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Rate of dark respiration of oats at various levels of copper supply

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Abstract

The aim of the present study was to determine the intensity of dark respiration of oat plants cv. 'Udycz Żółty' during their vegetation period. Plants were grown with addition of increasing doses of copper, applied at different stages of development. Up to heading of the control plants, copper-deficient plants showed low intensity of dark respiration as compared with the copper-sufficient plants. After heading, a strong increase in the rate of respiration in the former was noted. The high intensity of dark respiration in copper-deficient plants after heading was probably the result of ineffective utilization of assimilates in the absence of the panicle – the main acceptor of the photosynthesis products.

INTRODUCTION

There are numerous papers, available in the literature, concerning the influence of copper on the yield of cereals. Some of them are connected with the influence of copper on the growth and development of plants ⟨Brown et al., 1958; Graham, 1975; 1980; Nambiar, 1976, part I; Ostrovskaya, 1961; Rahimi and Bussler, 1973; Szukalski et al., 1980⟩. In others, genotypic differences in the degree of sensitivity to copper deficiency have been reported ⟨Nambiar, 1976, parts I and II⟩. The influence of copper deficiency on the structure of tissues of higher plants ⟨Rahimi and Bussler, 1973⟩ and on anatomo-morphological changes in the inflorescences ⟨Weryszko et al., 1983⟩ has been also described. There has been studied the effect of copper on photosynthesis ⟨Baszyński et al., 1978⟩ and on carbohydrate metabolism in plants ⟨Brown et al., 1958⟩. It has been attempted to elucidate why, under conditions of copper deficiency, plants do not set seeds ⟨Graham, 1975⟩. It has been found, that the processes occurring in plants in the generative phase requir a higher copper supply than those in the vegetative phase ⟨Brown et al., 1958; Graham, 1975; Nambiar, 1976, part I; Ostrovskaya, 1961⟩. More recently attention has been devoted to the problem how the date of copper application, in the form of soil fertilization or spraying the plants, influences the growth and development of plants as well as the yield of grain ⟨Graham, 1976; Nambiar, 1976, part I⟩. However, there are only few reports on the influence of copper on plant respiration. The earliest study ⟨Le Van – quoted by Ostrovskaya, 1961⟩ concerns the action of salts of various metals ⟨including Cu⟩ on respiration of white lupin plants.

Recently the influence of copper deficiency on crop plants with particular reference to cereals has been examined in details in the Laboratory of Plant Nutrition of the Institute of Soil Science and Cultivation of Plants in Puławy ⟨Łyszcz et al., 1976; Ruszkowska and Łyszcz, 1971; 1975; Ruszkowska et al., 1976; Wojcieska, 1982; parts I and II; 1983, parts III, IV; Zinkiewicz, 1978; Zinkiewicz et al., 1980; Zinkiewicz and Ślusarczyk, 1981⟩. On the basis of these investigations the present study was undertaken to elucidate the influence of copper on the rate of dark respiration of oats, at various developmental stages, at various levels of copper supply and at different dates of Cu application.

MATERIAL AND METHODS

Pot experiments were performed in the period 1976-1980 with oat plants ⟨*Avena sativa* L.⟩, cv. 'Udycz Żółty'. The plants were cultivated in pots filled with low peat ⟨0.8 kg DWt⟩ deficient in copper, pH ⟨KCL⟩ 6.7. From the beginning of plant vegetation the copper supply was as follows:

Cu – 0 – control ⟨severe deficiency⟩,
Cu – 5 – 5 mg Cu/pot ⟨moderate deficiency⟩. ⟨This treatment was introduced only in 1977 and 1979⟩,
Cu – 125 – 125 mg Cu/pot ⟨optimal supply⟩.

Copper was given in the form of $CuSO_4 \cdot 5\ H_2O$. The remaining mineral nutrients were supplied to the plants in optimal quantities before sowing and during their vegetation. To elucidate the influence of copper applied at various stages of development on the dark respiration rate, in 1979 and 1980 additional treatments were introduced. Namely, the optimal copper dose ⟨Cu – 125 mg/pot⟩ was given at the following stages: tillering, shooting, heading and flowering of oats. Up to mentioned stages the plants grew with a complete absence of copper. Plants receiving an optimal Cu supply immediately after emergence served as a control.

Dark respiration was measured by means of an Infralyt III gas analyser in a closed system. The results ⟨means of two determinations⟩ were expressed in $mg \cdot h^{-1} \cdot g^{-1}$ DWt. The data was statistically elaborated by the variance with the F test and Tukey's confidence semi-intervals analysis.

The measurements of dark respiration were preformed on the main shoot ⟨separately⟩ and on all tillers ⟨jointly⟩. Next fresh and dry weights of the analysed shoots were determined. The following developmental stages ⟨determined on the basis of the main shoot in the treatment Cu – 125⟩ were taken into account: shooting, before heading, heading, filling of grain and grain ripeness – milk, milk-dough, dough, dough-full and full. At the time of respiration measurement additional plants were harvested for determination of the dry weight yield.

RESULTS

It has been noted that copper significantly influenced the growth and development of oat plants. The results concerning the yield and its structure have been presented in detail in separate publications ⟨W o j c i e s k a, 1982, parts I and II⟩.

The degree of copper supply had a significant influence on the dark respiration rate of oat plants. This effect depended on the developmental stage of plants ⟨Fig. 1⟩. Up to heading and even as late as the middle stage of grain filling, there was observed higher rate of dark respiration in main shoots treated with Cu – 125 in comparison with the Cu – 0 one. From the heading or grain filling stages to the end of measurements, that is to the dough or full ripeness, the above mentioned dependence was reversed – the respiration rate of the main shoot in the Cu – 0 treatment was higher than in the plants well supplied with Cu. The difference became bigger with the age of the plants. In the tillers, however, the respiration intensity of Cu – 0 plants was always higher than that in shoots of the Cu – 125 treatment, notwithstanding the developmental stage of the plants ⟨Fig. 1⟩.

In the experiments in 1977 and 1979 the treatment Cu – 5 was introduced. It was stated that the respiration rate of plants in this treatment had an intermediate value in comparison with plants showing copper deficiency symptoms and those optimally supplied with this nutrient ⟨Fig. 1⟩. There were, however, certain differences: in 1977 the respiration rate of the Cu – 5 plants was close to the low value obtained for the Cu – 125 plants, whereas in 1979 it was closer to the higher intensity of respiration of the Cu-deficient plants ⟨Table 1⟩.

The respiration rate of tillers was always higher than that of the main shoots, copper supply independent ⟨Fig. 1⟩.

There were some statistical significant differences in dark respiration intensity, notwithstanding the developmental stages: between tillers of copper-deficient plants ⟨Cu – 0⟩ and those with abundant copper supply ⟨Cu – 125⟩, as well as between tillers of Cu – 0 and of moderate shortage ⟨Cu – 5⟩. Significant differences concernig individual stages were as followed: in the case of main shoots – only before heading between Cu – 0 or Cu – 5 plants, and Cu – 125 plants; in tillers – in the milk-dough, dough and full ripeness stages between Cu – 0 and Cu – 125 plants.

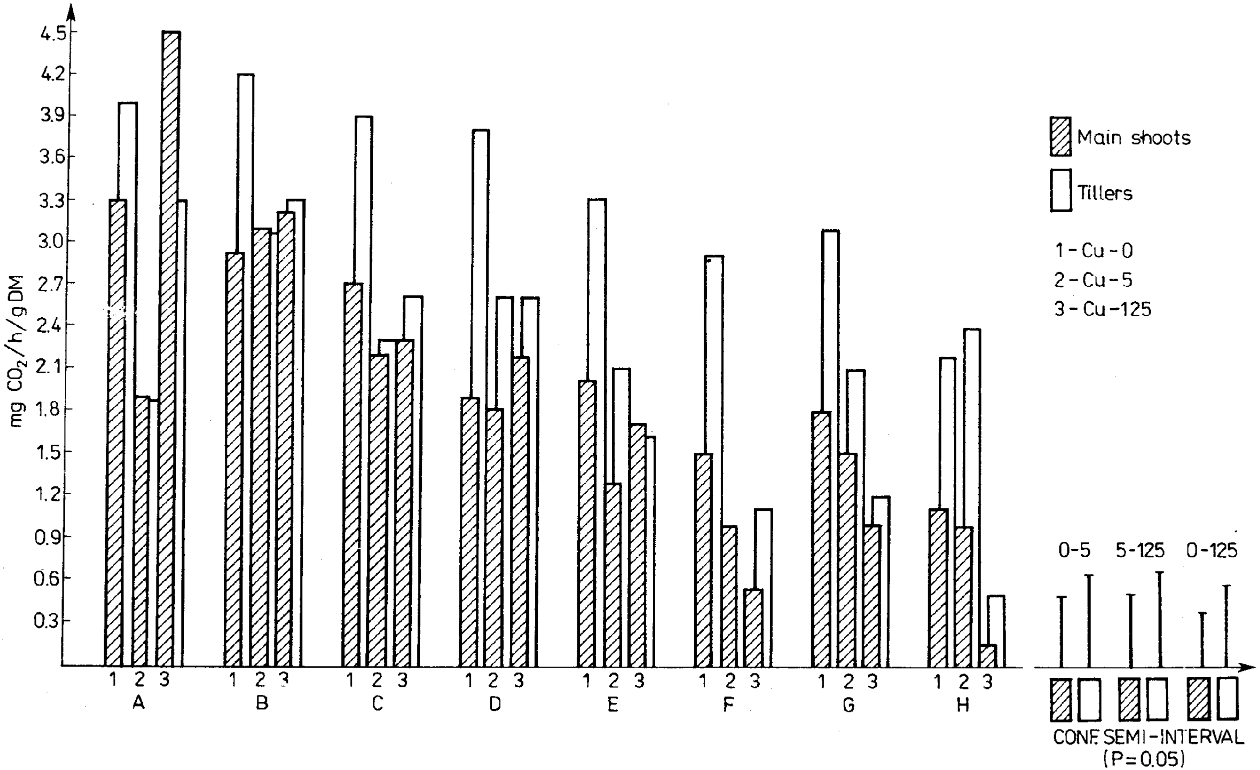

Fig. 1. Effect of copper on dark respiration rate of oat plants at different stages of development. 1 – Cu – 0, 2 – 5 mg Cu/pot, 3 – 125 mg Cu/pot given at sowing. Measurements in phase: A – before heading, B – heading, C – flowering, D – grain filling, E – milk stage, F – milk-dough stage, G – dough stage, H – full ripeness. ⟨Means of 5 years⟩. Confidence semi-intervals independent of date of measurement

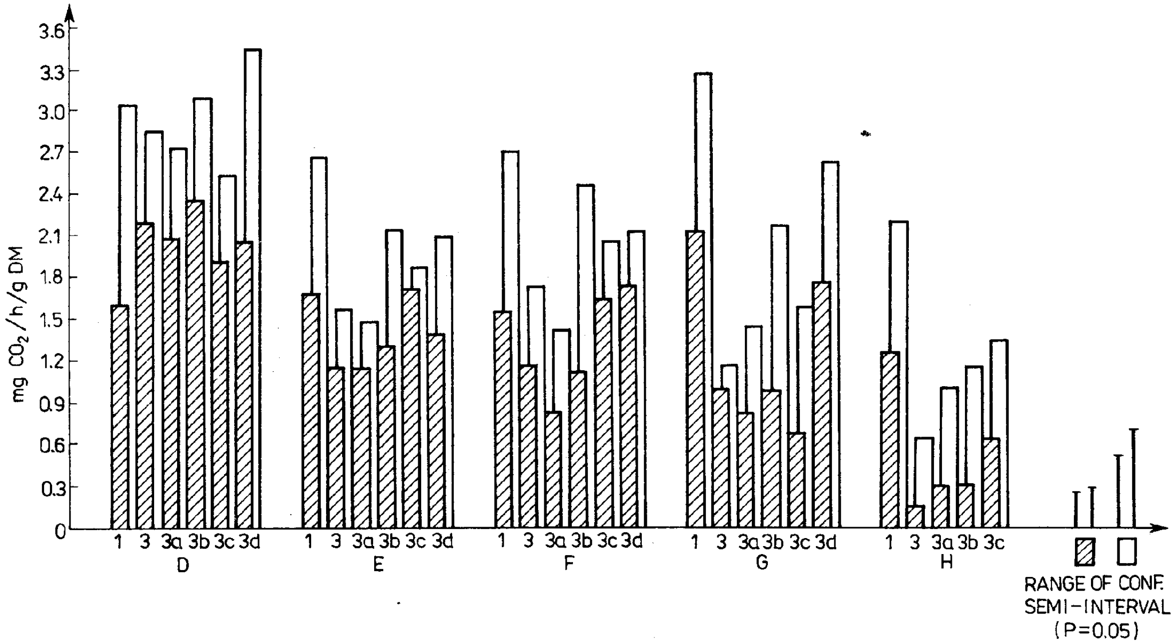

Fig. 2. Dark respiration with optimal copper dose supplied at different stages of plant development. 1 – Cu – 0, 3 – Cu – 125 mg Cu/pot given at sowing, 3a – tillering, 3b – shooting, 3c – heading, 3d – flowering. ⟨Means of 2 years⟩. Other explanations as in Fig. 1

Table 1

Effect of copper on dark respiration rate of oat plants at milk stage

Year	Kind of a shoot	Dark respiration rate – in mg · h^{-1} · g^{-1} DWt		
		Cu – mg/pot		
		0	5	125
1977	main	1.7	1.0	1.1
	shoot	2.5	1.1	1.1
1979	tillers	2.1	1.9	0.6
		2.7	2.3	0.9

The respiration intensity of oats varied during the vegetation but differences in respect of copper supply and part of plant were slight. The highest value of plant respiration rate in the treatment Cu – 0 and Cu – 5 was found at the stage of heading ⟨Fig. 1⟩. At the subsequent stages the intensity decreased, reaching the lowest value towards the end of the milk ripeness. For the Cu – 125 plants, the highest value of respiration intensity was noted in the period preceding heading. Upon these conditions the decrease in intensity was more pronounced, and the lowest value was found at full grain ripeness.

An addition of copper to Cu – 0 plants during tillering or shooting caused a reduction of the respiration intensity of plants ⟨especially of the main shoots⟩, as compared with the high respiration level of plants growing under the conditions of Cu deficiency ⟨Fig. 2⟩. At later stages ⟨heading and flowering⟩ copper supply did not depress the respiration intensity.

Statistical evaluation confirmed the significance of the differences in respiration intensity, both in the case of main and of lateral shoots. These differences were especially pronounced in plants treated with the optimal copper dose before emergence, during tillering and shooting as compared with plants growing the whole time under conditions of copper deficiency and also those which received Cu at heading or flowering.

DISCUSSION

The present investigations demonstrated that the changes in respiration intensity of oats dependent on the plant developmental stage and degree of copper supply exhibited a distinct character. Over all the years of the study, from the stage of heading or grain filling a higher intensity of respiration of the main shoots was observed in the treatment Cu – 0, as compared with that of plants receiving an optimal supply of Cu. In plants growing under conditions of copper deficiency ⟨mostly without heading⟩ it was probably caused by the excessive utilization of assimilates in the process of enhanced respiration. Whereas in plants optimally supplied with Cu, in which the respiration rate was markedly lower, the assimilates were mainly transported to the grain.

The phenomenon of unproductive respiration of plants caused by the influence of unfavourable factors has been observed, among others, by Kushnirenko ⟨1961⟩ in the case of root chilling in thermophilous plants and Stoy ⟨1965⟩ after ear cutting. The headed shoots showed a higher respiration rate as compared with the control, not only because they were physiologically younger, but also on account of the higher retention of soluble assimilates, serving as respiratory substrate. This has been confirmed by the results of Ślusarczyk ⟨1980⟩ concerning the carbohydrate content in plant material used in the experiments described in the present paper. The low hexose content in intensively respirating plants, which show symptoms of copper deficiency was an evidence of the high consumption of carbohydrates – main respiratory substrates.

The different intensity of plant respiration in the Cu – 5 treatment ⟨1977 and 1979⟩, as compared with that in plants with a high copper deficiency and those optimally supplied, is in good agreement with the above reported dependence. In the first year of measurements, the low degree of respiration of Cu – 5 plants observed from stage of milk ripeness may be explained by a greater transport of assimilates to the grain ⟨in 1977 the plants had panicle⟩, instead of their utilization in the process of unproductive respiration. In 1979, however, the oats did not from the panicle and the respiration rate was close to the high respiratory value in plants showing copper deficiency symptoms, which also did not from panicles. It has been known that in cases of severe copper deficiency heads and panicles did not from. The above discussed relation corresponded to the different copper contents in the plants in these two years ⟨Cú – 5 in 1977: leaves – 5.7 ppm Cu, culm – 3.8 ppm Cu, and in 1979: leaves – 2.4 ppm Cu and culm – 1.8 ppm Cu⟩.

The decreased respiration rate was found in copper-deficient plants when this nutrient was supplied at the tillering and shooting stages as compared with the high respiration intensity of plants growing throughout the vegetation period under conditions of Cu deficiency. That probably have been due to the fact that copper, involved in carbohydrate metabolism ⟨Grigoryuk et al., 1975, van Schreven, 1936 – quoted by Graham, 1980⟩, improves the utilization of the assimilates produced ⟨at earlier developmental stages⟩ in the grain filling. The high intensity of respiration of plants supplied with copper later than at the shooting stage ⟨as compared with plants supplied with Cu from the beginning of vegetation⟩ is probably one of the causes of the low grain yield. Graham ⟨1980⟩ has observed a rapid decrease in concentration of carbohydrates after fertilization in the treatment with a high Cu supply. He has attributed it to the translocation of these substances to the grain. Under the conditions of low copper level where, owing to sterility, no grain was produced, and thus there was no acceptor of soluble assimilates, they were accumulated in various tissues. According to this author, plants poor in copper contained less soluble assimilates at the beginning of the season and more at the late stages of development as compared with those receiving a sufficient Cu supply. The accumulation of soluble carbohydrates caused not only profuse tillering of the plants, characteristic of the late developmental stages of cereal plants deficient in copper, but also an enhanced respiration intensity.

The rapid increase in reducing sugar content observed by Brown and Harmer ⟨quoted by Brown et al., 1958⟩ in wheat plants well supplied in Cu, in contrast to deficient plants, seemed to indicate considerable differences in metabolism under the influence of copper. These changes have been also described by Ślusarczyk ⟨1980⟩. She has suggested that the break-down of glucose in the process of ration may occur, to a higher degree, on the pentosephosphate pathway, under the copper deficiency than under optimal conditions for the plant growth. This would explain, to some extent, the cause of enhanced respiration of copper-deficient plants, owing to the small amount of ATP arising in this process.

Suggestions presented there have been confirmed in detailed determinations of the content and composition of the individual sugar fractions in plants receiving copper at various stages of development, and will be the subject of a separate publication.

CONCLUSIONS

1. Copper supply had an important effect on the dark respiration rate of oat plants; this influence also depended on the plant developmental stage. Up to the heading or grain filling, the respiration intensity of the main shoot of plants deficient in copper ⟨Cu – 0⟩ was lower as compared with plants growing under optimal conditions of Cu supply ⟨Cu – 125⟩. At the further stages a reversed relation was observed.

The respiration rate of tillers of copper-deficient plants was, notwithstanding the developmental stage, higher than that in tillers of plants sufficiently supplied with copper.

2. In all copper treatments the intensity of respiration of tillers was higher than that of the main shoot.

3. Copper, supplied at the stage of tillering or of shooting to deficient plants, reduced the respiration rate as compared with the high respiratory level of plants growing throughout the vegetation period under conditions of Cu deficiency.

4. The enhanced respiration intensity of copper-deficient plants was the result of unproductive utilization of assimilates owing to the lack of the main acceptor of photosynthesis products which under normal conditions would be the developing grain.

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Intensywność oddychania ciemniowego owsa przy różnym zaopatrzeniu w miedź

Streszczenie

Celem pracy było wyjaśnienie wpływu miedzi na intensywność oddychania ciemniowego owsa odm. 'Udycz Żółty' w różnych fazach rozwoju roślin przy kilku poziomach zaopatrzenia w miedź i zróżnicowanym terminie jej stosowania.

Intensywność oddychania ciemniowego roślin owsa z niedoborem miedzi do fazy kłoszenia była niższa w porównaniu do roślin dobrze zaopatrzonych w ten składnik. Po kłoszeniu stwierdzono odwrotną zależność. Wysoka intensywność oddychania ciemniowego roślin owsa deficytowych w miedź po kłoszeniu była prawdopodobnie wynikiem nieproduktywnego zużywania asymilatów w przypadku braku głównego akceptora produktów fotosyntezy, jakim w normalnych warunkach są rozwijające się ziarniaki.

Dostarczenie miedzi w fazie krzewienia i strzelania w źdźbło roślinom pozbawionym tego składnika od początku wegetacji powodowało obniżenie natężenia oddychania w porównaniu do wysokiej intensywności oddychania roślin rosnących przez cały czas wegetacji w warunkach niedoboru tego pierwiastka.

We wszystkich kombinacjach zróżnicowanego nawożenia miedzią intensywność oddychania pędów bocznych była wyższa niż pędów głównych.