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Article

Allelopathy—A Tool to Improve the Weed Competitive Ability of Wheat with Herbicide-Resistant Black-Grass (*Alopecurus myosuroides* Huds.)

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Abstract: Controlling black-grass in winter wheat production in northern Europe is an increasing problem because of more frequent winter crops and development of herbicide resistance in weeds. Alternative weed management strategies are needed, e.g., use of more competitive cultivars. Factors that increase cultivar competitiveness include early vigor and straw length, but also allelopathy. Therefore, the allelopathic properties of wheat cultivars included in the Swedish national list or in the release pipeline were investigated using a bioassay with herbicide-resistant and herbicide-sensitive black-grass as receiver plants. Wheat-rye translocation lines were also included in this screening to identify possible sources of high allelopathic activity. The bioassay results were followed up in two-year field trials. The results revealed large variations in allelopathic activity between cultivars. Most cultivars showed interference with both herbicide-sensitive and herbicide-resistant black-grass, although the allelopathic effect was lower on the herbicide-resistant biotype. Cultivars with high allelopathic activity gave only half the black-grass biomass of low allelopathic cultivars. Dinaro, a triticale (wheat-rye hybrid) cultivar and the new wheat cultivar Nimbus showed the highest allelopathy and inhibition of black-grass growth. Only a few wheat lines with rye chromatin, all or part of a rye chromosome, showed high allelopathy. Use of cultivars with high allelopathic activity can thus be important in integrated weed management of black-grass.

Keywords: allelopathic; black-grass; field studies; herbicide resistance; weed competition; wheat-rye translocation lines

1. Introduction

Black-grass (*Alopecurus myosuroides* Huds.) is the most important herbicide-resistant weed in Europe, followed by ryegrass (*Lolium*), poppy (*Papaver rhoeas* L.) and wild oats (*Avena fatua* L.) [1]. Black-grass is mainly a problem in western and central Europe, but in recent years also in northern Europe, due to milder winters and more frequent autumn-sown crops. At infestation levels above 10 plants m^{-2}, yield decreases linearly with black-grass density and at a density of 100 plants m^{-2} the yield loss can be 1 t ha^{-1} or more [2]. The strong negative effect on wheat yield is a combination of competition and inhibition of wheat root growth by allelochemicals from the black-grass [3]. Kazinczi [4] were unable to confirm this finding. Neither aqueous leaf leachates nor shoot and root residues of black-grass retarded growth in their study of winter wheat. Naylor [5] also found that wheat was more competitive to black-grass than *vice versa* when the fertilizer level was sufficiently high.

Black-grass has developed resistance to several types of herbicides, such as phenyl-urea chlorotoluron, acetyl-CoA carboxylase (ACCase), aryloxyphenoxypropionate (AOPP), cyclohexanedione (CHD) and acetolactatesynthase (ALS)-inhibiting herbicides [1,6–8]. The mechanism behind the resistance is reported to be enhanced metabolism in the case of AOPP/CHD resistance [6] and target-site resistance in case of ACCase-inhibiting and ALS-inhibiting herbicides [7,8]. Black-grass is extremely disposed to develop herbicide resistance and there will soon be no effective herbicide left. The black-grass problem is so bad in some fields that they have to be taken out of production. The problems with herbicide-resistant weeds, black-grass in particular, have paved the way for non-herbicide weed-management practices [7,9]. In these, farmers are encouraged to use more cultural control measures such as ploughing, crop rotation and delayed drilling. However, little emphasis is placed on the competitive ability within the crop [7,10], although there are reports of this trait having strong effects on other weeds [11–13].

Allelopathy is one component of the competitive complex, besides vigorous root and shoot growth, leaf inclination and straw length, among others. There is increasing evidence that allelopathy can play a significant role in weed competition in wheat [11,13–15]. If wheat allelochemicals released by the living crop can suppress herbicide-resistant black-grass, this could have a great influence on wheat production in black-grass infested fields. The allelopathic effects on herbicide-resistant and herbicide-sensitive weeds have been studied before, but using extracts from residues. For example, Przepiokowski and Gorski [16] found that aqueous extracts of rye residues inhibited both herbicide-resistant and herbicide-sensitive horseweed (*Conyza canadensis* L.) and willowherb (*Epilobium ciliatum* Rafin). Wu *et al.* [17] showed that aqueous extracts of wheat shoot residues inhibited germination and root growth of a biotype of annual ryegrass resistant to several groups of herbicides, as well as herbicide-sensitive ryegrass. However, in that study herbicide-resistant ryegrass was generally more sensitive to several allelochemicals than herbicide-susceptible ryegrass.

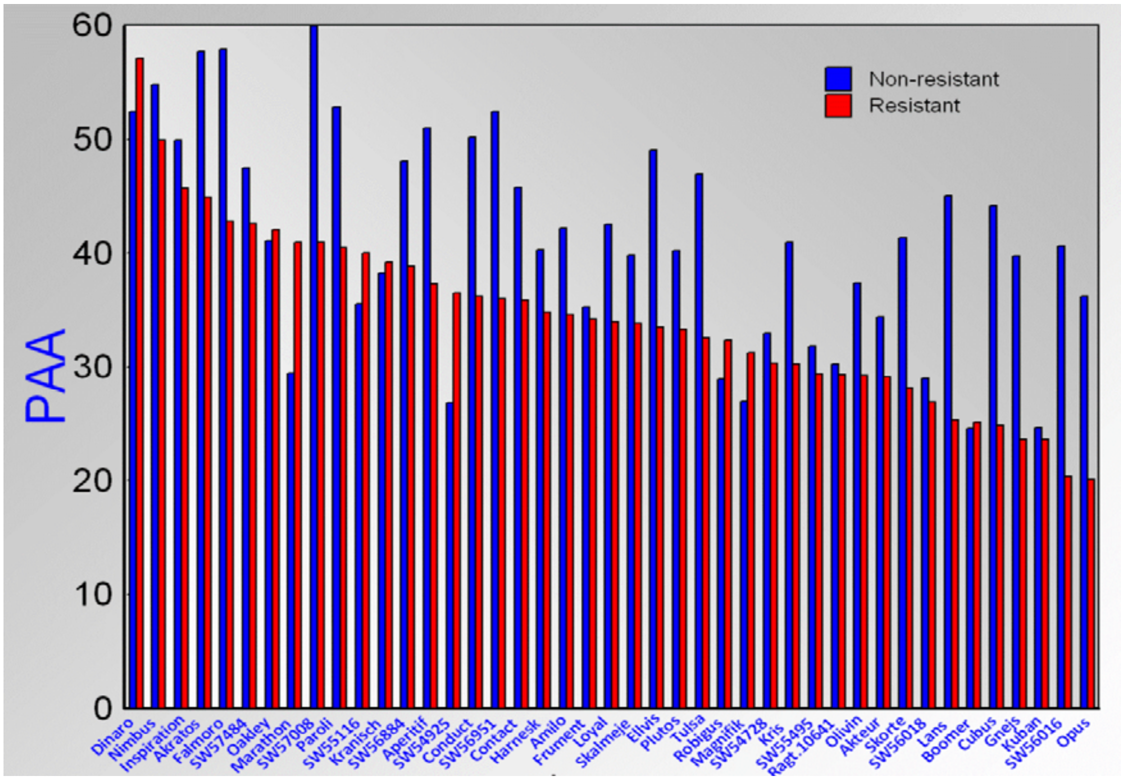
The aim of the present study was to examine allelopathic interference with herbicide-resistant and herbicide-sensitive black-grass by modern winter wheat cultivars either on the national cultivar list or in the release pipeline in Sweden. Wheat-rye translocation lines [18] were also included in the study to determine their potential as possible sources of high allelopathic activity. The growth inhibition of black-grass roots by wheat root allelochemicals was used as a measure of the potential allelopathic activity of each wheat cultivar. The allelopathy screenings were followed by field evaluations.

2. Results and Discussion

2.1. Allelopathic Potential of Modern Wheat, Triticale, Rye and Wheat Breeding Lines

Statistical analysis using ANOVA detected highly significant differences ($P < 0.001$) between wheat, triticale and rye cultivars, biotypes and biotype × cultivar interactions in their interference with herbicide-sensitive and herbicide-resistant black-grass. When herbicide-sensitive and herbicide-resistant black-grass were grown together with different cultivars on pure agar, their root growth was inhibited by between 25% and 60%, depending on the cultivar (Figure 1). The triticale cultivar Dinaro followed by the new wheat cultivar Nimbus showed the highest activity against both herbicide-sensitive and herbicide-resistant black-grass. The other triticale cultivar, Falmoro, showed higher activity to herbicide-sensitive black-grass than to herbicide-resistant black-grass. Rye is known to be allelopathic [19], but in this study, the rye cultivar Amilo showed only medium allelopathic activity. The reason for this finding, as also noted in previous studies, may be that the bioassay used is not adapted to rye [13]. This is because maximum allelopathic activity occurs much later in rye than in wheat and the plants were only observed for 10 days in the bioassay [20,21].

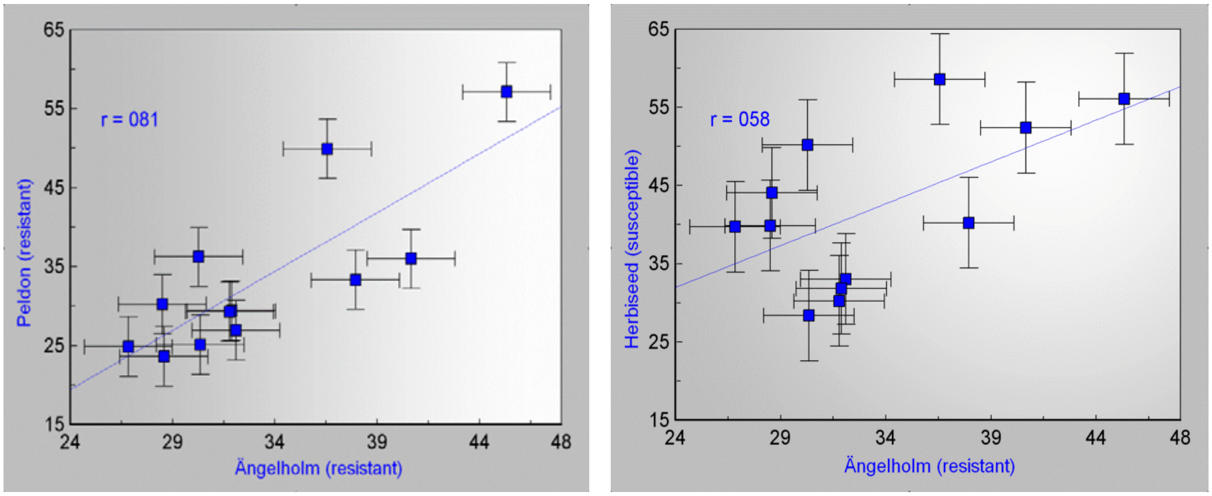
Figure 1. Potential allelopathic activity (PAA) calculated as percentage reduction in root growth of herbicide-resistant and herbicide-sensitive black-grass in the presence of 32 winter wheat cultivars and eight advanced breeding lines, two triticale cultivars (Dinaro and Falmaro) and one rye cultivar (Amilo) (95% confidence interval = 11.9).



Most cultivars showed similar interference with herbicide-sensitive and herbicide-resistant black-grass, but 12 cultivars showed significantly ($P < 0.05$) higher allelopathic interference with the herbicide-sensitive biotype and one showed significantly lower interference. The higher interference with the herbicide-resistant weed biotype contradicts previous findings by Wu *et al.* [17]. In their study with ryegrass as the model weed, 24 wheat cultivars were more allelopathic to herbicide-resistant ryegrass and only 12 cultivars to herbicide-sensitive ryegrass. In the present study, herbicide-resistant black-grass was clearly less affected by the wheat allelochemicals. There are several explanations for these differences. Firstly, not only different biotypes, but also different species were used, so even if ryegrass had evolved similar herbicide resistance to black-grass, there could still be differences between the species. Secondly, extracts were used in the study by Wu *et al.*, whereas we used exudates. Thirdly, those authors also found a significant cultivar x biotype interaction and hence the difference in results could be a matter of choice of cultivar. Przepiokowski and Gorski [16] found that rye extract inhibited the germination and growth of both herbicide-sensitive and herbicide-resistant forms of three different weeds.

The studies cited above and the present study show that allelochemicals, either extracted or exuded from wheat and rye, can inhibit both herbicide-sensitive and herbicide-resistant biotypes of weeds. The lower effect observed here on herbicide-resistant black-grass may not necessarily be related to herbicide resistance, but to biotype. However, a second resistant biotype collected near Ängelholm in southern Sweden showed a higher correlation with the resistant biotype Peldon than with the sensitive biotype from Herbiseed Ltd., England (Figure 2). Both biotypes are resistant to photosynthesis inhibitors, which may indicate that the differences in interference observed could be related to herbicide resistance. The reason for this behavior is still unknown, but one of the wheat allelochemicals (phenolic acid) is known to target the chlorophyll degradation pathways, as do some herbicides [22]. In fact, most, if not all, herbicides are based on allelochemicals found in plants. After minor rearrangements of the active molecule to make it more stable and active, it is used as the active ingredient in a commercial herbicide. Thus, allelochemicals and herbicides are closely related and it is possible that the activity of wheat allelochemicals was also affected by whether the black-grass was herbicide-resistant or not. This also raises the question of whether black-grass and other weeds can evolve resistance to wheat allelochemicals, a possibility that cannot be excluded. However, in the case of sorgoleone, an allelochemical exuded from root hairs of sorghum, there is no known resistance. The reason for this could be that sorgoleone inhibits both photosystem II and 4-hydroxyphenyl-puruvate-dioxygenase (HPPD), and it is unlikely that the two mutations at least required for the development of resistance will occur. Thus, during millions of years of evolution, the allelochemicals could have developed multiple target inhibitions [23] and hence are less likely to encounter resistance than herbicides.

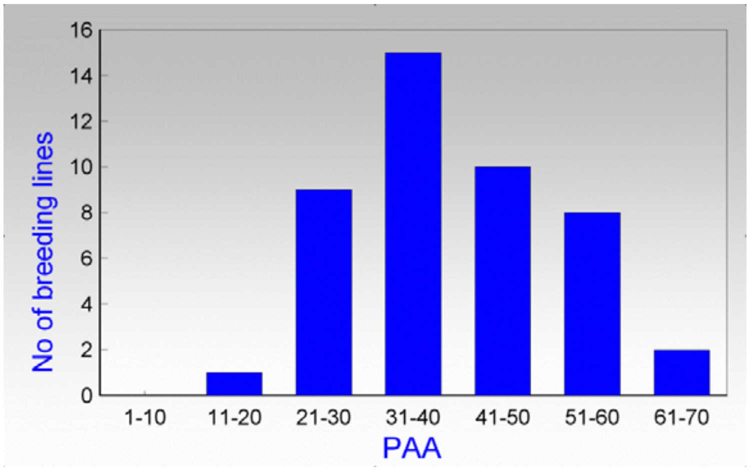
Figure 2. Relationship between potential allelopathic activity of a herbicide-resistant black-grass biotype from Ängelholm and the herbicide-resistant biotype Peldon from Essex (**left**), and the relationship between the resistant biotype from Ängelholm and the herbicide-susceptible biotype from England (**right**). Bars indicate two standard errors (SE). r denotes the linear correlation coefficients and it is significant if $r > 0.57$ ($P < 0.05$).



2.2. Allelopathic Potential of Wheat-Rye Translocation Lines

The allelopathic activity of the wheat-rye translocation lines ranged from 16% to 58%, but most lines had a PAA value between 31 and 40 (Figure 3). The two cultivars in the last bar in Figure 3 are triticales (Dagro and a triticale breeding line), with a PAA of 61 and 62, respectively. The 51–60 range included two wheat cultivars (Nimbus and Inspiration) and one triticale (Pinoccio). The three other wheat cultivars had a PAA value of less than 32. Thus, five wheat-rye translocation lines had a rather high allelopathic activity, a promising finding for future plant breeding work. However, when the D-genome was substituted by the whole rye genome (R), as in triticale, the allelopathic activity against black-grass was higher. As for rye, the wheat-rye substitution and translocation lines may be discriminated against by the bioassay used. It is also possible that black-grass is less sensitive to rye allelochemicals than to wheat and triticale allelochemicals. Rye and wheat interferences with different weeds differed in a previous study of different receiver plants [18]. The interference with *Chenopodium alba*, *Lolium perenne* and *Brassica napus* was similar, while the interference between rye and *Sinapis alba* was twice that for wheat. On-going field evaluations of wheat-rye translocation lines will ultimately demonstrate whether it is possible to improve weed susceptible ability in wheat by translocation or substitution of rye chromosomes or part of rye chromosomes. The part of the rye genome that is translocated or substituted has yet to be determined in all lines characterized in the present study. However, the substitutions are known in 11 of the lines and they showed a PAA value of 37 or lower. In most of these there is a 1R substitution, 2R in three lines and 1R+6R in three lines. The 1R and 2R substituted lines showed an evenly distributed PAA value below 37 and down to 18. All double-substituted lines 1R+6R showed low allelochemical activity. This result confirms earlier findings that it is difficult to relate a special rye chromosome to high allelopathic activity [18]. Since substitutions in the lines with the highest activity, with the exception of the three triticale breeding lines, are not known, more information about their genetics may change this preliminary conclusion.

Figure 3. Frequency distribution of potential allelopathic activity (PAA) of winter wheat-rye translocation lines including five wheat and three triticale cultivars (pooled standard error of PAA = 3.7).



2.3. Field Studies

A heavy infestation of black-grass in 2010, no black-grass in 2011 and winter die-off of four cultivars in 2012 affected our field studies. In addition, in 2012 the infestation of black-grass was low and unevenly distributed. Spreading herbicide-sensitive black-grass seeds and then raking them solved this problem, resulting in an even distribution of black-grass with a low sampling error . Unfortunately, the two wheat cultivars with high allelopathy did not survive the winter. However, in both years, there was a tendency (not significant) for a negative relationship between allelopathic activity of the wheat cultivars and black-grass biomass (Figure 4). Cultivars with high allelopathic activity had less black-grass biomass at heading of wheat than those with low activity. This is in line with previous findings of a relationship between laboratory bioassays and field screening [13,24]. None of the cultivars tested could fully outcompete the black-grass. However, in both years the triticale cultivar showed the highest competitive ability. This confirms findings in other trials on a mixture of monocotyledonous and dicotyledonous weeds [13]. The present study indicated that biomass growth of black-grass, herbicide-resistant or not, can be reduced by 33%–50% by choosing a more competitive crop cultivar. The problems with black-grass could be further reduced by greater use of cultural control options such as ploughing, crop rotation and delayed drilling [1,9].

This study was limited to cultivars available on the market, advanced breeding lines and wheat-rye translocation and substitution lines. It should be possible to select genotypes with higher allelopathic activity by screening a larger sample of breeding material, because there was no negative relationship between allelopathic activity and grain yield (Figure 5). The wheat cultivar Nimbus (No. 4 in Figure 5) is a good example of this finding: If there had been a negative relationship with yield, it could have been discarded in earlier generations. Nimbus is a newly released cultivar with high allelopathic activity, but it seems to lack some winter hardiness. However, it is not the only wheat cultivar with low winter hardiness and in fact there seems to be an overrepresentation of weak winter hardiness among cultivars with high allelopathic activity. It is not yet known whether this is a related trait, or simply a coincidence.

Figure 4. Relationship between potential allelopathic activity (PAA) of winter wheat cultivars (incl. the triticale cultivar Dinaro (1)) and total aboveground biomass of black-grass at time of heading of wheat in two different years. For cultivar identification codes see the Materials section. Bars indicate two standard errors (SE).

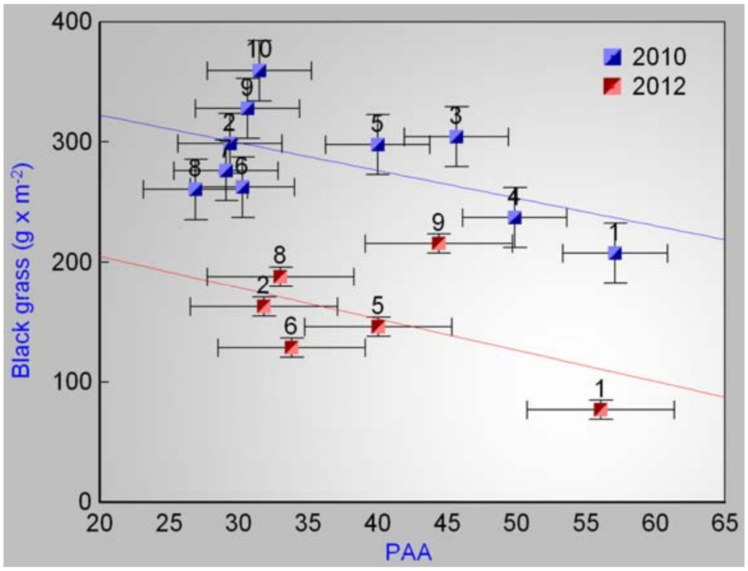
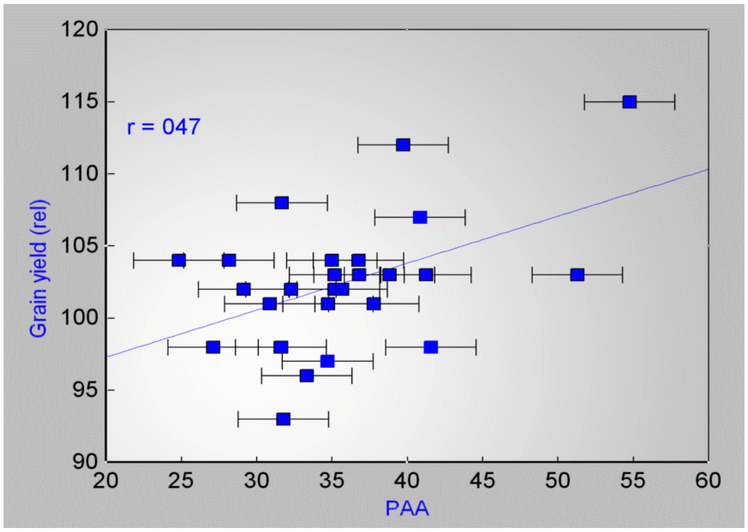


Figure 5. Relationship between potential allelopathic activity (PAA) and grain yield in Swedish official variety tests of winter wheat cultivars. Bars indicate two standard errors (SE). *r* denotes the linear correlation coefficients and is significant if $r > 0.38$ ($P < 0.05$).



3. Experimental Section

3.1. Materials

Winter wheat cultivars and breeding lines, either on the national variety list of Sweden or submitted to official Swedish variety testing in 2009, were collected from various owners or representatives. In a first set-up, 32 wheat cultivars, eight advanced breeding lines, two triticale cultivars and one rye cultivar were tested. In a second set-up, 40 wheat-rye translocation lines, two wheat cultivars and one rye cultivar were tested. Furthermore, two seed stocks of black-grass were obtained from Herbiseed Ltd., Berkshire, UK, one collected from Peldon, Essex, UK (herbicide multi-resistance to photosynthesis inhibitors Arelon® and Cougar®, ALS-inhibitors Lexus®1, Atlantis®2 partly and ACCase-inhibitors, Puma®), and the other collected by Herbiseed Ltd (herbicide-susceptible). A third seed stock was collected near Ängelholm, southern Sweden (resistant to photosynthetic electron transport inhibitors Arelon® and Cougar®).

3.2. Methods

3.2.1. Evaluation of Allelopathic Activity

The potential allelopathic activity (PAA) was evaluated using a bioassay adapted from Wu *et al*. [11] with modifications concerning the number of plants, number of receiver plants, gel concentration and gel quantity and length of test period [25]. These were selected to explain the variance in weed competitive ability in barley as far as possible. In the original method, ryegrass (*Lolium perenne* L.) was used as receiver plant, but here black-grass was used. In plastic tissue culture vials (Phytotech, 400 mL) filled with 20 mL 0.35% water agar, four pre-germinated wheat seedlings were planted in the center and eight pre-germinated black-grass seedlings in a circle around the vial wall. The cereal seeds were pre-germinated on filter paper in darkness for three days at 21 °C. The black-grass seeds were germinated on filter paper in light and pre-germinated seedling with root length between 2 mm and 10 mm were collected daily and stored at +4 °C up to three days until planting in the vials. The wheat seeds were soaked in 70% ethanol for one minute and rinsed with water and this process was then repeated to reduce the risk of infection. The vials were sealed with a lid that admitted some air and placed in a growth chamber with a light/dark cycle of 16/8 h at a temperature of 20 °C and inflorescent light of 52 µmol m^{-2} s^{-1}. After seven days, the root area (mm^2) of the black-grass was measured using an image analyzer (DIAS, Delta-T Devices, Cambridge, England), by placing them between two plates made of glass lying on black cloth. The plates were illuminated by four lamps (Osram h428 60W) shining at a 45-degree angle. Vials with only ryegrass were used as controls. PAA was calculated according to $PAA = (1 - A1/A2) \times 100$ with A1 = black-grass root area in the presence of wheat and A2 = black-grass root area without wheat. The cultivars were tested in six replicates with the three different biotypes of black-grass as receiver plants.

3.2.2. Field Studies

Nine winter wheat and one triticale cultivar were sown in trials following a randomized block design with three replicates in 2009/2010 and 2010/2011, and with four replicates in 2011/2012.

The cultivars were Dinaro (1) (triticale), SW55495 (2), Inspiration (3), Nimbus (4), Kranich (5), Magnifik (6), Akteur (7), SW56018 (8), SW56016 (9) and Robigus (10). The crops were drilled on 24 September 2009 at Esarp (55°38' N, 13°18' E), 23 September 2010 at Väståkra (55°40' N, 13°9' E) and 28 September 2011 at Väståkra (55°40' N, 13°9' E) in southern Sweden, on clay soils following winter rapeseed, spring barley and winter rapeseed, respectively. The plot size was 19.2 m^2 with 16 rows, a row spacing of 12 cm and 350 plants per m^2. The plots were fertilized with 120 kg N (Axan, Yara, Landskrona, Sweden) on 1 April 2008, and 60 kg N (Axan, Yara, Landskrona Sweden) on 26 March + 60 kg N (Axan, Yara, Landskrona Sweden) on 20 April 2009. In the trial at Esarp, the infestation of black-grass was massive, whereas at Väståkra in the second year there was no black-grass at all and therefore it had to be excluded from the analysis. Broad-leaved weeds were controlled by Ariane S®. The first year there were also spots in the field infested by Loose Silky-bent (*Agrostis spica-venti* L). These spots were avoided when sub-sampling for black-grass bioamass. The infestation was also low in 2011, but black-grass was spread by hand and raked in (about 200 seeds) on an area of 1 m^2 at two places in each plot. These plots later showed an even and rather heavy distribution of black-grass similar to that in the first year. At time of heading of triticale (in 2010) and wheat (in 2012), crop and black-grass biomass were analyzed by sub-sampling an area of 2 × 0.25 m^2 and determining the dry weight of aboveground biomass after seven days in a ventilated oven at 80 °C.

3.2.3. Data analysis

The bioassay of each cultivar and line was repeated six times over time. Two internal checks were included in each test run and when the two checks differed from other test runs, the values of all cultivars in that test run were corrected by subtracting the differences between the mean value of the two check cultivars and the mean value of the checks for all test runs. An ANOVA was performed on the bioassay data with genotype and two treatments (sensitive and resistant) as factors to determine treatment effects and pooled standard errors. The field data were subjected to ANOVA analysis with cultivars and replications (blocks) as factors. Relationships between bioassay and field mean data were studied by regression analysis. The ANOVA, regression analysis and frequency study were carried out using Statgraphics Pro (Manugistics, Inc., Rockville, MD, USA).

4. Conclusions

The study revealed large variations in allelopathic activity among the cultivars studied. Most cultivars showed interference with both herbicide-sensitive and herbicide-resistance black-grass, although the allelopathic effect was lower on the herbicide-resistant biotype. The cultivar that showed highest allelopathy and inhibition of black-grass was the triticale Dinaro, followed by the new wheat cultivar Nimbus. Cultivars with high allelopathic activity gave only half the black-grass biomass of cultivars with low allelopathic activity, a fact that may considerably contribute to either resistance prevention or management. Five of the wheat-rye translocation lines tested showed an activity similar to that of triticale and the best wheat cultivars. Thus it is possible that wheat-rye translocation lines could be a source when breeding high allelopathic wheat cultivars. Choice of cultivars with high allelopathic activity is likely to be important in integrated weed management of black-grass.

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