

Full Length Research Paper

Allelopathy regulates wheat genotypes performance at the enhancement stage by soil water and prohydrojasmon (PDJ)

Shengpeng Zuo^{1,2#}, Jinhu Zhi⁴, Hongbo Shao^{2,3,5#*} and Guangchao Zhao¹

¹College of Environmental Science and Engineering, Anhui Normal University, Wuhu 241000, China.

²State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling 712100, China.

³Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, China.

⁴College of Plant Sciences, Tarim University, Alaer 843300, China.

⁵Institute for Life Sciences, Qingdao University of Science and Technology, Qingdao 266042, China.

Accepted 28 July, 2010

Growth adaptation and allelopathic potential of four winter wheat (*Triticum aestivum* L.) accessions has been investigated in pot experiments by prohydrojasmon (PDJ, 10 - 5M) and soil water (75 and 45%) at the enhancement stage. This paper also presented the performance of photosynthesis, water use and weed suppression. The effect of soil water and PDJ on wheat performance displayed significant differences depending on tested wheat cultivars and measured parameters. Water deficit decreased plant biomass significantly and changed phenotypic characteristics like plant height and leaf area of wheat. However, PDJ was found to stimulate wheat root growth and development so as to enhance pressure resistance and induce strong allelopathic potential and weed resistance. Physiological response in var. Lankao 95 - 25 to water shortage and PDJ was significantly relative to net photosynthesis rate and water use efficiency. Water deficit and PDJ would lead to plant phenotype and photosynthesis change and consequently, influence allelopathic expression and weed suppression of wheat based on Canonical Correspondence Analysis (CCA). Water deficit would induce the production and accumulation of more allelochemicals in wheat by passive transport of energy cost. Differing the regulation mechanism of water stress, PDJ showed active transport of energy supply in allelopathic stimulation, which implied that PDJ mainly exhibited its hormone effect to regulate and control wheat growth and development such as improving phenotypic features on competition at the basis of increasing growth cost. Therefore, it was possible for artificial measures to regulate allelopathic potential and weed resistance capacity of winter wheat cultivars, especially, in the arid areas of Loess Plateau of China.

Key word: Allelopathic potential, inducible regulation and interaction, prohydrojasmon, soil water stress, weed suppression, winter wheat.

INTRODUCTION

On the Loess Plateau, China, soil drought is the main limiting factors influencing the growth and yield of wheat. As a widely planted crop, wheat has acquired two kinds of

significant response systems to long drought pressure.

One is that wheat can change its growth and developmental phenotype to deal with an arid environment through long ecological adaptation, which is more linked with allelopathic regulation. The other anti-drought mechanism is that wheat can conduct a short-rapid physiological acclimatization where it will maintain water balance of the plant by closing leaves stoma and decreasing water loss due to transpiration effect (Shao et al., 2005, 2008c, 2009).

*Corresponding author. E-mail: shaohongbochu@126.com. Tel: +86 532 84023984.

#These authors contributed equally to this paper

Drought can lead to the closing of leaf stoma for a short term, which shows a complex procedure of physiological response. The direct phenomenon is the change of photosynthesis parameter of gas exchange (Shao et al., 2008 a,b). Farquhar and Sharkey (1982) deduced that the decline of stoma conductance of plant leaf would significantly affect the photosynthesis rate. Of course, after a long period for environmental adaptation, plants can adapt to the optimum circumstance. Meanwhile, it also endures abrupt changes of nature. Under environmental pressure, plants compete with other plants for limited resources by physical capacity to a lesser extent, but more by chemical techniques (Pare and Tumlinson, 1997). Emeterio et al. (2004) concluded that in the mixture treatment of *Lolium rigidum* Gaud, results showed stronger allelopathic potential to inhibit root growth of other plants under drought conditions. Oueslati et al. (2005) discovered that the auto-toxic effect of *Hordeum vulgare* L. grown in an arid region was correlated closely with water conditions in the growth season; with more serious drought it would become stronger. Therefore, it is presumed that in the arid season, more allelochemicals will be induced to produce and accumulate in a short period so that it exhibits allelopathic effect for its high concentration of allelochemicals. Tang et al. (1995) observed that *Tagetes erecta* under water stress could be induced to exude a higher concentration of phenolics compared with the control as normal water.

Propyl dihydro-jasmonate/prohydrojasmon (PDJ), as an important hormone substitute in plant growth and development, not only regulates key growth and development process, but also modulates markedly important physiological responses and functions. Especially, PDJ was synthesized and had similar functions with endogenous jasmonic acids or jasmonate (Koshiyama et al., 2003). When apple trees were treated by PDJ, the photosynthesis rate of leaves were enhanced and root vigor and endogenous abscisic acid (ABA) increased, leaf stoma closed so as to enhance resistance capacity to an adverse environment (Liu et al., 1999). PDJ can increase significantly anti-drought capacity of earthnut under drought condition, as it can promote the rapid accumulation of leaf proline (Pro) and soluble sugar as well as maintain high water content, delay the decline of enzyme activity such as superoxide dismutase (SOD) and catalase (CAT), gradually and stably enhance the activity of peroxidase (POD) and decrease malondialdehyde (MDA) content (Shao et al., 2005, 2008 a, b, c, 2009; Dong et al., 2002; Chen and Wang, 1997). In addition, the analogues of PDJ, jasminates, also showed significant effect on inducible regulation of drought resistance and the allelopathic effect of plants. Especially, in water shortage circumstance, tea seedlings could improve photosynthesis efficiency with methyl jasmonate (MJ) application, propel root development and enhance water use efficiency, so that the anti-drought capacity increased (Su, 2004). On rice allelopathy induction, exogenous jasminates induced the synthesis of functional allelochemicals whether in an inside or outside condition, whose effect connect significantly with the concentration and the and the inducible

period of jasminate utilization. Although exogenous MJ would induce the synthesis of abundant allelochemicals, the effects only maintain very short interval with the change of outside factor dynamics. When treated with 0.14 mol/L for 48 h, MJ displayed the strongest inducible effect on rice allelopathy. Meanwhile, different rice accessions exhibited various responses to MJ effect of allelopathic induction (Kong et al., 2004).

Under PDJ application and moderate drought, plants can increase leaf metabolism activity, which implies that both synergisms possibly affected the adaptive style of crops to adverse environments, including drought (Shao et al., 2009, 2008a; Hassan, 2006). However, there is no information on PDJ inducible effect on crop allelopathy and relative physiological and biochemical mechanisms, especially the regulatory effect of multiple resistances to exterior stress. Thus, it is necessary to study the relationship of PDJ and allelopathic characteristics. In addition, on the Loess Plateau, it is important to know how to apply PDJ to regulate crop growth and weed suppression under drought pressure and its management in crop production practices by investigating physiological mechanisms such as photosynthesis and allelopathy. In the present study, the effect of allelopathic expression of different wheat varieties was with PDJ soaking before seed sowing and water treatment in a continuous period of artificial control of 45 and 75% field water capacity since greening. The objectives of the present study are: (1) To investigate water stress and PDJ effect on allelopathic expression as well as the interaction effect; (2) to explore physiological mechanisms from the viewpoint of photosynthesis effect; (3) to analyze the synergistic effect on water use efficiency and allelopathy by exterior factors like water and hormone analogues such as PDJ.

MATERIALS AND METHODS

Pot test

Pot experiments were carried out in the greenhouse of the Institute of Water and Soil Conservation, Chinese Academy of Sciences. In the present study, we took neutral soil as a test sample. The soil contains 0.11% total nitrogen, water hydrolyzed nitrogen of 118.43 mg.kg⁻¹, 1.32% organic matters, 75 kg/hm⁻² phosphorus as P₂O₅, 20.05% field water capacity. In addition, the soil contained water of 22.34% before wheat seeds were sowed.

Four typical wheat (*Triticum aestivum* L.) cultivars with different allelopathic behavior, grown widely on the Loess Plateau, were selected and treated by full random design of two factors. At first, seeds were soaked by 10⁻⁵ mol/l PDJ (Treatment X) before being sown. The control group was not PDJ treated (0 mol/l, Treatment O). The chemical formula of PDJ, provided by Dr. Kunitaka Tachibana of Japan Meiji Seika Kaisha, Ltd. Co., and its analogue MJ are shown in Figure 1. After that, wheat materials were treated by normal water conditions of normal (75%, 1) and stress (45%, 2) conditions from the greening stage. Four wheat accessions of Lankao 95 - 25, No 6 Xiaoyan, Yumai 66 and Lankao 217 exhibited non-significant difference in one thousand seeds weight (40.58 ~ 42.33 g). They belonged to late mature varieties with weak winter property. These seeds were arranged in 96 pots by six replications, sowing with 10 seeds in even design after being soaked by PDJ

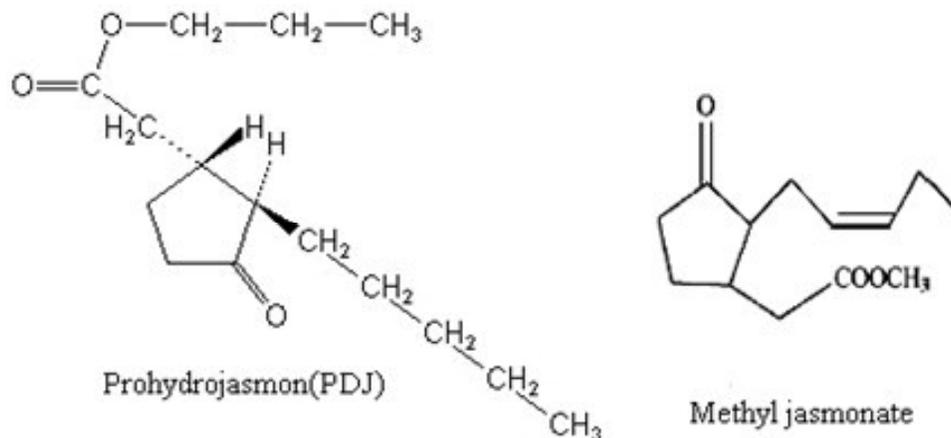


Figure 1. Chemical formula of PDJ and its analogue methyl jasmonate.

according to the method of Zuo et al. (2005).

Tested methods

In the enhancement stage of wheat, four wheat genotypes were investigated for leaf area index, plant height, mean node distance, chlorophyll content of flag leaf, above-ground biomass, root biomass, number of weed plant per pot and total weed biomass per pot at fresh weight, respectively.

At 9.00-11.00 am in a sunny day, photosynthesis parameters such as the photosynthesis rate of flag leaf or inverse second leaf (P_n , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), stoma conduction rate (G_s , $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), cellular CO_2 concentration (C_i , $\mu\text{L}\cdot\text{L}^{-1}$), transpiration rate (E , $\text{mol}/\text{g}\cdot\text{s}$) and water use efficiency (WUE) were measured with four replications per treatment by an Li-6400 photosynthesis system instrument (LI-COR, USA). While surveying the above indices, mean CO_2 concentration and gas velocity in the air were $375 \pm 6 \mu\text{L}\cdot\text{L}^{-1}$ and $5 \text{ ml}\cdot\text{min}^{-1}$, respectively. The value of L_s photo-system in the leaf was calculated according to the methods of Farquhar and Sharkey (1982) as $L_s = 1 - C_i/\text{Ca}$.

In the enhancement stage, all aboveground biomass and underground roots of wheat materials were cut, divided and stored for further treatment after being cleaned and then naturally dried. That is to say, samples were frozen for 48 h under -4°C and then freeze dried under -50°C . All were reduced to powder, which was immersed for 24 h per sample in water with a weed to water ratio of 1:10 (w/w). After that, the solution was extracted with ultrasonic for 30 min and filtered so as to acquire a super-stratum solution for aqueous extract. *T. aestivum* var. No 1 Jinchun was adopted as the tested acceptor for later allelopathic bioassays based on the method of Zuo et al. (2005).

From the formula, $R = T/C^{-1}$, the relative parameters such as R - RI and S - RI for allelopathic indices of aboveground parts and underground, roots, respectively were deduced. Meanwhile, weed resistance indices like WN (weed plants per pot) and WB (total weed biomass per pot, fresh weight) indicated wheat suppressing weed capacity according to weed plant numbers and total weed biomass per pot. The results were analyzed using the allelopathic assessment method designed by Williamson and Richardson, (1988). The rate of acceptor indices in the treatments (T) and the control (C) formed the comparison index. The allelopathic reaction index (RI) equals $(T/C)^{-1}$. A positive RI value indicates a stimulating effect. A negative RI value indicates an inhibitive effect. The absolute value of RI reflects the intensity of the allelopathic effect. Four wheat accessions were treated by random procedures,

marked as PDJ and 75% soil water (X - 1), PDJ and 45% soil water (X - 2), no PDJ and 75% soil water (O - 1) and no PDJ and 45% soil water (O - 2). Among these treatments O - 1 was hypothesized as the control, given the value of 1. Then, the other three treatments can get their values for (X - 1)/ (O - 1), (X - 2)/ (O - 1) and (O - 2)/ (O - 1) as treatments like X - 1, X - 2 and O - 2.

Statistical analysis

All data were analyzed using the Statistical Package for the Social Sciences (SPSS) 13.0 software for statistical analyses like one-way analysis of variance (ANOVA) and Fisher's Least Significant Difference (LSD) analysis of multiple comparisons. Relationship analysis was conducted by using CCA software in Cacono 4.5.

RESULTS

Growth response of different wheat genotypes under water and PDJ treatments

Growth response showed significant differences dependent on different wheat genotypes and various tested indicators under water and PDJ treatments (Figure 1). Generally, PDJ exhibited two typical types of influential effects mainly on roots development for root stimulation (Figure 2C and D) and root inhibition (Figure 2A and B). Var. Lankao 95 - 25 displayed non-significant differences in leaf area and chlorophyll content under water and PDJ treatment compared with the control. However, plant height and mean node distance decreased, but without significant effect. The underground biomass declined significantly. The three treatments, X - 1, X - 2 and O - 2 were 31, 50 and 62% less than the control, respectively. Similarly, root biomass of X - 1 was 27% lower than normal growth (Figure 2A). Var. No 6 Xiaoyan showed a significant decline in plant biomass for 32 - 62% of aboveground biomass and 10 - 49% of root biomass, less than the control under water and PDJ treatment, without significant difference in other tested indicators (Figure 2B).

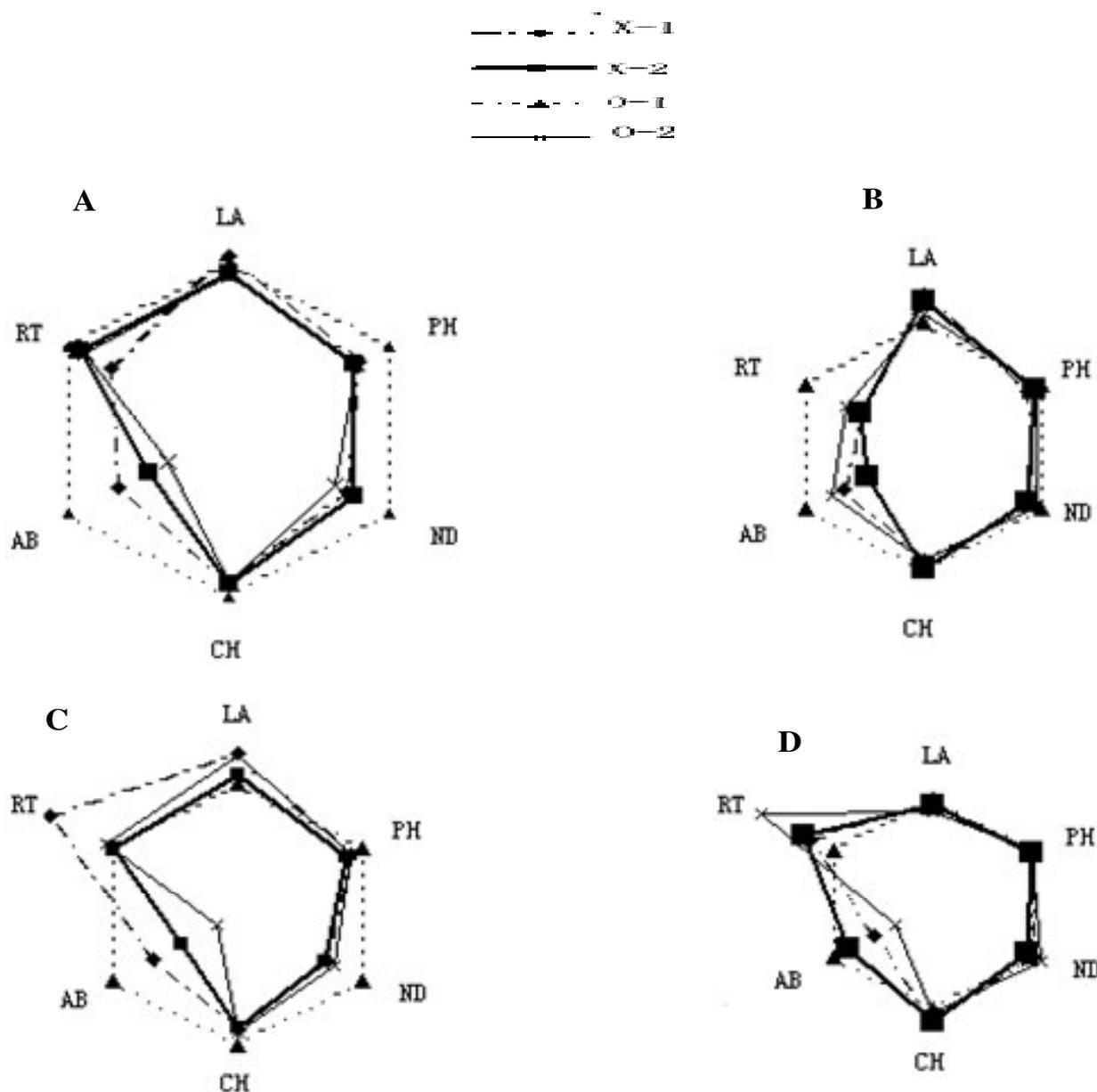


Figure 2. Growth dynamic of wheat genotypes at the enhancement stage under water stress and PDJ pretreatments. The treatment O - 1 in four wheat genotypes was considered as the control, given the value 1. Other parameters' values were calculated from the rate of the treatment to the control. Based on four treatments and six tested indicators in four wheat genotypes, their growth dynamics in equilateral hexagons is shown. Among the Figures, the center was the beginning as the value 0, the distance from the center to the acme was 1. Some relative signals were exhibited as treatments for X (+PDJ), O (-PDJ), 1 (75% soil water) and 2 (45% soil water); wheat accessions for A (var. Lankao 95 - 25), B (var. No 6 Xiaoyan), C (var. Yumai 66) and D (var. Lankao 217); tested indicators for LA (leaf area), PH (plant height), ND (node distance), CH (chlorophyll content), AB (aboveground biomass) and RT (root biomass).

Var. Yumai 66 displayed different changes in various parameters. All treatments showed non-significant difference in plant height and chlorophyll, but all three treatments showed mean node distance of 26% lower than that of the control and the aboveground biomass exhibited in decreasing order a decline rate of the treatment to the control from O - 2 (84%), to X - 2 (54%), to X - 1 (32%). However, with PDJ regulation and water control,

in all treatments, wheat flag leaf area increased significantly by 8 - 24%. Roots biomass in X - 1 treatment increased significantly by 51% compared with the control, but not in O - 2 and X - 2 treatments (Figure 2C). Var. Lankao 217 showed similar changes of no significant difference with Var. No 6 Xiaoyan in these parameters: Flag leaf area, plant height, mean node distance and chlorophyll content under PDJ regulation and water

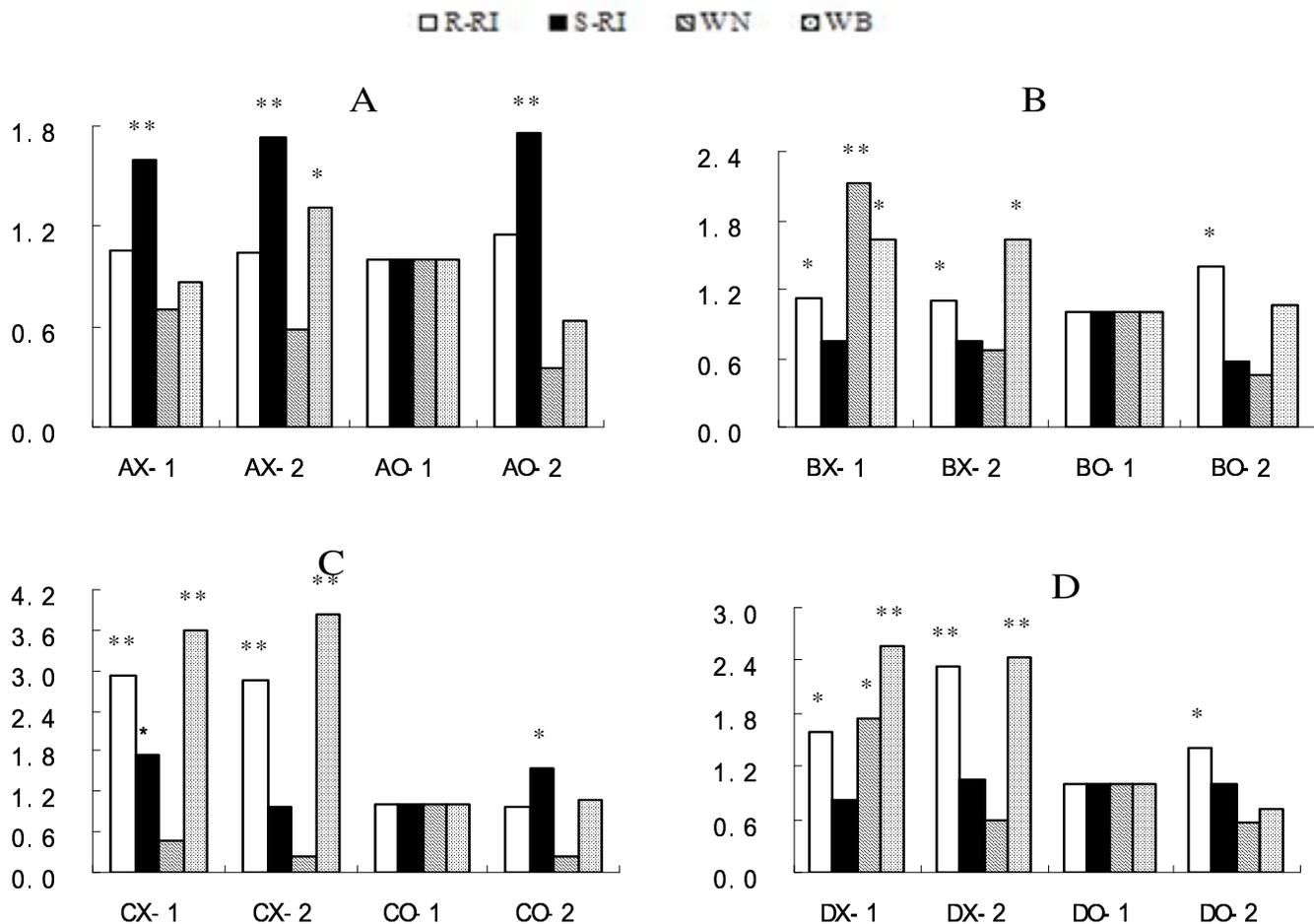


Figure 3. Effects of water and PDJ on allelopathic expression and weed resistance of four typical wheat cultivars at the enhancement stage. In all treatments, O - 1, as the control, was presumed as the value (1.0), Y axis showed the rate of the treatment to the control. Some relative signals were exhibited as treatments for X (+PDJ), O (-PDJ), 1 (75% soil water) and 2 (45% soil water); wheat accessions for A (var. Lankao 95 - 25), B (var. No 6 Xiaoyan), C (var. Yumai 66) and D (var. Lankao 217). Water and PDJ as well as wheat accessions designed randomly made up of 16 treatments (from AX-1 to DO-2). Allelopathic indicators as R - RI and S - RI mean root response index and aerial parts response index, respectively. Weed resistance capacity was displayed by WN (weed plants per pot) and WB (total weed biomass per pot, fresh weight). * Suggested least significant difference on 5% level (LSD). Some indices were measured as R - RI (response index of receptor seedling roots to donor allelopathy), S - RI (response index of receptor seedling stems to donor allelopathy), WN (suppressive effect of weeds number in wild tests by donor materials) and WB (suppressive effect of weeds biomass in wild tests by donor materials).

management. Three treatments, O - 2, X - 1 and X - 2, caused a significance decrease of the aboveground biomass by 15 - 60%. Unlike the aboveground biomass, roots increased by 73% (O - 2), 23% (X - 1) and 30% (X - 2) (Figure 2D).

Summarizing from the above description, soil water stress (O - 2) will possibly inhibit or delay the growth and development of plants. However, under the inducible effect of exterior factors, plants can culture an adaptive strategy of active change with a dynamic environment by inner physiological mechanisms like PDJ production, accumulation and regulation, which are generally considered a great strategy named as life history choice. PDJ, as a growth hormone alternative, is discovered scarcely in plant body due to its limited content or particular circumstance. In the present study, its addition (X - 1)

showed two effects depending on wheat cultivars, concentration and growth indices. Firstly, PDJ can enhance plant resistance to an adverse environment like water deficit (X - 2). Secondly, PDJ can promote root growth of acceptor plants, so it possesses similar properties to hormones like ethylene.

Effect of water and PDJ on allelopathic expression of different wheat accessions

Allelopathic expression and weed resistance capacity can be induced to increase under water and PDJ treatment (Figure 3). Allelopathic potential of roots of var. Lankao 95 - 25 was weaker than that of aerial parts under water and PDJ treatment. In contrast, var. No 6 Xiaoyan, var. Yumai

66 and var. Lankao 217 roots allelopathic potential would be stronger than that of aboveground parts due to the inducible effect of water stress and PDJ regulation. So, water and PDJ showed various effects on wheat resistance capacity depending on varieties, growth period and development part.

Compared with the control (O - 1), the three treatments, O - 2, X - 1 and X - 2 could enhance allelopathic potential of aerial parts of Lankao 95 - 25 accessions. Their allelopathic potential was increased by 1.76 (O - 2), 1.60 (X - 1) and 1.73 (X - 2) times of the control, respectively. Under the synergistic effect of water and PDJ (X - 2), weed growth was suppressed significantly (Figure 3A). In contrast with var. Lankao 92 - 25, root allelopathic potential in var. No 6 Xiaoyan would be increased by water control and PDJ regulation. In normal water supply, PDJ addition would enhance significantly allelopathic potential of var. No 6 Xiaoyan roots as well as its weed resistance capacity of inhibiting weeds number and their biomass. Especially, X - 2 treatments not only enhanced root allelopathy of var. No 6 Xiaoyan, it also inhibited subsequent growth of surrounding weeds significantly (Figure 3B).

Var. Yumai 66, PDJ showed significant effect on allelopathic expression and weed suppression capacity and that water stress (O - 2) could enhance allelopathic potential of the aerial parts of wheat plants. PDJ treatment (X - 1) can increase allelopathic expression of intact plant and significantly inhibit weed infection under normal water conditions. In addition, PDJ under water stress would increase allelopathic potential of var. Yumai 66 roots and decrease weed biomass (Figure 3C). To var. Lankao 217, water and PDJ displayed similar effects on allelopathic potential of weed resistance with those of var. No 6 Xiaoyan, although both acquired different levels of inducible effect. In short, allelopathic expression and weed resistance capacity in var. Lankao 217 is stronger than that of var. No 6 Xiaoyan under water control and PDJ regulation (Figure 3D).

It is implied that water supply and PDJ addition would enhance drought resistance of wheat to a certain degree due to two different influence mechanisms of crop plants (Figure 3). Drought stress mainly showed its direct inducible effect on the allelopathic potential of wheat. PDJ expressed its indirect inducible effect on the allelopathic potential of crop plants mainly because it could promote root growth of acceptor plants and increase phenotype competitive capacity. Generally, water and PDJ would induce allelopathic potential of tested plants, depending on their genotype background, relative tested parameter and growth stage. They could enhance allelopathic expression of roots of tested plants and decrease weeds biomass so as to inhibit weed growth.

Leaf gas exchange and water use of wheat accessions at the enhancement stage under water control and PDJ regulation

Water and PDJ displayed different effects on various photosynthesis parameters (Figure 4). Water and PDJ

enhanced photosynthesis effect and WUE of var. Lankao 95 - 25 significantly taking treatment 3 (O - 2) as the control. From review of photosynthesis characteristics of var. Lankao 95 - 25, water and PDJ would markedly increase the photosynthesis rate and stoma conductance although water deficit in certain ranges enhanced transpiration rate and stoma resistance. On the whole, the interaction of water and PDJ could improve the WUE of wheat, especially under normal water condition; PDJ (Treatment 1) leads to the super-expression of photosynthesis property of var. Lankao 95 - 25. Compared with the control, three important parameters such as photosynthesis rate, stoma conductance and WUE were enhanced by 137, 96 and 27%, respectively (Figure 4A).

While water and PDJ effects were related to concrete tested parameters in var. No 6 Xiaoyan, water and PDJ (Treatment 1, 2 and 4) induced and increased leaf stoma conductance and transpiration rate by 11 - 50% and 17 - 39%, respectively, as well as photosynthesis rate by 0 - 24%. In contrast, leaf stoma resistance and whole WUE were decreased in var. No 6 Xiaoyan. Differing from var. Lankao 95 - 25, under treatment 1, the photosynthesis effect was inhibited and WUE declined, the mechanism possibly being that lower stoma resistance would cause a more rapid transpiration rate so that corresponding WUE was decreased significantly (Figure 4B). In var. Yumai 66, PDJ with enough water would induce a reduction of leaf stoma resistance and photosynthesis rate, but increase wheat WUE. Under water deficit, it showed another style of increasing expression of photosynthesis effect and declining WUE. Based on treatment 1 and 2, water and PDJ showed synergistic effects on photosynthesis effect and WUE of wheat, with water inducing the improvement of photosynthesis features and PDJ decreasing leaf stoma resistance (Figure 4C).

However, in var. Lankao 217, whether with sufficient water or water deficit, PDJ would lose its inducible effect due to increasing photosynthesis rate and WUE of the wheat crop. It can assure that water deficiency without PDJ would significantly inhibit photosynthesis effect of var. Lankao 217 with no significant change of WUE (Figure 4D). We can conclude that water and PDJ showed inducible effects on photosynthesis effect and WUE related with wheat accessions (Figure 4). While meeting with hormone analogue PDJ regulation, different wheat varieties displayed different adaptive properties like inducible difference of photosynthesis effect and WUE.

Relationship of allelopathic expression and key traits of wheat accessions

Based on Canonical Correspondence Analysis (CCA), the specific relationship of allelopathic suppression of weeds and relative physiological factors by X- and Y- axis as two dimension orderable figures (Figure 5) were simply mapped. From Figure 5, four types of relationship were very significant. Firstly, allelopathic potential of aerial parts is significantly related with root allelopathy ($P < 0.001$) in four wheat accessions. Secondly, on the whole,

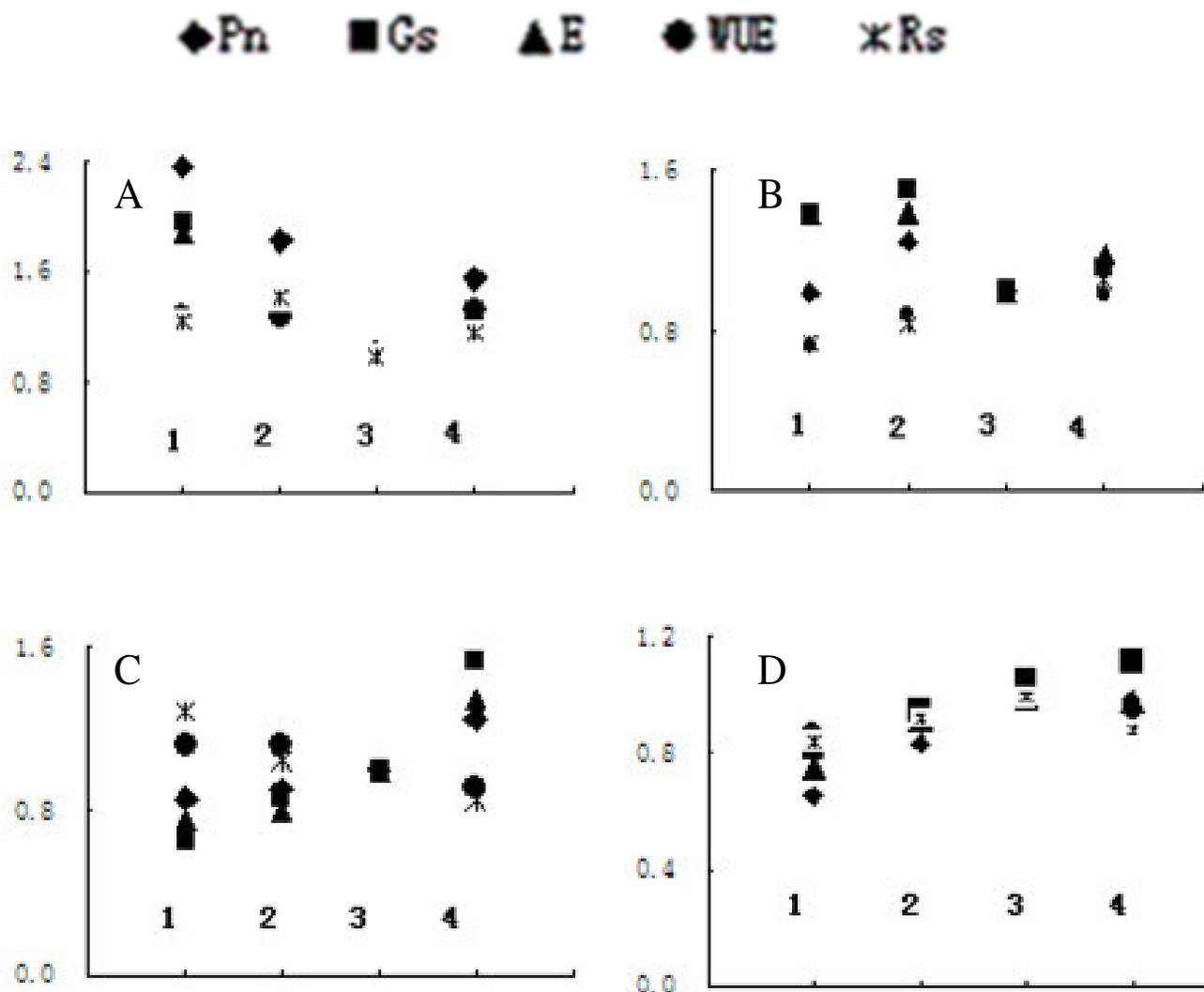


Figure 4. Leaf gas exchange and water use efficiency of four wheat accessions at the enhancement stage under water control and PDJ regulation. In four wheat cultivars, all treatments were compared to the rate of the control (O - 1, 1.0) as the relative value, also shown in Y-axis by relative indicators. Treatment figures were exhibited as treatments for 1 (X - 1, +PDJ and 75%), 2 (X-2, +PDJ and 45%), 3 (O - 1, -PDJ and 75%) and 4 (O - 2, -PDJ and 45%). Some relative measures indicated wheat accessions for **A** (var. Lankao 95 - 25), **B** (var. No 6 Xiaoyan), **C** (var. Yumai 66) and **D** (var. Lankao 217). Other parameters were **Pn** (photosynthesis rate), **Gs** (stoma conductance), **E** (transpiration rate), **WUE** (water use efficiency) and **Ls** (stoma limitation value as qualifying gas resistance).

allelopathic potential in intact wheat plants showed a significant relationship with weed suppression capacity of decreasing weed biomass, but not weed density. It suggested that self-allelopathy in crop plants can inhibit weed infection and reduce their biomass, which have been observed in field trials.

Thirdly, weed resistance characteristics showed a significant positive relationship with photosynthesis rate, transpiration rate and WUE and a significant negative relationship with aboveground biomass, plant height, node distance, stoma conductance except leaf area, leaf chlorophyll content and root biomass. Fourthly, allelopathic potential showed similar relationships to weed resistance capacity with the above indicators. It was concluded that early vigor and allelopathic property would

enhance competitive capacity in spring barley and spring wheat. During the course in wheat, early crop biomass explained 14 - 21% of the observed genotypic variance across 4 years, allelopathic activity explained 0 - 21% and combined, explained 27 - 37% of the observed genotypic variance. Model predictions suggested that new cultivars with increased early vigor and allelopathic activity offer a potential to further reduce weed interference. In the present study, we discovered that to enhance allelopathic weed capacity would consume energy and cost necessary metabolism by interior balance regulation. So it can explain the decrease of aboveground biomass plant height and node distance of wheat plants while increasing allelopathic weed capacity under water control and PDJ regulation.

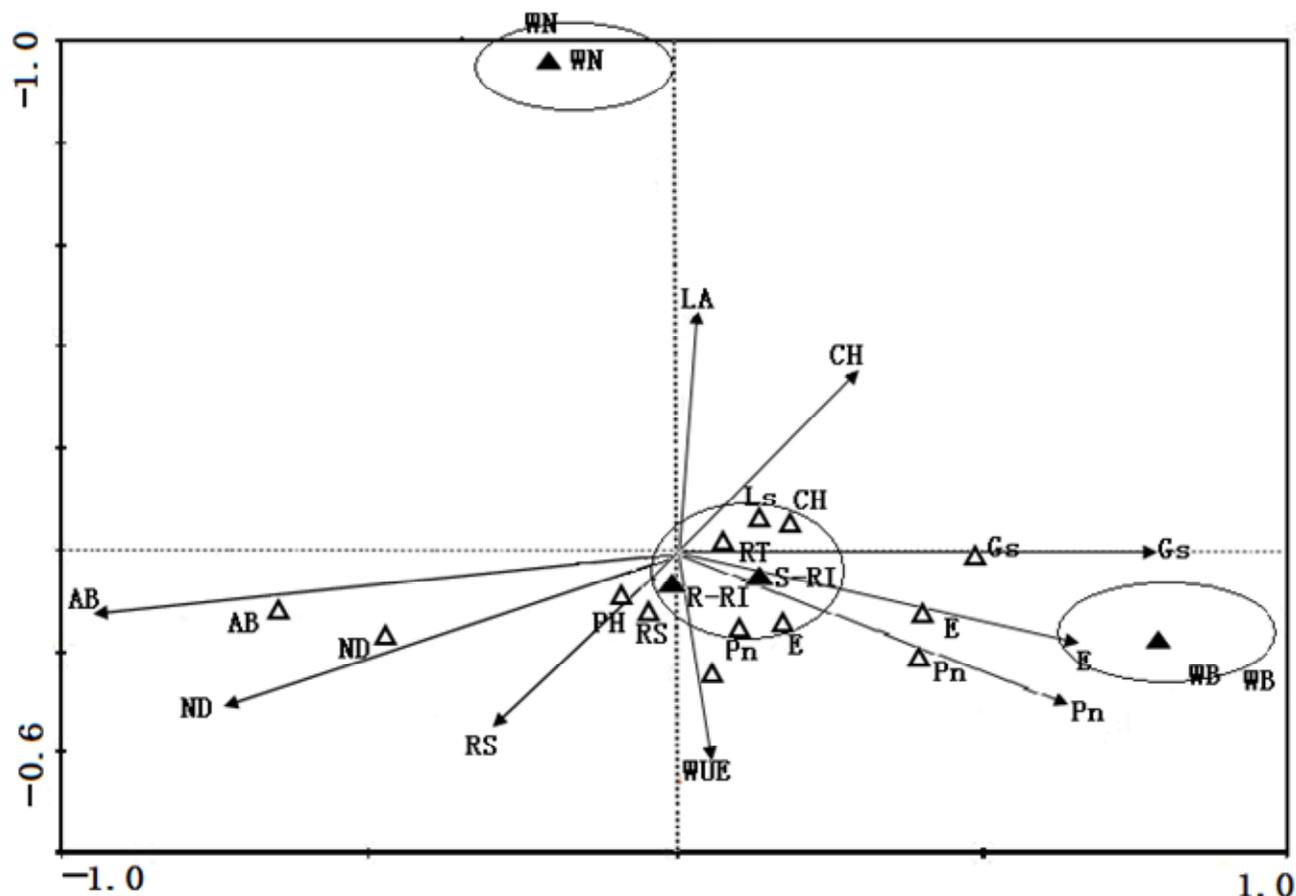


Figure 5. Relationship of allelopathic expression and key traits of wheat accessions at the enhancement under water and PDJ treatment. In four wheat cultivars, all treatment was calibrated to the rate of the control (0 - 1, 1.0) as the relative value (0 - 1), also shown in X- and Y-axis by relative indicators. Treatments were exhibited as 75 and 45% soil water and PDJ or not. Four wheat accessions included var. Lankao 95 - 25, var. No 6 Xiaoyan, var. Yumai 66, and var. Lankao 217. four allelopathic expression indicators included allelopathic potential such as R - RI and S - RI implying roots response index and aerial parts response index and weed resistance capacity displayed by WN (weed plants per pot) and WB (total weed biomass per pot, fresh weight). (▲ symbol) 11 tested physiological indicators meant LA (leaf area), PH (plant height), ND (node distance), CH (chlorophyll content), AB (aboveground biomass) and RT (root biomass); and Pn (photosynthesis rate), Gs (stoma conductance), E (transpiration rate), WUE (water use efficiency), and Ls (stoma limitation value as qualifying gas resistance) (Δ symbol). The growth, photosynthesis and allelopathic weed suppression in four wheat cultivars under water and PDJ treatment was conducted by Canonical Correspondence Analysis (CCA) to explore their relationship of allelopathic traits and physiological response in the enhancement stage.

DISCUSSION

Under environmental stress, allelopathic potential in plants would be induced and enhanced. The pressure caused not only significant increase of allelochemicals, but also further enhancement of allelopathic intensity. Hall et al. (1982) discovered that with the increase of nutrient stress, phenolics produced by *Helianthus annuus* would show higher concentration. Under this circumstance, it also displayed stronger allelopathic inhibition of *Amaranthus retroflexus* seed germination. Josep and Joan, (1997) concluded that monoterpene content in *Rosmarinus officinalis* significantly increased with CO₂ concentration increasing in the environment. Especially, monoterpene exuded content was higher in the season with high temperatures than that of other seasons. Kong et al. (2004) discovered

that in an adverse environment with water deficit and fertilizer shortage, allelopathic potential in *Ageratum conyzoides* was very strong, which was related to the sudden increase of preconcene in the plant directly. With the gradual decline of nutrient level, the volatile oils in *A. conyzoides* showed stronger allelopathic potential.

In the present study, under water stress allelopathic potential in aboveground parts was firstly induced. For example, in 45% soil water, different wheat accessions had variable allelopathic stimulation such as var. Lankao 95-25(15%), var. No 6 Xiaoyan (39%), var. yumai 66(6%) and var. Lankao 217(45%). In addition, the water press would induce var. No 6 Xiaoyan and var. Yumai 66 having stronger suppression of weeds. In this case, a possible mechanism could be that stress including water deficit, would induce the synthesis of functional allelochemicals

in aerial parts, which would enter the rhizosphere by mass flow and diffuse to roots so as to influence surrounding plants growth. On the other hand, the pressure would enhance use efficiency of limited resources such as water, nutrients, light and increase relative competitive capacity of life resources (Chapin et al., 1987).

It is worth noting that water stress sometimes would change allelopathic potential and weed suppression properties. In our study, water stress reduced mean 53% of allelopathic potential of var. no 6 Xiaoyan and var. Yumai 66. It also decreased weed inhibitive capacity of var. Lankao 95 - 25 and var. Lankao 217, with decreases ranging from 29 - 36%. Therefore, environmental stress had specific inducible effects, mainly stimulating more allelochemicals production and higher concentration accumulation. However, due to other factors involved in allelopathy such as nutrient, water, soil and biological factors in the field (Rice 1984), the inducible effects was scarcely observed in field trials. Especially, allelochemicals released into the soil were difficult to isolate, identify and monitor. That is to say, the allelopathic dynamic was decided by many factors, including selecting press from the environment. Surely, it should be determined by mutual adaptation, regulation and long bilateral co-evolution (Singh and Usha, 2003).

In nature, there is a novel endogenous growth hormone named "jasmonic acids" (JA), which can inhibit plant growth and promote plant senescence and falling off. It can delay the germination of non-dormant seeds, significantly inhibit root growth, and stimulate tuber development and shows important medium effects as a key chemical signal in plant wound and infestation by pathogens (Imamura, 2004). But JA analogue PDJ, synthetic product, showed wide application in plant resistance and quality improvement. PDJ exhibited strong inhibition of cucumber mosaic virus (CMV) in *Nicotiana glauca* leaf, whose effect was negatively related to PDJ concentration (Cai et al., 2003). Besides, PDJ can induce the expression of osmotin genes of *Nicotiana attenuata* seedlings and alleviate the harm of *Phytophthora parasitica* var. *nicotiana*. PDJ in 100 mg/L can control 69.57% of *Nicotiana* harm and persist for about 15 d (Xu et al., 2005). Other studies reported that PDJ can enhance the drought resistance capacity of peanuts and anti-freeze and frost of fruit trees (Sekozawa, 2005).

In regulating economic crop quality, PDJ also displayed significant effects. When sprinkled on *Pyrus bretschneideri* by 0.5 mL/L PDJ, 15 d before the flowering peak, blossom thinning was very significant. In grape tests, PDJ showed significant effect on color stabilization of the fruit (Hidehiko et al., 2005). Further study showed that PDJ had specific and selective regulatory effect on allelopathic weed suppression of different wheat accessions in our research. Our findings were similar with those of Kong et al. (2004). PDJ as well as MJ possessed an inducible effect on allelopathic potential. In the present study, PDJ could stimulate allelopathic expression of acceptor roots and weed suppression capacity in the field of var. No 6 Xiaoyan and var. Lankao 217. In specific circumstance, it also induces allelopathic potential of

aerial parts of var. Lankao 95 - 25. Except var. Lankao 217, PDJ showed significant regulation effect on allelopathic potential in normal water supply, but not in water deficit. The possible explanation was that water press and PDJ simultaneously had antagonistic effect to a certain degree.

MJ as a PDJ analogue was discovered to possess allelopathic potential. In the Great Basin Desert, *Artemisia tridentata* produced MJ volatiles and inhibited seeds germination of *Nicotiana tabacum* in the vicinity. Consequently, seeds bank of *N. tabacum* was influenced significantly, so we presumed that PDJ should show its regulative effects on allelopathic expression by two aspects: (1) PDJ can promote crops growth and increase their resources competitive capacity so as to enhance allelopathic potential; (2). PDJ could possibly weaken certain allelopathic potential. For example, PDJ would decline 37.5% of aboveground biomass of var. Lankao 217. So PDJ would cause allelopathic press to tested crops, which requires further research for its reasonable application.

When plants were stimulated by exterior factors, they produce some signals and regulating phenotype and physiological changes by emergency responses and adaptive adjustments. So changing dynamics of soil water, nutrients and environment would affect photosynthesis effect of plants, whose procedure was mainly sensed by leaf stoma and leaf cells (Shao et al., 2008a). Shao et al. (2005) did a study suggesting that drought resistance of wheat was related closely to its photosynthesis effect. In arid circumstances, dryland wheat cultivars possessed a higher rate of photosynthesis effect. PDJ in a dry environment could promote accumulation of leaf Pro and soluble sugar, as well as maintain high water content of living tissues, delay subsequent decline of active enzyme of SOD and CAT and gradually enhance the activity of POD and decrease MDA content, which showed similar effects with ABA in drought resistance capacity (Shao et al., 2005, 2008 a,b,c, 2009).

In the present study, under different soil water content, with PDJ addition, photosynthesis rate of wheat materials was enhanced significantly, also including WUE of var. Lankao 95 - 25 and var. no 6 Xiaoyan, whereas PDJ showed certain inhibition of photosynthesis of var. Yumai 66 and var. Lankao 217. The result came from the different response of wheat accessions to PDJ. Based on CCA analysis of allelopathic expression and physiology of wheat materials, allelopathic potential displayed significant relationship with weed suppression capacity; meanwhile, the weed resistance capacity was positively related with WUE, photosynthesis rate and transpiration rate, negatively combining with aboveground biomass, plant height, node distance and stoma conductance. Therefore, allelopathic potential and weed suppression in crops need risk cost (Siemens et al., 2002), which include matter consumption and energy input. The organic process was a mixture of active and passive responses by producing secondary metabolites (Chapin et al., 1987).

The production and efficient accumulation of secondary metabolites was driven by passive and active transfer

procedure according to the hypothesis of response mixture theory by active and passive transfer of allelopathic expression. Water stress led to the increase of allelopathic expression, which implied the passive transfer process of energy change. Whereas PDJ implemented its positive regulative effect like hormone and increase cost input to improve crops competition. When PDJ is sprayed on wheat leaves in the enhancement and seeds filling stage, dry matters production and inner storage in stems transporting to the spikes after finishing spike was promoted significantly. Especially, early PDJ input would enhance seed number, thousand seeds weight and increase the final yield. Our results meant PDJ positive regulation as well as negative adjustment of water stress would induce allelopathic expression of wheat crops in the enhancement period.

It is necessary to study the types of allelochemicals produced, their concentration and impact on crop growth in water control and PDJ regulation during the life history of crops including wheat and rice. It is also worth studying how artificial selection and natural evolution affect allelopathic expression induced by exterior stimulants like field management and hormone analogues as well as the genes involved in the regulation process in allelopathic inducible effect by stress factors or regulative measurements. So we should keep and stabilize the property of allelopathic expression in crops production and future breeding. In short, these issues call for deeper and broader studies. Meanwhile, allelopathic potential and competition capacity of wheat should be separated precisely, especially in wild condition. Song et al. (2008) successfully used allelopathy-competition separation (ACS) approach to explore the biointerference relationship between rice accessions and barnyardgrass exposed to different nitrogen supplies in hydroponics. So, further experiment is needed to confirm whether it is really allelopathic effect in test materials or not.

ACKNOWLEDGEMENTS

This work was supported jointly by National Natural Science Fund of China (30870403), University Natural Science Research Project of Anhui Province of China (KJ2008B192), Anhui Normal University of China for Youths (2008xqn75) and for Ph.D talents (160 - 750717), Tarim University President Foundation (TDZKSS08002), One hundred-Talent Plan of Chinese Academy of Sciences (CAS), the CAS-local government Cooperative Project and the CAS/SAFEA International Partnership Program for Creative Research Teams for financial support. Dr. William J. Gale, the foreign teacher of Northwest A & F University provided help with the editing and English revision of this manuscript.

Abbreviations

PDJ, Prohydrojasmon; **CCA**, canonical correspondence analysis; **ABA**, abscisic acid; **Pro**, proline; **SOD**,

superoxide dismutase; **CAT**, catalase; **POD**, peroxidase; **MDA**, malondialdehyde; **MJ**, methyl jasmonate; **WUE**, water use efficiency; **RI**, reaction index; **JA**, jasmonic acids; **CMV**, cucumber mosaic virus.

REFERENCES

- Cai LH, Chen JS, Xu BJ (2003). Influence of cucumber mosaic virus loading by a synthesized jasmonic acid analogue in plant. (in Chinese). *J. Zhejiang Univ. Agric. Life Sci.* 29: 534-538.
- Chapin FS, Arnold JB, Christopher BF, John ML (1987). Plant response to multiple environmental factors. *Bioscience*, 37: 49-77.
- Chen GX, Wang WJ (1997). Influence of PDJ on the grain filling and bearing for two line japonica hybrid rice. *J. Huazhong Agric. Univ.* 16: 538-542.
- Dong DF, Jiang LG, Nie CR, Lin JH (2002). Effects of long-lasting brassinosteroid TS303 and Propyl Dihydrojasmonate on peanut resistance to drought (in Chinese). *J. Peanut Sci.* 31: 29-32.
- Emeterio LS, Arroyo A, Canals RM (2004). Allelopathic potential of *Lolium rigidum* Gaud. on the early growth of three associated pasture species. *Grass For. Sci.* 59: 107-112.
- Farquhar GD, Sharkey TD (1982). Stomatal conductance and photosynthesis. *Ann. Rev. Plant Physiol.* 33: 317-345.
- Hall AB, Blum U, Fites RC (1982). Stress modification of allelopathy in *Helianthus annuus* L. debris on seed germination. *Am. J. Bot.* 69: 776-7831.
- Hassan IA (2006). Effects of water stress and high temperature on gas exchange and chlorophyll fluorescence in *Triticum aestivum* L. *Photosynthetica*, 44: 312-315.
- Hidehiko K, Zaynab O, Albert E, Mirokura L (2005). Effect of n-propyl dihydrojasmonate (PDJ) on intro growth of yam (*Dioecorea* spp.) explants. *Jpn. J. Trop. Agric.* 49: 59-60.
- Imamura K (2004) n-Propyl dihydro-jasmonate (PDJ). (In Japanese). *Plant Growth Regul.* 38: 35-39.
- Josep P, Joan L (1997). Effects of carbon dioxide, water supply, and seasonally on terpene content and emission by *Rosmarinus officinalis*. *J. Chem. Ecol.* 23: 979-9931.
- Kong CH, Hu F, Zhang CX, Lv DF (2004). Inducible effects of methyl jasmonate on allelochemicals from rice. (in Chinese). *Acta Ecologica Sinica*, 24: 177-180.
- Kong CH, Xu XH, Zhou B, Zhang CX (2004). Two compounds from allelopathic rice accession and their inhibitory activity on weeds and pathogens. *Phytochemistry*, 65: 786-772.
- Koshiyama M, Seto H, Kamuro Y, Kateora M (2003). A jasmonic acid analog, PDJ, comes into practical use as a plant growth regulator. (in Japanese). *Plant Growth Regul.* 38: 35-47
- Liu ZM, Ma HP, Chen HJ, Li XH, Wang ZQ (1999). Preliminary Study of PDJ on the Photosynthesis and Endogenous ABA Content in Malus (in Chinese). *Plants Acta Horticult. Sinica*, 26: 87-90.
- Oueslati O, Ben HM, Ghorbal MH, Orienta H (2005). Barley autotoxicity as influenced by varietal and seasonal variation. *J. Agron. Crop Sci.* 191: 249-254.
- Pare PW, Tumlinson JH (1997). Induced synthesis of plant volatiles. *Nature*, 385: 30-31.
- Rice EL (1984). *Allelopathy*. 2nd ed. New York: Academic Press Inc., pp. 267-290.
- Sekozawa Y (2005). Resistance to freeze and cold in fruit tree by n-Propyl dihydrojasmonate(PDJ). (in Japanese). *Plant Growth Regul.* 39: 352-358.
- Shao HB, Chu LY, Jaleel CA, Zhao CX (2008a) Water-deficit stress-induced anatomical changes in higher plants. *Comptes Rendus Biologies*, 331: 215-225.
- Shao HB, Chu LY, Lu ZH, Kang CM (2008c). Primary antioxidant free radical scavenging and redox signaling pathways in higher plant cells. *Int. J. Biol. Sci.* 4: 8-14
- Shao HB, Chu LY, Shao MA (2008b). Calcium as a versatile Plant Signal Transducer under Soil Water Stress. *BioEssays*, 30: 634-641.
- Shao HB, Jaleel CA, Shao MA (2009). Understanding Water Deficit Stress-induced Changes in Basic Metabolisms of Higher Plants for biotechnologically and sustainably Improving Agriculture and Ecoenvironment in Arid Regions on the Globe. *Crit. Rev. Biotechnol.* 29: 131-151.

- Shao HB, Liang ZS, Shao MA (2005). Changes of some physiological and biochemical indices for soil water deficits among 10 wheat genotypes at seedling stage. *Colloids Surf.ace B: Biointerface*, 42: 107-113.
- Siemens DH, Garner SH, Mitchell-Olds T, Farmeris U (2002). Cost of defense in the context of plant competition: *Brassica rapa* may grow and defend. *Ecology*, 83: 505-517.
- Singh B, Usha K (2003). Salicylic acid induced physiological and biochemical changes in wheat seedlings under water stress. *Plant Growth Regul.* 39: 137-141.
- Song B, Xiong J, Fang C, Qiu L, Lin R, Liang Y, Lin W (2008). Allelopathic enhancement and differential gene expression in rice under low nitrogen treatment. *J. Chem. Ecol.* 34: 688-695
- Su JW (2004). Effects of methyl jasmonate on photosynthetic properties in tea shoots under drought stress. (In Chinese). *J. Fujian Agric. For. Univ. Nat. Sci. Edition*, 33: 190-194.
- Tang CS, Cai WF, Kohl K, Orianta H (1995). Plant stress and allelopathy. *ACS. Symp. Ser.*, 582: 142-147.
- Williamson GB, Richardson D (1988). Bioassays for allelopathy: Measuring treatment responses with independent controls. *J. Chem. Ecol.* 14: 181-187.
- Xu HJ, Ding XY, Liu F, Farmeris U (2005). The control effect of PDJ to tobacco black shank and the influence of PDJ to osmotin gene expression. (in Chinese). *Acta Tabacaria Sinica*, 11: 31-34.
- Zuo SP, Ma YQ, Deng XP (2005) Allelopathy in wheat genotypes during the germination and seedling stages. *Allelopathy J.* 15: 21-30.