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ROLE OF THE CHROMOSOME 4B IN SUPPRESSING FROST RESISTANCE IN WINTER WHEAT (*Triticum aestivum* L.)

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SUMMARY

Frost resistance of different monosomic lines were investigated under controlled environment conditions. In the case of Cheyenne, Mironovskaya 808 and Rannaya 12 a reduction in the degree of frost resistance was observed when chromosomes 5A, 3B, 3A, 5B or 7A were missing. In two of the monosomic series there was also a drop in the level of frost resistance in monosomic lines 5D and 7B. The frost resistance of monosomic line 4B, on the other hand, was significantly better than that of the disome in two of the three cultivars. In previous experiments using substitution lines, the presence of a 4B chromosome originating from a variety with better frost resistance also led to an increase in frost resistance. The results suggest that a gene suppressor for frost resistance may be located on chromosome 4B.

Index words: *Triticum aestivum*, monosomic series, frost resistance, hardening, gene suppressor

INTRODUCTION

Under the climatic conditions of the Carpathian Basin the winter wheat yield is influenced not only by genes directly concerned with yield and for disease tolerance, but also to a great extent by genes for winter hardiness (Lelley, 1956; Rajki, 1980). During the winter, young wheat seedlings are exposed to many kinds of stress: direct frost effects, cold winds, snow cover, intense freezing and glaciation of the soil, frost lifting in spring and various diseases which thrive in or can withstand the cold. Frost tolerance is one of the most important components of winter hardiness. If seedlings are frost resistant, it means that they can survive the frost effect without any considerable damage (Lelley and Rajh  thy, 1955).

Several genetic studies have been conducted to determine the gene action controlling the expression of frost resistance in wheat. Valuable results concerning the frost resistance of hexaploid wheat have been obtained not only through the analysis of hybrid generations, but also by studying aneuploids. Monosomic and substitution analysis have made it possible to identify chromosomes determining cold resistance (Jenkins, 1971; Cahalan and Law, 1979). Despite the difficulties encountered when using monosomics, many researchers have used monosomic analysis in the study of cold tolerance. Goujon et al. (1968) tested F₂ monosomic hybrids derived from the Chinese Spring monosomics crossed to six winter and spring wheat varieties for cold tolerance at the coleoptile stage. Chromosomes 5A, 2D and 5D were found to carry genes responsible for cold tolerance, while chromosomes 7A, 2D

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This paper reports the behaviour of three sets of monosomics in the varieties Cheyenne, Mironovskaya 808 and Rannyaya 12 to freezing and the detection of a gene suppressor for frost resistance on chromosome 4B.

The monosomic lines were grown in a randomised design in wooden boxes, the internal dimensions of which were 38x26x11 cm. Thirty lines were sown in each box, with 5 plants per line. Eighteen replications were used in the experiment, so that 90 plants were evaluated from each monosomic line. Seeds were germinated for 2 days in petri dishes and then transferred to the wooden boxes containing a 4:1 mixture of good quality garden soil and

Before freezing, the seedlings were grown under long daylength (Table 1). The intensity was 15,000 lux, $Q=260\mu\text{Es}^{-1}\text{m}^{-2}$ per hour day (Tischner et al., 1997). After cold hardening none of the lines reacted differently when transferred to the frost testing chamber. The temperature was reduced to -4°C within 1 hour from 0°C to -4°C . The plants were then kept at -17°C . After 24 hours of freezing the temperature was further reduced, down to -17°C . After 24 hours of freezing the temperature was increased per hour to $+1^{\circ}\text{C}$, and the plants were kept at $+1^{\circ}\text{C}$. The plants were then transferred to a growth chamber at a night temperature of 15°C for 21 days. After 21 days, plants which had died were distinguished from those which had survived. Plants which had died off were scored as 0 points).

	1	2
Day	15.0	10.0
Night	10.0	5.0
Day	70	75
Night	75	80

The evaluation of the experimental variance. Differences between means were tested (ANOVA, $P < 0.05$, 0.01 and 0.001).

sand (Tischner et al., 1997b) and raised for six weeks. At first the plants were watered with tap water, then from the third week onwards with Vollunger nutrient solution. During the one-week hardening period (6th week), the plants were given less nutrient solution, and during freezing they were not watered at all. Following freezing they were again given the optimum quantity of nutrient required for regrowth. The plants were raised and hardened in Conviron PGV-36 plant growth chambers, frozen in C-812 frost rooms and placed on GB-48 growth benches (Tischner et al., 1997a) for recovery.

Before freezing, the seedlings were subjected to gradually decreasing temperatures and daylength (Table 1). The intensity of illumination during both these periods of treatment was 15,000 lux, $Q=260\mu\text{Es}^{-1}\text{m}^{-2}$ using Sylvania Gro-Lux-WS fluorescent tubes, with a 14 hours day (Tischner et al., 1997). Due to the relatively low temperature during growth and hardening none of the lines reached floral initiation. After hardening the boxes were transferred to the frost testing chamber, where the temperature was reduced by 1°C per hour from 0°C to -4°C. The plants were hardened for another 2 days at -4°C, then the temperature was further reduced, depending upon the experiment, either to -15°C, -16°C or -17°C. After 24 hours of freezing without illumination the temperature was raised by 1°C per hour to +1°C, and the plants were kept at this temperature for 15 hours. After this the boxes were transferred to a growth bench for recovery at a day temperature of 16°C and a night temperature of 15°C for 21 days. After freezing, the leaves were cut off with scissors a few centimetres above the soil, so that regrowth could be more accurately evaluated. After 21 days, plants which had survived freezing and showed regrowth could be clearly distinguished from those which had died. A 0-5 scale was used to score each plant (those which had died off were scored as 0, while well-developed, tillering plants were given 5 points).

Table 1

The FDA climatic programme

	Weeks					
	1	2	3	4	5	6
Temperature (°C)						
Day	15.0	10.0	10.0	5.0	5.0	2.0
Night	10.0	5.0	5.0	0.0	0.0	0.0
Relative humidity (%)						
Day	70	75	75	*	*	*
Night	75	80	80	*	*	*

* At temperatures below 5°C the humidity is not regulated to avoid frost damage to the equipment

The evaluation of the experimental data was carried out using single factor analysis of variance. Differences between means were tested by least significant differences (LSD) ($P = 0.05, 0.01$ and 0.001).

RESULTS

The frost testing of each of the monosomic series of Mironovskaya 808, Rannaya 12 and Cheyenne was carried out at the freezing temperatures given in Table 2.

Table 2

Frost resistance of the lines of monosomic series

Monosomic series	Cheyenne		Mironovskaya 808		Rannaya 12	
Monosomic lines	Score	Deviation from the variety	Score	Deviation from the variety	Score	Deviation from the variety
1A	1.24	-0.02	1.40	-0.47	1.51	-0.33
2A	1.60	0.42	2.02	0.15	1.84	0.00
3A	1.00	-0.26	1.22	-0.65*	0.88	-0.96***
4A	1.20	-0.06	1.77	-0.10	1.92	0.08
5A	0.74	-0.52*	0.92	-0.95***	0.95	-0.89***
6A	0.56	-0.70**	1.90	0.03	2.30	0.46
7A	0.86	-0.40	0.96	-0.91***	1.38	-0.46
1B	0.90	-0.36	1.58	-0.29	1.78	-0.06
2B	1.44	0.18	-	-	2.44	0.60
3B	0.16	-1.10***	1.20	-0.67*	1.00	-0.84***
4B	1.86	0.60**	2.18	0.31	2.74	0.90***
5B	0.72	-0.54*	1.47	-0.40	1.60	-0.24
6B	1.32	0.06	1.66	-0.21	2.06	0.22
7B	0.64	-0.62**	2.24	0.37	1.12	-0.72**
1D	1.28	0.02	1.96	0.09	1.62	-0.22
2D	1.58	0.32	1.50	-0.37	2.06	0.22
3D	1.22	-0.04	1.93	0.06	1.48	-0.36
4D	1.18	-0.08	1.54	-0.33	2.15	0.31
5D	0.58	-0.68**	1.12	-0.75**	1.98	0.14
6D	1.10	-0.16	1.92	0.05	2.65	0.80**
7D	1.26	0.00	2.26	0.39	1.74	-0.10
Disome	1.26		1.87		1.84	
Freezing temperature	-17°C		-16°C		-15°C	

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively

The development of the 2B monosomic line of Mironovskaya 808 has not yet been completed, so this line could not be tested. The various freezing temperatures and the frost resistance values achieved at these temperatures also express the frost sensitivity levels of the individual monosomic series. The lack of chromosomes 5A and 3B caused a large drop in frost resistance in all three monosomic series. The frost resistance of monosomic lines 3A, 7A and 5B also decreased, but the difference from the original variety was not significant for all three series. In two series the loss of chromosomes 5B and 7B caused a significant reduction. The frost resistance of the 4B monosomic lines, however, was better

than that of the disomes. The 6A monosomic line of Rannaya 12 had better frost resistance than the disomes. The 6A monosomic line of Cheyenne was increased in the 6A monosomic line of Mironovskaya 808 6A monosomic line of Rannaya 12 had better frost resistance than the disomes.

In the present experiments, we found to increase when chromosomes 4B and 5B were present in the analysis (Sutka and Rajki, 1979). The presence of the 4B chromosome increased the percentage survival of the chromosome 4B, which in certain chromosomes. Its functioning can be inhibited by homoeologous pairing (1995) on chromosomes 2D, 3D, 4D, 5D, 6D, 7D, 8D, 9D, 10D, 11D, 12D, 13D, 14D, 15D, 16D, 17D, 18D, 19D, 20D, 21D, 22D, 23D, 24D, 25D, 26D, 27D, 28D, 29D, 30D, 31D, 32D, 33D, 34D, 35D, 36D, 37D, 38D, 39D, 40D, 41D, 42D, 43D, 44D, 45D, 46D, 47D, 48D, 49D, 50D, 51D, 52D, 53D, 54D, 55D, 56D, 57D, 58D, 59D, 60D, 61D, 62D, 63D, 64D, 65D, 66D, 67D, 68D, 69D, 70D, 71D, 72D, 73D, 74D, 75D, 76D, 77D, 78D, 79D, 80D, 81D, 82D, 83D, 84D, 85D, 86D, 87D, 88D, 89D, 90D, 91D, 92D, 93D, 94D, 95D, 96D, 97D, 98D, 99D, 100D, 101D, 102D, 103D, 104D, 105D, 106D, 107D, 108D, 109D, 110D, 111D, 112D, 113D, 114D, 115D, 116D, 117D, 118D, 119D, 120D, 121D, 122D, 123D, 124D, 125D, 126D, 127D, 128D, 129D, 130D, 131D, 132D, 133D, 134D, 135D, 136D, 137D, 138D, 139D, 140D, 141D, 142D, 143D, 144D, 145D, 146D, 147D, 148D, 149D, 150D, 151D, 152D, 153D, 154D, 155D, 156D, 157D, 158D, 159D, 160D, 161D, 162D, 163D, 164D, 165D, 166D, 167D, 168D, 169D, 170D, 171D, 172D, 173D, 174D, 175D, 176D, 177D, 178D, 179D, 180D, 181D, 182D, 183D, 184D, 185D, 186D, 187D, 188D, 189D, 190D, 191D, 192D, 193D, 194D, 195D, 196D, 197D, 198D, 199D, 200D, 201D, 202D, 203D, 204D, 205D, 206D, 207D, 208D, 209D, 210D, 211D, 212D, 213D, 214D, 215D, 216D, 217D, 218D, 219D, 220D, 221D, 222D, 223D, 224D, 225D, 226D, 227D, 228D, 229D, 230D, 231D, 232D, 233D, 234D, 235D, 236D, 237D, 238D, 239D, 240D, 241D, 242D, 243D, 244D, 245D, 246D, 247D, 248D, 249D, 250D, 251D, 252D, 253D, 254D, 255D, 256D, 257D, 258D, 259D, 260D, 261D, 262D, 263D, 264D, 265D, 266D, 267D, 268D, 269D, 270D, 271D, 272D, 273D, 274D, 275D, 276D, 277D, 278D, 279D, 280D, 281D, 282D, 283D, 284D, 285D, 286D, 287D, 288D, 289D, 290D, 291D, 292D, 293D, 294D, 295D, 296D, 297D, 298D, 299D, 300D, 301D, 302D, 303D, 304D, 305D, 306D, 307D, 308D, 309D, 310D, 311D, 312D, 313D, 314D, 315D, 316D, 317D, 318D, 319D, 320D, 321D, 322D, 323D, 324D, 325D, 326D, 327D, 328D, 329D, 330D, 331D, 332D, 333D, 334D, 335D, 336D, 337D, 338D, 339D, 340D, 341D, 342D, 343D, 344D, 345D, 346D, 347D, 348D, 349D, 350D, 351D, 352D, 353D, 354D, 355D, 356D, 357D, 358D, 359D, 360D, 361D, 362D, 363D, 364D, 365D, 366D, 367D, 368D, 369D, 370D, 371D, 372D, 373D, 374D, 375D, 376D, 377D, 378D, 379D, 380D, 381D, 382D, 383D, 384D, 385D, 386D, 387D, 388D, 389D, 390D, 391D, 392D, 393D, 394D, 395D, 396D, 397D, 398D, 399D, 400D, 401D, 402D, 403D, 404D, 405D, 406D, 407D, 408D, 409D, 410D, 411D, 412D, 413D, 414D, 415D, 416D, 417D, 418D, 419D, 420D, 421D, 422D, 423D, 424D, 425D, 426D, 427D, 428D, 429D, 430D, 431D, 432D, 433D, 434D, 435D, 436D, 437D, 438D, 439D, 440D, 441D, 442D, 443D, 444D, 445D, 446D, 447D, 448D, 449D, 450D, 451D, 452D, 453D, 454D, 455D, 456D, 457D, 458D, 459D, 460D, 461D, 462D, 463D, 464D, 465D, 466D, 467D, 468D, 469D, 470D, 471D, 472D, 473D, 474D, 475D, 476D, 477D, 478D, 479D, 480D, 481D, 482D, 483D, 484D, 485D, 486D, 487D, 488D, 489D, 490D, 491D, 492D, 493D, 494D, 495D, 496D, 497D, 498D, 499D, 500D, 501D, 502D, 503D, 504D, 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837D, 838D, 839D, 840D, 841D, 842D, 843D, 844D, 845D, 846D, 847D, 848D, 849D, 850D, 851D, 852D, 853D, 854D, 855D, 856D, 857D, 858D, 859D, 860D, 861D, 862D, 863D, 864D, 865D, 866D, 867D, 868D, 869D, 870D, 871D, 872D, 873D, 874D, 875D, 876D, 877D, 878D, 879D, 880D, 881D, 882D, 883D, 884D, 885D, 886D, 887D, 888D, 889D, 890D, 891D, 892D, 893D, 894D, 895D, 896D, 897D, 898D, 899D, 900D, 901D, 902D, 903D, 904D, 905D, 906D, 907D, 908D, 909D, 910D, 911D, 912D, 913D, 914D, 915D, 916D, 917D, 918D, 919D, 920D, 921D, 922D, 923D, 924D, 925D, 926D, 927D, 928D, 929D, 930D, 931D, 932D, 933D, 934D, 935D, 936D, 937D, 938D, 939D, 940D, 941D, 942D, 943D, 944D, 945D, 946D, 947D, 948D, 949D, 950D, 951D, 952D, 953D, 954D, 955D, 956D, 957D, 958D, 959D, 960D, 961D, 962D, 963D, 964D, 965D, 966D, 967D, 968D, 969D, 970D, 971D, 972D, 973D, 974D, 975D, 976D, 977D, 978D, 979D, 980D, 981D, 982D, 983D, 984D, 985D, 986D, 987D, 988D, 989D, 990D, 991D, 992D, 993D, 994D, 995D, 996D, 997D, 998D, 999D, 1000D, 1001D, 1002D, 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1146D, 1147D, 1148D, 1149D, 1150D, 1151D, 1152D, 1153D, 1154D, 1155D, 1156D, 1157D, 1158D, 1159D, 1160D, 1161D, 1162D, 1163D, 1164D, 1165D, 1166D, 1167D, 1168D, 1169D, 1170D, 1171D, 1172D, 1173D, 1174D, 1175D, 1176D, 1177D, 1178D, 1179D, 1180D, 1181D, 1182D, 1183D, 1184D, 1185D, 1186D, 1187D, 1188D, 1189D, 1190D, 1191D, 1192D, 1193D, 1194D, 1195D, 1196D, 1197D, 1198D, 1199D, 1200D, 1201D, 1202D, 1203D, 1204D, 1205D, 1206D, 1207D, 1208D, 1209D, 1210D, 1211D, 1212D, 1213D, 1214D, 1215D, 1216D, 1217D, 1218D, 1219D, 1220D, 1221D, 1222D, 1223D, 1224D, 1225D, 1226D, 1227D, 1228D, 1229D, 1230D, 1231D, 1232D, 1233D, 1234D, 1235D, 1236D, 1237D, 1238D, 1239D, 1240D, 1241D, 1242D, 1243D, 1244D, 1245D, 1246D, 1247D, 1248D, 1249D, 1250D, 1251D, 1252D, 1253D, 1254D, 1255D, 1256D, 1257D, 1258D, 1259D, 1260D, 1261D, 1262D, 1263D, 1264D, 1265D, 1266D, 1267D, 1268D, 1269D, 1270D, 1271D, 1272D, 1273D, 1274D, 1275D, 1276D, 1277D, 1278D, 1279D, 1280D, 1281D, 1282D, 1283D, 1284D, 1285D, 1286D, 1287D, 1288D, 1289D, 1290D, 1291D, 1292D, 1293D, 1294D, 1295D, 1296D, 1297D, 1298D, 1299D, 1300D, 1301D, 1302D, 1303D, 1304D, 1305D, 1306D, 1307D, 1308D, 1309D, 1310D, 1311D, 1312D, 1313D, 1314D, 1315D, 1316D, 1317D, 1318D, 1319D, 1320D, 1321D, 1322D, 1323D, 1324D, 1325D, 1326D, 1327D, 1328D, 1329D, 1330D, 1331D, 1332D, 1333D, 1334D, 1335D, 1336D, 1337D, 1338D, 1339D, 1340D, 1341D, 1342D, 1343D, 1344D, 1345D, 1346D, 1347D, 1348D, 1349D, 1350D, 1351D, 1352D, 1353D, 1354D, 1355D, 1356D, 1357D, 1358D, 1359D, 1360D, 1361D, 1362D, 1363D, 1364D, 1365D, 1366D, 1367D, 1368D, 1369D, 1370D, 1371D, 1372D, 1373D, 1374D, 1375D, 1376D, 1377D, 1378D, 1379D, 1380D, 1381D, 1382D, 1383D, 1384D, 1385D, 1386D, 1387D, 1388D, 1389D, 1390D, 1391D, 1392D, 1393D, 1394D, 1395D, 1396D, 1397D, 1398D, 1399D, 1400D, 1401D, 1402D, 1403D, 1404D, 1405D, 1406D, 1407D, 1408D, 1409D, 1410D, 1411D, 1412D, 1413D, 1414D, 1415D, 1416D, 1417D, 1418D, 1419D, 1420D, 1421D, 1422D, 1423D, 1424D, 1425D, 1426D, 1427D, 1428D, 1429D, 1430D, 1431D, 1432D, 1433D, 1434D, 1435D, 1436D, 1437D, 1438D, 1439D, 1440D, 1441D, 1442D, 1443D, 1444D, 1445D, 1446D, 1447D, 1448D, 1449D, 1450D, 1451D, 1452D, 1453D, 1454D, 1455D, 1456D, 1457D, 1458D, 1459D, 1460D, 1461D, 1462D, 1463D, 1464D, 1465D, 1466D, 1467D, 1468D, 1469D, 1470D, 1471D, 1472D, 1473D, 1474D, 1475D, 1476D, 1477D, 1478D, 1479D, 1480D, 1481D, 1482D, 1483D, 1484D, 1485D, 1486D, 1487D, 1488D, 1489D, 1490D, 1491D, 1492D, 1493D, 1494D, 1495D, 1496D, 1497D, 1498D, 1499D, 1500D, 1501D, 1502D, 1503D, 1504D, 1505D, 1506D, 1507D, 1508D, 1509D, 1510D, 1511D, 1512D, 1513D, 1514D, 1515D, 1516D, 1517D, 1518D, 1519D, 1520D, 1521D, 1522D, 1523D, 1524D, 1525D, 1526D, 1527D, 1528D, 1529D, 1530D, 1531D, 1532D, 1533D, 1534D, 1535D, 1536D, 1537D, 1538D, 1539D, 1540D, 1541D, 1542D, 1543D, 1544D, 1545D, 1546D, 1547D, 1548D, 1549D, 1550D, 1551D, 1552D, 1553D, 1554D, 1555D, 1556D, 1557D, 1558D, 1559D, 1560D

than that of the disomes. The 6A monosomic lines of the three varieties behaved in different ways: in Cheyenne the loss of 6A led to a significant reduction in frost resistance, which was increased in the 6A monosomic of Rannaya 12. The frost resistance score of the Mironovskaya 808 6A monosomic was the same as that of the variety. The monosomic 6D line of Rannaya 12 had better frost resistance than that of the disomics.

DISCUSSION

In the present experiments, when monosomic lines were frozen the frost resistance was found to increase when chromosome 4B was missing. At the same time, in F_2 monosomic analysis (Sutka and Rajki, 1979) and in tests on substitution lines (Sutka et al., 1986) the presence of the 4B chromosome from a variety (Cheyenne) with better frost resistance also increased the percentage survival. It is probable that a suppressor gene is located on chromosome 4B, which in certain cases inhibits the manifestation of genes on other chromosomes. Its functioning can be compared with that of the gene on chromosome 5B, which inhibits homoeologous pairing (Feldman, 1968), or the genes identified by Stracke et al. (1995) on chromosomes 2D, 3D, 4A, 4B and 5A, which suppress mildew resistance.

The results of tests on various monosomic and substitution series confirm the hypothesis that genes responsible for frost resistance are to be found on certain chromosomes. On the basis of tests on monosomic and ditelosomic series (Veisz and Sutka, 1993) and F_2 monosomic and substitution analysis (Sutka et al., 1986) chromosomes 5A, 5D and 5B carry genes for frost resistance, as reported by Law and Jenkins (1970), Cahalan and Law (1979) and Poysa (1984). Chromosomes 3A, 3B, 6A and 6D carry genes for frost susceptibility in the varieties Rannaya 12 and Arthur (Sutka and Rajki, 1979; Sutka, 1981).

In the monosomic lines the functioning of frost resistance genes on other chromosomes was not suppressed when chromosome 4B was absent. It may be that in the course of F_2 monosomic and substitution analysis this inhibitory effect was not expressed due to changes in the genetic background, but it is also possible that the substituted 4B chromosome did not have a frost resistance-increasing effect, but simply had no inhibitory effect. According to another hypothesis, there could be a gene or genes on chromosome 4B for increased susceptibility to freezing. It is difficult to distinguish between these two possibilities. There is also no unequivocal explanation for the effect of the gene on the 6D chromosome of Rannaya 12, but it is clear from the present and earlier research that this chromosome plays some role in the development of frost resistance (Sutka and Rajki, 1979).

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GENETIC ANALYSIS

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Tolerance to low temperatures in winter wheat. In the process of breeding it is important to know the genetic base of low temperature tolerance. Rana Niska, Saitama, UPI 301, N. Mladenov, 1995. To determine the genetic base of low temperature tolerance of the F₁ hybrids was partial dominance and lower mean value dominated were determined. The predominant mode of inheritance was determined. gene effects were found. Frost tolerance was determined in Saitama x Sava and NS-5260 x Saitama. In the process of winter wheat breeding the effects predominate, since those effects predominate for cold tolerance. The selection should be more successfully.

Key words: wheat, low temperature tolerance

Any environmental factor can limit the yield of wheat below their genetic potential (Christiansen 1985). It is estimated that 15% of the wheat yield is lost at low temperatures (Christiansen 1985). The wheat yields that are 30 to 40% higher than the average winter wheat is prerequisite for the quantitative character conditions (Christiansen 1965; Gullord, 1975; Fowler 1975). The important component of winter wheat production under cold conditions can be quite severe. The selection should be more successfully attaining high and stable yields.

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