biochem. Cultiv. Plants* **2013**, *45*, 113–126.
9. Hara, M.; Furukawa, J.; Sato, A.; Mizoguchi, T.; Miura, K. Abiotic Stress and Role of Salicylic Acid in Plants. In *Abiotic Stress Responses in Plants. Metabolism, Productivity and Sustainability*; Ahmad, P., Prasad, M.N.V., Eds.; Springer: New York, NY, USA, 2012; pp. 235–251.
10. Rivas-San, V.M.; Plasencia, J. Salicylic acid beyond defense: Its role in plant growth and development. *J. Exp. Bot.* **2011**, *62*, 3321–3338.

11. Li, Z.-H.; Wang, Q.; Ruan, X.; Pan, C.-D.; Jiang, D.-A. Phenolics and Plant Allelopathy. *Molecules* **2010**, *15*, 8933–8952, doi:10.3390/molecules15128933.
12. Lutts, S.; Benincasa, P.; Wojtyla, L.; Kubala, S.; Pace, R.; Lechowska, K.; Quinet, M.; Garnczarska, M. Seed Priming: New Comprehensive Approaches for an Old Empirical Technique. In *New Challenges in Seed Biology—Basic and Translational Research Driving Seed Technology*; Araujo, S., Balestrazzi, A., Eds.; InTech: London, UK, 2016; pp. 1–49.
13. Grigoryuk, I.A.; Tkachev, V.I.; Savinski, S.V.; Musiyenko, N.N. *Modern Methods of Investigations and Assessment of Drought and Heat Tolerance in Plants. Methodic Guide*; Nauk. Svit: Kyiv, Ukraine, 2003; 139p.
14. Pleshkov, B.P. *Practical Work on Plant Biochemistry*; Agropromizdat: Moscow, Russia, 1985, 255p.
15. Komarov, M.N.; Nikolaev, L.A.; Regir, V.G.; Tesov, L.S.; Kharitonova, N.P.; Shatokhina, R.K. (Eds.) Phytochemical analysis of medicinal plants. In *Methodical Guide for Laboratory Works*; CPHPA: Saint Petersburg, Russia, 1998; pp. 30–35.
16. Grodzinski, A.M.; Kostroma, E.Ю.; Shrol`, T.S.; Khokhlova, I.G. Methods of direct bioassay of soil and metabolites of microorganisms. In *Allelopathy and Plant Productivity*; Grodzinski, A.M., et al., Eds.; Naukova Dumka: Kyiv, Ukraine, 1990; pp. 121-124.
17. Grodzinsky, A.M. *Plant Allelopathy and Soil Sickness: Selected Works*; Naukova Dumka: Kyiv, Ukraine; 1991; 432p.
18. Rinkis, G.Y.; Nollendorf. V.F. *Macro and Micronutrients in Balanced Nutrition of Plants*; Zinatne, Riga, USSR: 1982; 202 p.
19. Antomonov, M.Y. *Mathematical Processing and Analysis of Medical and Biological Data*; Publishing House "Maly Druk": Kyiv, Ukraine, 2006; 558p.
20. Alexieva, V.; Ivanov, S.; Sergiev, I.; Karanov, E. Interaction between stresses. *Bulg. J. Plant Physiol.* **2003**, 1–17. Barkosky, R.R.; Einhellig, F.A. Allelopathic interference of plant-water relationships. *Bot. Bull. Acad. Sin.* **2003**, *44*, 53–58, doi:10.1007/BF00993692.
21. Kolupaev, Y.Y.; Obozny, O.I. Active forms of oxygen and antioxidant system at cross-adaptation of plants to the action of abiotic stressors. *Bull. Kharkiv Natl. Agrar. Univ. Ser. Biol.* **2013**, *3*, 18–31.
22. Romero-Romero, T.; Sánchez-Nieto, S.; SanJuan-Badillo, A.; Cruz-Ortega, R. Comparative effects of allelochemical and water stress in roots of *Lycopersicon esculentum* Mill. (*Solanaceae*). *Plant Sci.* **2005**, *168*, 1059–1066.
23. Weir, T.L.; Park, S.W.; Vivanco, J.M. Biochemical and physiological mechanisms mediated by allelochemicals. *Curr. Plant Biol.* **2004**, *7*, 472–479.
24. Blum, U.; Gerig, T.M. Relationships between phenolic acid concentrations, transpiration, water utilization, leaf area expansion, and uptake of phenolic acids: Nutrient culture studies. *J. Chem. Ecol.* **2005**, *31*, 1907–1932, doi:10.1007/s10886-005-5934-5.
25. Mierziak, J.; Kostyn, K.; Kulma, A. Flavonoids as Important Molecules of Plant Interactions with the Environment. *Molecules* **2014**, *19*, 16240–16265, doi:10.3390/molecules191016240.
26. Fragasso, M.; Iannucci, A.; Papa, R. Durum wheat and allelopathy: Toward wheat breeding for natural weed management. *Front. Plant Sci.* **2013**, *4*, 375. Doi:10.3389/fpls.2013.00375.
27. Zaimenko, N.V.; Pavliuchenko, N.A.; Ellanska, N.E.; Kharytonova, I.P. The effect of drought on allelopathic, biochemical, microbiological characteristics of the system plant-soil-microorganisms. *Bull. Kharkiv Natl. Agric. Univ. Ser. Biol.* **2014**, 286–294.
28. Inderjit Weiner, J. Plant allelochemical interference or soil chemical ecology? *Perspect. Plant Ecol. Evol. Syst.* 2003, *4*, 3–12, doi:10.1078/1433-8319-00011.