ISSN 1062-3590, Biology Bulletin, 2022, Vol. 49, No. 3, pp. 133–141. © Pleiades Publishing, Inc., 2022.
Russian Text © The Author(s), 2022, published in Izvestiya Akademii Nauk, Seriya Biologicheskaya, 2022, No. 3, pp. 237–245.

BIOCHEMISTRY

Secondary Metabolites of Micromycetes in Plants of the Family Brassicaceae (Cruciferae)

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Received July 23, 2020; revised January 21, 2021; accepted January 21, 2021

Abstract—Indirect competitive enzyme immunoassay was used to detect the occurrence of 16 mycotoxins in wild herbaceous plants of the Brassicaceae (Cruciferae) family typical for biocenoses of Central Russia. Alternariol, cyclopiazonic acid, and the total of ergot alkaloids were detected with a frequency of 52–100% in all species studied, representing 13 genera. The rest of the substances analyzed (i.e., fusariotoxins and metabolites peculiar to micromycetes of other taxa, including ochratoxin A, citrinin, sterigmatocystin, aflatoxin B_1, mycophenolic acid, emodin, PR toxin, and roridin A) were either absent or detected less frequently in quantities close to the detection limit of the method. In a number of plants, T-2 toxin, deoxynivalenol, diacetoxyscirpenol, and other minor components were detected more frequently. Patterns determining the distribution of mycotoxins in vegetative and generative organs of the bird rape (*Brassica campestris* L.), winter cress (*Barbarea arcuata* (Opiz ex J. et C. Presl) Reichenb.), and hill mustard (*Bunias orientalis* L.) have been identified; however, no clearly manifested seasonal dynamics of mycotoxin accumulation was noted for these plants.

Keywords: wild cruciferous plants, mycotoxins, enzyme-linked immunosorbent assay (ELISA)

DOI: 10.1134/S1062359022030050

INTRODUCTION

Herbaceous vascular plants are unique biological objects featuring perfect adaptation mechanisms to multiple environmental factors, including fungal communities, both external and internal (Zhang et al., 2006; Rodriguez et al., 2009). Plants and microscopic fungi can implement a wide range of contacts and relationships: from simple competitive reactions to diverse coexistence forms (Zabalgogeazcoa, 2008). Many associated microscopic fungi are known to be able to biosynthesize toxic metabolites (Weidenbörner, 2001), but their contribution to and degree of participation in the life of the host organism remained unclear for a long time. The statement of this problem became possible thanks to the development of a unified immunochemical analysis methodology making it possible to detect mycotoxins with various structures both selectively and sufficiently sensitively (Kononenko and Burkin, 2002). A survey of plants belonging to several taxonomic groups of the family Fabaceae made it possible to collect the first data on species-specific features of and seasonal changes in the accumulation of toxic metabolites produced by associated micromycetes (Burkin and Kononenko, 2018; Kononenko and Burkin, 2018, 2019). A study of cruciferous plants representing an integral component of meadow ecosystems in Central Russia became the next step in this scientific field.

The purpose of this study was to examine the occurrence and content of mycotoxins in cruciferous herbaceous plants belonging to various genera and to assess the variability of the metabolic profile over the growing season and for individual organs.

MATERIALS AND METHODS

The objects of this study were 289 wild herb specimens representing 13 genera of the family Brassicaceae (Cruciferae): garlic mustard (*Alliaria petiolata* (Bieb.) Cavara et Grande), alyssum (*Alyssum hirsutum* Bieb.), wild horse radish (*Armoracia rusticana* Gaertn., Mey. et Scherb.), winter cress (*Barbarea arcuata* (Opiz ex J. et C. Presl) Reichenb.), bird rape (*Brassica campestris* L.), hill mustard (*Bunias orientalis* L.), shepherd's purse (*Capcella bursa-pastoris* (L.) Medik.), erysimum (*Erysimum aureum* Bieb.), joined charlock (*Raphanus raphanistrum* L.), marsh cress (*Rorippa palustris* (L.) Bess.), hedge mustard (*Sisymbrium* spp.), white mustard (*Sinapis alba* L.), and field pennycress (*Thiaspi arvense* L.). The plant species were identified using keys (Gubanov et al., 2003; Skvortsov, 2004).

The aboveground parts of whole plants cut at a height of 3–5 cm from the soil surface were collected

on a regular basis (at weekly intervals) in May–July 2017–2019 in three meadow areas in Moscow and Tver oblasts. The sampling areas were selected for the greatest diversity of cruciferous plant species. After transportation over a short distance, some of the collected plants were divided into fragments (stems, leaves, flowers, and siliques and silicules with seeds). Then the specimens were stored in a ventilated chamber at room temperature to reach the air-dry condition; prior to the analysis, the samples were ground in a laboratory mill. A mixture of acetonitrile and water (volume ratio: 84 : 16; amount: 10 mL per gram of specimen) was used for extraction. After the tenfold dilution with a buffer solution, the extracts were used for indirect competitive enzyme immunoassay. Mycotoxins (T-2-toxin (T-2), diacetoxyscirpenol (DAS), deoxynivalenol (DON), zearalenone (ZEN), fumonisins (FUM), ergot alkaloids (EA), alternariol (AOL), roridin A (ROA), aflatoxin B_1 (AB_1), sterigmatocystin (STE), cyclopiazonic acid (CPA), emodin (EMO), ochratoxin A (OA), citrinin (CIT), mycophenolic acid (MPA), and PR-toxin (PR)) were analyzed using certified enzyme immunoassay test systems (Kononenko et al., 2015). The lower quantitative measurement limits were equal to 2 (T-2, EA, and AB_1), 4 (OA, STE, and ROA), 15 (AOL, ZEN, and EMO), 20 (CIT and MPA), 50 (DON), 60 (FUM and CPA), and 100 (DAS, PR) μg/kg and corresponded to an 85% antibody binding level. The standard repeatability and intermediate precision deviations were consistent with the authorized values of these parameters (State Standard 31653–2012).

RESULTS AND DISCUSSION

A common feature clearly manifested in all plants studied is the high occurrence of AOL, CPA, and EA with a frequency of 52–100% (Tables 1, 2). In terms of their accumulation levels, the above metabolites form the following series: CPA > AOL > EA; the content of AOL, a known metabolite of *Alternaria* fungi, amounts in this series to tens of μg/kg with the highest value of 75 μg/kg in *Armoracia rusticana*. For CPA and EA synthesized by other fungal taxa, this parameter varies from hundreds to tens and units of μg/kg (in field pennycress and alyssum). As in the preliminary study (Kononenko and Zotova, 2019), ROA was not found in the plants studied, even though some fungal species of the genus *Myrothecium* can produce it.

Annual cruciferous plants are either not contaminated with toxins produced by *Fusarium* fungi or their contamination is limited to T-2 or DAS (Table 1); these toxins were not detected in the sole joined charlock specimen available for analysis. By contrast, all perennials with long and interrupted development cycles are contaminated with T-2 and FUM. In winter cress, this combination is supplemented with DON; in marsh cress, with DAS; in garlic mustard, with ZEN; and in hill mustard, with all three of these metabolites together (Table 2). The presence of all fusariotoxins in four unidentified representatives of the genus *Sisymbrium* indicates that they also belong to perennials; one of them was indeed identified as *S. volgense* Bieb. Ex Fourn. Different combinations of fusariotoxins in such plants can be determined by the species composition of their associated fungal groups. Concurrently, T-2 is more frequently detected in marsh cress, T-2 and DON in winter cress, and DAS in hill mustard, and the content ranges of the above toxins in these plants are extended towards higher amounts, which can be determined by the intensity of their colonization. In this regard, it is necessary to note a recent study of meadow plants belonging to the family Leguminosae (Orina et al., 2017, 2018): the obtained data show that the content of fungal DNA of the genus *Fusarium* in perennials is significantly higher than that in annual plants.

The joint presence of metabolites known to be concertedly biosynthesized by fungi was identified in the plants studied: OA and CIT (*Penicillium viridicatum* Westling), STE and AB_1 (*Aspergillus flavus* Link and *A. parasiticus* Speare), and MPA and PR (*P. roqueforti* Thom); the ratios between the amounts of CIT and OA on the one hand and the amounts of MPA and PR on the other hand are consistent with those determined in cultures (Weidenbörner, 2001). This contamination type is typical for all perennial plants, but it is rarely detected in annuals (only in shepherd's purse and field pennycress) (Tables 1, 2). In the future, it is planned to perform a comparative assessment of the infection of these plants with toxin-secreting species using quantitative PCR.

The origin of the anthraquinone metabolite EMO in plant objects is still a matter of debate (Izhaki, 2002). In cruciferous plants, it was found in species of the genus *Sisymbrium* in amounts from 40 to 98 μg/kg, and in all other plants studied, except for joined charlock, alyssum, wild horse radish, and garlic mustard, at levels of 18–29 μg/kg (Tables 1, 2).

A comparison of the data presented in Tables 1 and 2 shows that shepherd's purse and hill mustard are the leaders among the cruciferous plants in terms of the component composition of mycotoxins, which makes them the most promising objects for in-depth studies of the role played by these compounds. In recent years, the identification of plants that can be used as convenient models for general metabolomics analysis used to solve biochemical, physiological, environmental, and taxonomic problems has become increasingly relevant (Kotlova et al., 2016).

Overall, mycotoxin accumulation levels in the meadow cruciferous plants studied are lower in comparison with legumes; accordingly, their mycotoxin loads should be recognized as low as well. Of course, such a conclusion cannot be considered final taking the significant diversity of cruciferous plants: more than 75 species in Central Russia alone (Gubanov

Table 1. Occurrence frequency (%) and content of mycotoxins in the aboveground parts of annual cruciferous plants

Mycotoxin	Bird rape *Brassica campestris* $n = 17$	Field pennycress *Thiaspi arvense* $n = 21$	Shepherd's purse *Capcella bursa-pastoris* $n = 39$	Erysimum *Erysimum aureum* $n = 14$	Allysum *Alyssum hirsutum* $n = 17$
T-2	–	5 5	21 2–**9**–34	21 3–**5**–6	–
DON	–	–	–	–	–
DAS	– ($n = 13$)	– ($n = 16$)	– ($n = 32$)	–	6 130
ZEN	–	–	–	–	–
FUM	–	–	–	–	–
AOL	71 12–**34**–59	91 24–**41**–105	77 19–**43**–150	64 16–**31**–40	53 18–**36**–84
OA	–	33 4–**8**–12	23 5–**7**–10	7 **8**	59 4–**6**–10
CIT	6 40	–	8 21–**28**–32	–	–
STE	6 13	14 12–**14**–17	8 6–**11**–15	64 15–**21**–28	24 6–**25**–83
AB_1	–	38 2–**3**–5	13 2–2–3	–	–
CPA	76 32–**150**–300	62 98–**175**–315	97 32–**200**–610	93 100–**140**–205	100 100–**145**–200
MPA	–	10 24, 33	31 9–**30**–100	7 33	–
EA	88 2–**20**–190	52 2–**9**–30	100 2–**15**–54	100 2–**20**–105	100 2–**7**–15
EMO	29 12–**18**–30	29 12–**29**–69	21 15–**21**–30	21 15–**17**–20	–
PR	–	–	5 390, 400	–	–

The upper line represents the share of toxin-positive specimens (%); the lower line represents the mycotoxin content (μg/kg): min value–**mean value**–max value; (–) mycotoxin not detected; and *n* is the number of specimens analyzed (applies to Tables 1 and 2).

et al., 2003; Skvortsov, 2004). In the family Leguminosae, plants with contrasting mycotoxicological statuses were identified even within the same genera, for instance, in *Trifolium* L. (Kononenko and Burkin, 2018) and in *Lathyrus* L. (Kononenko and Burkin, 2019).

As is known, domestic cruciferous plants fall out of cultivation easily and successfully adapt to natural communities (Gubanov et al., 2003; Skvortsov, 2004). Unfortunately, the degree of impact of habitat conditions on the profile of fungal metabolites is still poorly researched. However, analysis of 11 wilding white mustard (*Sinapis alba*) specimens shows its similarity to cultivated white mustard in the following aspects: low general mycotoxin load; regular occurrence of AOL, CPA, and EA; rare detection of AB_1, STE, EMO, and MPA; and single cases of OA, CIT, T-2, and FUM detection (Burkin et al., 2019).

Seasonal variations in the concentrations of endogenous secondary metabolites in vascular plants and the heterogeneity of their distribution between plant organs indicate their involvement in adaptation mechanisms to external impacts (Arbona et al., 2013; Kushalappa and Gunnaian, 2013; Hong et al., 2016). Fluctuations in the content of mycotoxins from the beginning of plant growth to flowering were described for the following legumes: meadow clover, white clover (Kononenko and Burkin, 2018), species of the genera *Medicago* and *Melilotus* (Burkin and Kononenko, 2018), meadow peavine, and cow vetch (Kononenko and Burkin, 2019). In cultivated white mustard, the composition of mycotoxins and the quantitative ratios

Table 2. Occurrence frequency (%) and content of mycotoxins in the aboveground parts of perennial cruciferous plants

Mycotoxin	Winter cress *Barbarea arcuata* $n = 62$	Hill mustard *Bunias orientalis* $n = 30$	Wild horse radish *Armoracia rusticana* $n = 8$	Garlic mustard *Alliaria petiolata* $n = 32$	Marsh cress *Rorippa palustris* $n = 33$
T-2	16 2–**7**–49	27 2–**3**–4	25 3, 5	6 3, 4	30 2–**6**–25
DON	48 46–**81**–130	7 50, 76	–	–	–
DAS	– ($n = 54$)	42 100–**200**–400 ($n = 24$)	–	– ($n = 22$)	9 100–**110**–125
ZEN	–	13 24–**33**–49	–	3 17	–
FUM	2 89	3 129	13 73	3 105	12 60–**67**–81
AOL	60 15–**30**–42	67 19–**35**–59	100 63–**75**–100	91 19–**36**–92	85 18–**33**–52
OA	3 8, 8	10 8–**8**–9	–	34 4–**8**–13	15 4–**6**–11
CIT	29 26–**34**–42	3 50	25 30, 33	25 25–**33**–47	9 33–**41**–45
STE	5 11–**13**–15	20 6–**11**–25	50 7–**8**–9	16 6–**14**–21	45 8–**12**–16
AB_1	–	17 2–**2**–2	63 2–**3**–3	38 2–**4**–5	18 2–**2**–2
CPA	95 63–**285**–645	93 82–**220**–515	100 130–**225**–300	75 63–**145**–250	91 76–**205**–470
MPA	3 19, 24	23 12–**27**–47	–	9 12–**13**–15	39 17–**23**–31
EA	86 2–**13**–160	83 2–**25**–95	100 6–**35**–63	75 4–**17**–56	100 3–**28**–125
EMO	–	27 10–**20**–30	–	53 16–**28**–77	18 14–**22**–32
PR	3 400, 415	3 205	–	–	6 270, 300

between them generally remain the same during the growing season; however, as the plants mature, the content of AOL and CPA goes down (Burkin et al., 2019). No significant and regular seasonal fluctuations in the occurrence and content of mycotoxins were identified in meadow cruciferous plants; however, common features, both general and specific, were identified in the distribution of mycotoxins between vegetative and generative organs (Tables 3–5).

The set of typical metabolites (i.e., AOL, CPA, and EA) is present in both vegetative and generative organs, which indicates a uniform distribution of associated fungi that biosynthesize these toxins. Leaves accumulate more AOL, CPA, and EA in comparison with stems and may contain toxins absent in the stems (Tables 3–5). Interestingly, in wild horse radish (*Armoracia rusticana*) and winter cress (*Barbarea arcuata*), no differences were identified between leaves growing in the upper and lower tiers and differing in shape (Kononenko et al., 2019). An elevated content of mycotoxins in leaves combined with an expansion of the component composition has already been described for white mustard (Burkin et al., 2019) and sunflower, a representatives of the family Asteraceae (Zotova et al., 2017). This phenomenon can be explained by the concentration of many dynamic functions of the organism in leaf blades.

Table 3. Occurrence (n^+) and content of mycotoxins in the vegetative and generative organs of annual cruciferous plants

Mycotoxin	Bird rape *Brassica campestris*				Field pennycress *Thiaspi arvense*	Shepherd's purse *Capcella bursa-pastoris*
	stems $n = 2$	leaves $n = 2$	flowers $n = 4$	siliques $n = 5$	silicules $n = 6$	silicules $n = 6$
T-2	–	–	–	–	–	–
DON	–	–	3 79–**81**–86	–	–	–
DAS	–	–	4 195–**240**–295	Not determined	Not determined	Not determined
ZEN	–	–	4 25–**29**–39	–	–	–
FUM	–	–	4 120–**145**–170	–	–	–
AOL	1 19	2 26, 28	4 38–**50**–63	2 12, 17	5 16–**37**–78	3 35–**36**–37
OA	–	–	–	–	6 5–**8**–10	2 6, 10
CIT	–	1 25	–	–	–	–
STE	–	1 8	–	–	3 15–**16**–19	3 12–**16**–23
AB_1	–	–	–	–	3 2–**2**–2	1 2
CPA	2 85, 195	2 300, 350	4 110–**140**–160	3 30–**37**–40	3 115–**140**–165	5 97–**145**–175
MPA	–	–	4 16–**21**–26	1 20	–	–
EA	2 2, 3	2 21, 43	2 2, 3	5 1–**3**–6	3 3–**6**–10	5 2–**5**–10
EMO	–	–	4 22–**25**–26	4 10–**14**–16	–	2 19, 24
PR	–	–	2 350, 515	–	–	–

The upper line represents the number of toxin-positive specimens (n^+); the lower line represents the mycotoxin content (μg/kg): min value–**mean value**–max value; (–) mycotoxin not detected; *n* is the number of specimens analyzed; and "not determined" means that the specimen was not analyzed for the presence of this toxin (applies to Tables 3–5).

Earlier, it was established that the composition of fungal metabolites in white mustard flowers is richer in comparison with its leaves (Burkin et al., 2019); this phenomenon was also revealed in the annual bird rape: the mycotoxin profile is supplemented with fusariotoxins (except for T-2), as well as MPA, EMO, and PR (Table 3). The set of mycotoxins in flowers of perennial plants (wild horse radish, winter cress, and hill mustard) differs from that in leaves in the opposite way: the composition of metabolites in flowers is poorer in comparison with the vegetative parts of the plant (Tables 4, 5). These unique traits identified in a few plants undoubtedly deserve further research, and larger samples of annuals and perennias should be used for data collection.

A number of distinct features have been identified in the fruits (siliques and silicules of various degrees of maturity) in comparison with flowers (bird rape, winter cress, and hill mustard) and the total phytomass. In annuals (bird rape, field pennycress, and shepherd's

Table 4. Occurrence (n^+) and content of mycotoxins in the vegetative and generative organs of winter cress-and hill mustard

Mycotoxin	Winter cress *Barbarea arcuata*				Hill mustard *Bunias orientalis*			
	stems $n = 7$	leaves $n = 7$	flowers $n = 8$	siliques $n = 7$	stems $n = 10$	leaves $n = 12$	flowers $n = 14$	silicules $n = 11$
T-2	4 2–**3**–5	2 2, 2	–	–	4 4–**7**–9	8 2–**4**–7	2 2, 5	1 2
DON	1 64	4 60–**81**–97	4 89–**99**–105	–	–	1 49	1 66	2 52, 53
DAS	–	–	–	Not determined	1 150	6 325–**400**–600	3 125–**165**–210 $n = 8$	2 200, 225 $n = 2$
ZEN	–	–	–	–	1 46	6 25–**40**–51	6 24–**29**–43	5 15–**43**–98
FUM	–	–	–	–	5 50–**105**–150	2 49, 49	–	1 47
AOL	7 25–**34**–51	6 25–**54**–160	4 24–**57**–130	1 38	7 13–**72**–315	9 20–**35**–59	5 13–**30**–67	4 10–**33**–53
OA	1 5	1 5	–	1 6	–	–	1 4	2 4, 5
CIT	–	–	–	2 26, 26	3 34–**38**–42	6 38–**48**–52	–	–
STE	–	1 15	–	2 13, 13	1 7	2 7, 8	–	1 19
AB_1	1 8	4 2–**6**–18	2 2; 16	–	–	3 2–**2**–2	1 2	–
CPA	7 155–**205**–305	7 295–**480**–760	8 200–**255**–385	5 65–**200**–365	7 97–**205**–365	12 155–**320**–630	9 63–**115**–185	3 38–**110**–250
MPA	2 20, 43	3 20–**35**–63	3 32–**40**–56	1 19	–	1 19	6 15–**20**–40	–
EA	7 3–**11**–32	7 2–**17**–76	5 2–**12**–48	4 2–**11**–20	7 3–**17**–42	12 2–**15**–47	5 2–**4**–5	1 8
EMO	2 19, 37	1 40	1 50	–	1 16	5 16–**26**–40	7 10–**30**–83	–
PR	–	2 265, 355	–	–	1 115	5 125–**160**–215	–	–

Table 5. Occurrence (n^+) and content of mycotoxins in vegetative organs and flowers of wild horse radish-and in siliques of garlic mustard

Mycotoxin	Wild horse radish *Armoracia rusticana*			Garlic mustard *Alliaria petiolata*
	stems $n = 9$	leaves $n = 7$	flowers $n = 4$	siliques $n = 10$
T-2	–	–	–	3 2–**3**–4
DON	–	–	–	3 83–**120**–155
DAS	–	–	–	Not determined
ZEN	–	–	–	2 25, 32
FUM	–	–	–	–
AOL	3 12–**13**–14	7 19–**20**–22	3 13–1**4**–14	10 24–**61**–105
OA	–	–	–	9 4–**16**–50
CIT	–	–	–	5 24–**30**–38
STE	–	–	–	4 12–**19**–27
AB_1	–	1 5	2 4, 4	8 2–**4**–4
CPA	1 100	7 97–**160**–205	–	7 78–**120**–160
MPA	–	2 25, 25	–	3 13–**15**–17
EA	–	7 4–**5**–7	–	8 8–**13**–20
EMO	–	–	–	6 14–**26**–54
PR	–	–	–	2 310, 330

purse), fusariotoxins are absent (Table 3), and the same effect was observed in winter cress (Table 4). By contrast, in two other perennials, hill mustard and garlic mustard, they are present among the contaminants (Tables 4, 5). A downward trend in the AOL and CPA accumulation levels was observed in bird rape (Table 3) and winter cress; while in hill mustard, it was more clearly pronounced for CPA and EA (Table 4). Out of the components found in aboveground parts of the plants with a frequency of more than 20%, EMO was absent in silicules of field pennycress; MPA, in shepherd's purse (Tables 1, 3); and EMO, MPA, and AB_1, in hill mustard (Tables 2, 4). Apparently, the decrease in the metabolic background noted in fruits of cruciferous plants, which was first discovered in white mustard (Burkin et al., 2019), is associated with the general vector of maturation processes in these plants. Unfortunately, the amount of information on the distribution of secondary metabolites between the organs of plants belonging to this family is still very low. It was shown that the content of phenolic compounds in seeds and valves of field pennycress silicules is significantly lower in comparison with the whole plant (Tartynskaya, 2013), while flavonols accumulate in the leaves, buds, and flowers of hill mustard in greater amounts in comparison with its stems (Mikhovich et al., 2018).

As is known, fungi belonging to the constitutive and induced mutualism groups are involved in mutu-

ally beneficial symbiosis with plants; these fungi inhabit aerated parts of the plant organism and can remain metabolically inactive for a long time with a relatively low fungal biomass. But under certain circumstances, their growth can significantly intensify (Carroll, 1988). All the mycotoxins analyzed, except for ROA, were detected in plants of the community studied (although with different frequencies); therefore, it can be concluded that the set of associated micromycetes is represented by a variety of toxin-secreting species. Elevated accumulation levels observed in some cases for individual metabolites can indicate the formation of conditions favorable for the growth of the respective fungi in the host organism or the fullest implementation of their genetically determined biosynthetic capacity.

CONCLUSIONS

In recent years, biological science has made persistent efforts to study comprehensively the cruciferous plants of European Russia, including their geographical distribution, floristic diversity, typification of taxa of various ranks (Dorofeev, 2002), and invasive activity as agriophytes (Grigor'evskaya et al., 2013). The assessment of these plants in terms of their contamination with mycotoxins the appearance of which is associated with the colonization of cruciferous plants by specific endophytes, as well as pathogenic and parasitic fungi, has just begun; this line of research remains highly relevant due to the ever-increasing use of these plants for food, medicinal, and forage purposes.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflicts of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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Translated by L. Emeliyanov