Research Article

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Selection of oat (*Avena sativa* L.) drought-tolerant genotypes based on multiple yield-associated traits

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Abstract

BACKGROUND: Most plant breeding and agricultural practices are based on selecting genotypes for yield. However, this is inadequate to screen crop varieties for specific attributes, such as drought tolerance. In this study, we quantified the response of oat (*Avena sativa* L.) plant physiological and morphological traits to drought stress and selected some key traits to establish a genotype by yield*trait (GYT)-based method for ranking 30 oat genotypes. The effectiveness of this method was also evaluated under drought conditions.

RESULTS: Water-deficit treatment significantly reduced leaf chlorophyll, root morphological traits, groat yield and associated components, such as mean grain weight. We observed that the genotypes 'JUSTICE' and 'BOLINA' had the smallest and largest yield loss, respectively, after exposure to drought stress, but showed opposite trends in the biomass allocation of roots and grains. This indicated that drought tolerance was highly dependent on the distribution of photoassimilates. Our results also illustrated that the GYT method is a trade-off approach and more effective in selecting oat ideotypes under drought conditions than the yield-related index method because it combines yield, yield stability, and related agronomic traits in the calculation process.

CONCLUSION: Drought-tolerant genotypes had more biomass allocated to roots and grains with higher chlorophyll content and better root structure, e.g. longer root lengths than drought-sensitive lines. By integrating yield and yield-related traits, the GYT approach is more practical than traditional single-trait selection methods when assessing drought tolerance.

Supporting information may be found in the online version of this article.

Keywords: water deficiency; phenotyping; tolerant index; GYT biplot; genotype selection

INTRODUCTION

Oat (*Avena sativa* L.) is becoming increasingly popular due to its healthy and nutrient-rich properties for human consumption.[1] Improvement of oat production is of importance and required by the domestic and international markets.[2] However, oat crops are often grown in harsher environments and are frequently subjected to various abiotic stresses.[3] Water scarcity is one of the most important abiotic stresses and significantly reduces yield and grain quality.[4] A previous study reported a 69% reduction in oat yield after 15 days of drought stress, but the yield drop was highly genotype-dependent.[5] This means that oat genotypes with strong drought tolerance can reduce yield losses in drought years compared to drought-sensitive genotypes. Therefore, selecting drought-tolerant genotypes with greater yield potential is essential for oat producers to cope with drought events.

To date, many efforts have been attempted in breeding and agronomic management studies to identify superior genotypes. Traditionally, data analysis from crop variety trials has often been limited to grain yield,[6] and some yield-based metrics have been proposed, such as yield index and yield stability index for crop genotype selection.[7] However, error-prone decisions are easily made based on yield alone because the highest yielding cultivars may not be stable across environments,[3,8] or yield losses prior to assessment due to bird damage or crop lodging. The decision to select the appropriate genotype must take into account multiple traits for high and reliable yields, combined with desirable levels

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of other traits. This is because an ideotype is defined as an optimal combination of morphological and physiological traits, resulting in a genotype that effectively matches its environment.[9] Based on this principle, a genotype by yield*trait (GYT) biplot approach was proposed for the genotype assessment of multiple traits. This approach could tackle the problem of genotype evaluation on multiple traits under different growth environments. The assumption is that yield is the most important trait, and the superiority of a genotype should be judged by the combination level of its yield and other target traits, rather than by its level on individual traits.[9] This process is enabled by the visual display of GYT data in biplots, which can easily show which genotype wins in which environment for which traits, as well as the genotypes are ranked according to their overall superiority in yield–trait combinations, such as the combination of yield–drought tolerance and yield–root morphology as shown in this study. The advantage of this method is that genotypes can be ranked effectively and reliably based on their superiority in yield and other target traits, such as photosynthetic ability while showing genotype strengths and weaknesses.[10] Although this approach has been proposed for general breeding selection, it has not been used to screen oat genotypes with better tolerance to drought stress in arid environments.

When recommending ideal genotypes using the GYT method, the most important step is to select agronomic traits for calculation. In general, the key attributes of reflecting plant health status from different perspectives are used. For example, traits of leaf chlorophyll and fluorescence parameters are usually included, as they directly elucidate the photosynthetic capacity of plants, an activity necessary for plants to accumulate biomass through assimilation with nutrients and light energy.[11] Likewise, root structure is closely related to the water and nutrient uptake capacity of plants.[12] The selection of these traits as predictors, therefore, has profound implications for crop yield, yield stability and grain quality under drought conditions. The objectives of this study were to (i) quantify the responses of oat yield and related traits to water deficit stress, (ii) select key agronomic traits for the GYT method establishment, and (iii) evaluate the performance of the GYT method in selecting ideal oat genotypes under drought conditions. We hypothesized that the responses of plant traits to drought stress are genotype-specific, and the established GYT method based on the selected traits would perform well in oat genotype selection under drought stress. The results of this work will assist oat breeders to identify genotypes with superior drought tolerance and help oat growers choose the ideotypes to mitigate drought stress, thereby minimizing yield and economic loss.

MATERIALS AND METHODS

Oat genotypes

Thirty oat genotypes were used in this study, including 15 from eastern Canada and 15 from western Canada. The basic characteristics of each cultivar are shown in Supporting Information Table S1, according to long-term observations by oat breeders of Agriculture and Agri-Food Canada.

Experimental design and management

The study was conducted under glasshouse conditions at Ottawa Research and Development Centre of Agriculture and Agri-Food Canada, a 30 × 2 factorial experiment in a randomized complete block (RCB) design with four replications. Plastic cone containers (6 cm in diameter × 15 cm in height as shown in Fig. 1) were filled with soil mix (topsoil–vermiculite–peat moss–perlite at a ratio of 6:1:1:1 *v/v*). The holes in the bottom of the cones were sealed with duct tape but left four needle holes to allow air access. Before planting, the dried and wet soil [soaked in water for 24 h, taken out and drained until there is no dripping water, to give 100% water holding capacity (WHC)] were measured to calculate and guide the amount of water being added for each treatment during the water deficient period. Additional four replicates of each treatment were used as a reference to calculate the daily water requirement to maintain the water treatment level. Then, soil mix was irrigated thoroughly to ensure seed germination. Each cone was sown with eight grains and thinned to four seedlings at 10 days after seeding. From germination to heading, all plants were watered daily to maintain the container soil with 75–85% WHC. At 39 days after planting (heading stage), the plants were subjected to two watering treatments for 15 days: well-watered control (80–85% WHC) *versus* drought, i.e. water-deficit (35–45% WHC). During the treatment period, soil moisture was monitored twice a day (9:00 and 17:00), and manual irrigation was performed to maintain the target soil water levels. Each container received 0.1 g NPK (nitrogen–phosphorus–potassium, 20:20:20) fertilizer every 2 weeks after planting, for a total of four times. Throughout the experiment, the glasshouse environment was set at 25/18 °C and 50 ± 5% relative humidity with a 16h:8 h day/night cycle. Supplementary light was provided with a minimum of 300 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) on cloudy days. Air temperature, relative humidity, and PPFD of the growing room were continuously monitored with an ARGUS control platform. The experiment was run twice from April to November 2021.

Determination of groat yield and yield-associated traits

At 10 days after starting drought treatment, two plants were randomly selected from each cone and their flag leaf chlorophyll and fluorescence were measured with a chlorophyll meter (SPAD-502 Chlorophyll Meter; Minolta Camera Co. Ltd, Osaka, Japan) and a fluorimeter (OS30p+; Opti-Sciences, Hudson, NH, USA), respectively. At maturity, after recording plant height, the plants were cut at the root crown, separated into shoots, grains, and hulls, and grain number was counted. Groat yield, aboveground biomass, culm, and hull weight per plant and mean grain weight were determined after being dried at 80 °C for 72 h.

After removing the aboveground part, the container was soaked thoroughly, and the roots were removed, cleaned with tap water and scanned with a scanner (Epson Expression 1640XL; Epson America, Inc., Los Alamitos, CA, USA). The obtained root images were analysed with the WinRHIZO system (Regent Instrument Inc., Quebec, Canada) to determine root length, surface area, and volume. Finally, root dry biomass was determined after being dried at 80 °C to constant weight. The shoot-to-root ratio was calculated based on their dry mass. Specific root length was calculated by dividing root length by the corresponding root dry weight. The root mass fraction was calculated as root dry mass divided by the corresponding whole plant dry mass.

Data analysis

Statistical analysis on yield and yield-associated traits

Analysis of variance was conducted using the MIXED procedure in SAS (SAS version 9.4; SAS Institute, Cary, NC, USA) to investigate the main effects of cultivar, drought treatment, and their

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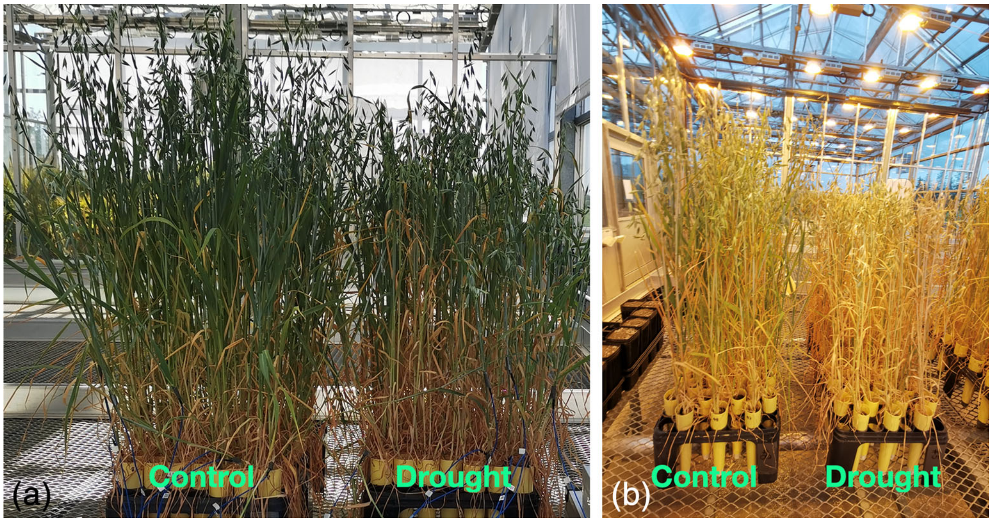


Figure 1. The growing status of oat plants at 7 days (a) and 15 days (b) after watering treatment, respectively. The cone containers were 6 cm in diameter and 15 cm in height, filled with topsoil, vermiculite, peat moss, and perlite at a ratio of 6:1:1:1 *v/v*.

interaction on yield, biomass, and leaf and root traits. The cultivar and watering treatment were treated as fixed effects while the experiment (two runs) and replicate (block) as random effects. The residual normality was tested using the Shapiro–Wilk's statistic for each trait and the residual plots were employed to verify the homogeneity of variances. The appropriate data transformation was used based on the Box–Cox recommendation when the response variable did not meet the normality assumption. Specifically, yield and grain number per plant data were transformed with square root, SPAD values with raising to the power of 2, and hull mass and shoot-to-root ratio with log transformation before conducting the analysis of variance. When the main effects were significant, the protected least significant difference (LSD) test was performed to compare the differences among treatment levels. The Pearson correlation analysis was conducted between yield and yield-related traits using the corr function of Pandas package (version 1.3.0) with method = 'pearson' of Python programming language (version 3.9.6; Python Software Foundation) after centring (i.e. subtracting the mean values) and scaling (dividing the centred values by the standard deviation within each GYT combination) the dataset. The significant level in this study was set as $P \leq 0.05$.

Genotype selection methods

Four methods were used for oat genotype selection, including groat yield-based method, drought-tolerance index (DTI), genotype superiority index (GSI), and GYT index. In the yield-based method, the genotype with the highest groat yield under drought (water-deficit) conditions is regarded as the desirable line while the lowest yield genotype is treated as the worst genotype.[13] The DTI[14] and GSI[15] were calculated as follows: $\mathrm{DTI}=\frac{Y_\mathrm{d}}{Y_\mathrm{c}}$, and $\mathrm{GSI}=\sqrt{(Y_\mathrm{c}-\mathrm{MY}_\mathrm{c})^2+(Y_\mathrm{d}-\mathrm{MY}_\mathrm{d})^2}$, respectively, where Y_c and Y_d represent seed yield collected under control and drought conditions, MY_c and MY_d refer to the maximum grain yield under control and drought conditions. The DTI is the ratio of yield under drought stress to that under control conditions, while the GSI defines the Euclidean distance between the yield response under water limiting and the maximum yield response under control conditions for a specific genotype. Therefore, a higher DTI score or a smaller GSI value indicates a better genotype.

The GYT method was established based on the following procedures.[16] First, selection of traits as predictors, which must meet the following criteria before being included: (i) the trait could be used to clearly distinguish drought from normally watered plants, i.e. response of the trait to watering levels must be significant; and (ii) only one trait can be selected if two traits showed significant linear correlation ($r^2 > 0.5$). Second, constructing a GYT table by multiplying each trait by yield to form the yield*trait combination and thus converting the genotype-by-trait table to a GYT table. Third, standardizing the GYT table by centring and scaling. Fourth, GYT index calculation and GYT biplot establishment. The GYT index was calculated from this standardized GYT table for each genotype, which is the mean across all standardized yield–trait combinations. The GYT biplot, which can visually rank the genotypes, was completed with the GGE biplot program (version 8.0; Ottawa, Canada).

RESULTS

Responses of traits to drought stress

Different levels of watering treatment greatly impacted oat plant growth (Fig. 1). We observed a significant yield reduction in 29 of the 30 genotypes (except for JUSTICE with $P = 0.059$) under drought stress (Fig. 2(a)). This was mainly due to the negative responses of yield and yield-associated traits (including biomass, harvest yield, grain number, and mean grain weight) to drought stress. The limited watering reduced grain number per plant and mean grain weight by an average of 25% and 12.5%, respectively (Fig. 2 and Supporting Information Fig. S1), and it also resulted in a 2–29% and 4–36% reduction in culm and hull mass compared to the well-watered plants (Fig. 2). Drought stress reduced plant height, aboveground biomass, and root mass by more than 8%, but increased biomass allocated to roots, with a 35% higher root mass fraction (Table 1). Some attributes of different genotypes responded differently to drought stress. For example, drought treatment reduced the yield of BOLINA by up to 56%, but did not significantly alter the yield of JUSTICE (Fig. 2(a)). In general,

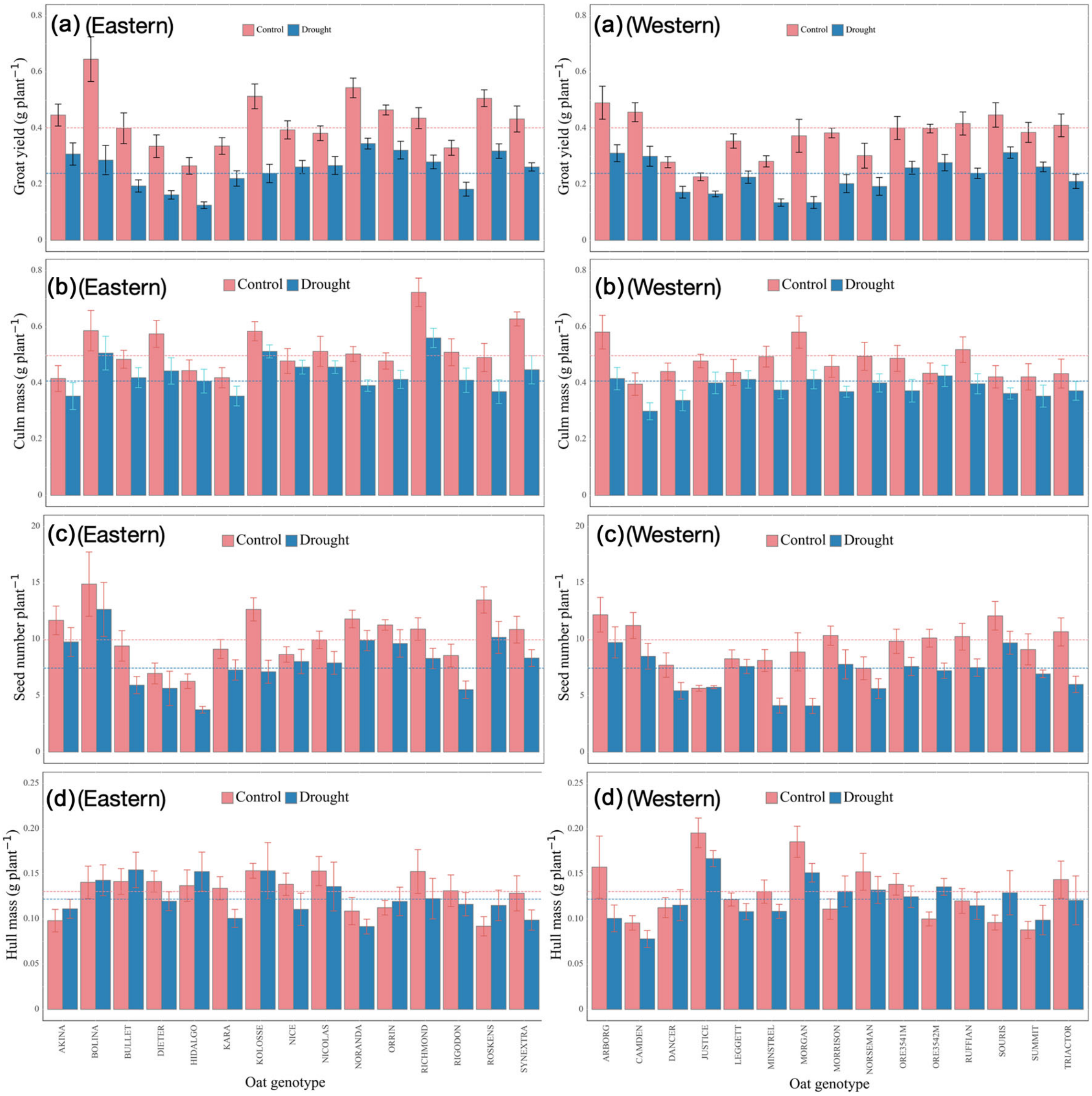


Figure 2. The variations in yield (a) and yield components, including culm mass (b), grain number (c), and hull mass (d) of different eastern and western genotypes in response to different watering treatments.

genotypes with higher grain numbers had lower mean grain weight, such as BOLINA (Table 1). Similarly, genotypes with higher levels of shoot-to-root ratio generally had lower levels of root mass fraction. Therefore, genotypes had specific abilities to allocate biomass to roots and grains under drought conditions.

Leaf and root physiological and morphological traits were significantly affected by watering treatment. On average, drought stress reduced SPAD values, Fo, and Fv by 16%, 31%, and 72%, respectively (Fig. S1). HIDALGO had the highest average SPAD reading of 50.4 and ROSKENS had the lowest value of 44.2 (Fig. S2). Drought stress reduced the average root volume by 33.3% and density by 17% (Table 1), but increased specific root length by 17–24% and root average diameter by 3–6% (Table 1). The responses of these root characteristics to drought stress varied widely among oat genotypes. For example, drought stress reduced root length by more than 50% in HIDALGO, but not in ROSKENS compared to well-watered plants (Table S2).

Traits selection for GYT method

All traits measured in this study were significantly impacted by genotype and watering treatment (Table 1), suggesting that they were important for oat genotype selection under drought conditions. However, according to Pearson's correlation analysis, some traits can be substituted by other parameters and can therefore be excluded from the calculation of the GYT index (Fig. 3). Our analysis showed that SPAD reading, Fo, Fv, and Fm were positively correlated with each other, as were root architectural traits. For example, root length was closely correlated with root volume ($R^2 = 0.8$), root tips ($R^2 = 0.9$), and surface area ($R^2 = 1.0$), but longer roots generally had smaller root diameter. Therefore, a total of 18 traits (Table 2) were included for GYT index calculation and GYT biplot graphing.

Yield-based index and GYT genotype selection

The results showed that NORANDA and HIDALGO were considered as be the best and worst genotypes, respectively because

Table 1. Effects of drought stress on groat yield (mg plant^{-1}), aboveground biomass (SDM, mg plant^{-1}), root biomass (RDM, mg plant^{-1}), shoot-to-root ratio (SRR), plant height (PH, cm), chlorophyll content (SPAD), harvest index (HI), grain number (SN, n plant^{-1}), mean grain weight (SW, mg grain^{-1}), culm mass (CM, mg plant^{-1}), hull mass (HM, mg plant^{-1}), root mass fraction (RMF, %), specific root length (SRL, m g^{-1}), root density (RD, mg cm^{-3}), root surface area (RA, cm^3 plant^{-1}), root length (RL, dm plant^{-1}), root average diameter (RAD, µm), root volume (RV, cm^3), root tips (RT, n plant^{-1}) and leaf fluorescence of Fo, Fv, Fm, Fv/Fm, and Fv/Fo of 30 oat genotypes[a]

Treatment	Yield	SDM	RDM	SRR	PH	SPAD	HI	SN	SW	CM	HM	RMF	SRL	RD	RA	RL	RAD	RV	RT	Fo	Fv	Fm	Fv/Fm	Fv/Fo
Genotypes																								
AKINA	377	0.87	40	26	57	46.6	0.43	10.7	36	384	105	4.5	59	539	13.6	21	211	73	1085	144	212	356	0.51	1.42
ARBORG	401	1.03	35	24	62	46.2	0.39	10.9	37	498	129	4.5	50	478	12.0	15	264	80	835	149	106	254	0.27	0.61
BOLINA	466	1.15	63	27	55	46.8	0.38	13.8	34	546	142	6.0	48	464	22.1	27	264	144	1526	156	214	370	0.51	1.33
BULLET	297	0.89	73	16	58	46.1	0.32	7.7	38	452	148	7.4	36	764	17.8	25	236	101	1270	134	153	288	0.40	1.09
CAMDEN	378	0.81	34	26	55	47.3	0.46	9.8	40	347	87	4.1	70	430	15.7	23	225	85	1076	140	233	373	0.62	1.65
DANCER	225	0.73	62	15	55	45.5	0.31	6.6	36	389	114	7.8	47	564	20.2	28	237	115	1313	179	271	450	0.52	1.43
DIETER	249	0.89	48	31	59	46.8	0.28	6.3	40	509	131	5.2	65	461	18.8	28	228	101	1569	138	247	385	0.53	1.59
HIDALGO	195	0.76	39	29	53	50.4	0.25	5.0	38	425	145	4.9	61	381	17.3	24	247	102	1387	131	213	344	0.53	1.44
JUSTICE	196	0.82	41	21	61	45.2	0.24	5.7	34	439	181	5.3	32	662	9.8	13	255	62	579	123	166	289	0.44	1.16
KARA	279	0.78	24	41	52	50.3	0.35	8.2	34	386	117	3.1	84	317	12.9	18	234	76	997	149	185	334	0.40	1.06
KOLOSSE	376	1.08	73	21	56	49.0	0.33	9.9	37	548	153	6.2	40	529	19.7	23	287	137	1199	159	220	379	0.42	1.22
LEGGETT	290	0.83	51	20	60	45.0	0.34	7.9	36	425	115	5.9	45	573	15.1	19	253	95	820	126	186	312	0.46	1.24
MINSTREL	208	0.76	40	26	56	47.3	0.27	6.1	36	434	119	4.8	54	365	16.7	21	268	109	993	140	175	315	0.41	1.12
MORGAN	254	0.92	46	23	54	45.8	0,26	6.5	39	497	168	4.7	63	395	19.8	26	246	121	1640	158	211	369	0.42	1.27
MORRISON	293	0.82	46	16	57	49.2	0.35	9.0	32	414	121	6.2	33	616	11.9	15	259	77	650	177	286	463	0.61	1.59
NICE	328	0.92	52	22	61	44.6	0.36	8.3	40	467	125	5.3	48	469	16.6	21	258	105	1080	145	195	340	0.41	1.17
NICOLAS	324	0.95	28	47	55	45.0	0.34	8.9	37	484	145	2.8	84	383	13.6	19	229	78	1165	146	111	257	0.26	0.74
NORANDA	444	0.99	47	28	56	47.6	0.44	10.8	41	447	100	4.3	48	475	15.8	20	259	100	1062	174	284	458	0.49	1.46
NORSEMAN	247	0.84	53	13	58	46.1	0.28	6.5	37	447	142	7.4	56	584	17.9	28	204	90	1514	132	105	237	0.30	0.70
ORE3541M	330	0.89	70	11	56	45.8	0.37	8.7	38	430	132	9.9	61	384	30.1	40	240	181	1853	156	254	410	0.49	1.46
ORE3542M	338	0.89	39	33	56	46.0	0.38	8.7	39	430	118	4.6	54	300	17.7	20	319	129	833	175	206	381	0.40	1.09
ORRIN	393	0.96	51	29	58	48.8	0.41	10.4	38	445	116	4.9	37	512	15.0	19	276	94	940	167	236	403	0.45	1.29
RICHMOND	358	1.14	34	46	57	45.9	0.31	9.6	37	642	138	2.8	89	326	19.0	28	227	104	1959	176	241	417	0.48	1.35
RIGODON	256	0.84	23	48	57	44.8	0.30	7.0	37	459	124	2.8	173	245	20.2	31	215	108	1690	145	189	333	0.40	1.10
ROSKENS	412	0.94	45	29	59	44.2	0.44	11.8	36	430	103	4.8	67	436	17.7	24	248	107	1211	173	289	461	0.57	1.61
RUFFIAN	328	0.90	40	21	58	48.3	0.36	8.9	37	458	117	5.3	39	745	10.2	15	232	57	823	153	248	400	0.58	1.57
SOURIS	380	0.89	49	25	60	47.1	0.42	10.9	35	392	113	5.2	46	560	15.8	23	267	91	1123	137	180	316	0.41	1.05
SUMMIT	324	0.80	48	19	56	44.6	0.41	8.0	42	388	93	6.1	43	527	15.6	21	248	92	1034	142	210	352	0.47	1.23
SYNEXTRA	347	1.00	43	35	63	49.0	0.35	9.6	36	538	114	3.9	77	333	19.8	26	263	125	1634	149	259	409	0.53	1.56
TRIACTOR	310	0.84	65	16	57	45,8	0.36	8.3	37	403	132	7.8	50	566	20.9	30	234	119	1544	131	190	321	0.53	1.41
LSD$_{0.05}$	65	0.14	2	2	5	3.3	0.05	2.1	5	80	32	2	29	116	1.4	7	30	29	572	32	98	117	0.21	0.61
Watering levels																								
Normal	401 a	1.01 a	59 a	33 a	60 a	50.7 a	0.38 a	9.9 a	40 a	497 a	130 a	4.3 b	56 b	513 a	20.5 a	28 a	253 a	120 a	1488 a	177 a	326 a	503 a	0.62 a	1.82 a
Drought	239 b	0.78 b	43 b	22 b	55 b	42.8 b	0.32 b	7.4 b	35 b	407 b	122 b	5.8 a	66 a	424 b	13.6 b	18 b	240 b	80 b	977 b	123 b	91 b	214 b	0.30 b	0.71 b
ANOVA: levels of significance (*P* values)																								
Cultivar (C)	***	***	***	***	***	***	***	***	***	***	*	***	***	***	***	***	*	***	***	***	***	***	***	***

Table 1. Continued

Treatment	Yield	SDM	RDM	SRR	PH	SPAD	HI	SN	SW	CM	HM	RMF	SRL	RD	RA	RL	RAD	RV	RT	Fo	Fv	Fm	Fv/Fm	Fv/Fo
Watering (W)	***	***	***	***	***	***	***	***	**	***	***	***	***	***	***	**	***	***	***	**	**	**	*	*
C × W	*	ns[a]	***	***	***	ns	ns	ns	ns	ns	ns	**	ns	ns	**	**	***	*	**	ns	ns	ns	ns	ns

[a] ns, no significance at $P \leq 0.05$. Within a column between the watering levels, means followed by the same letter are not significantly different according to the $LSD_{0.05}$ test. $LSD_{0.05}$ values were presented for comparing the significance among cultivars for each measured trait. * presents significant difference at $0.01 < P \leq 0.05$, **significant at $0.001 < P \leq 0.01$, and ***significant at $P \leq 0.001$.

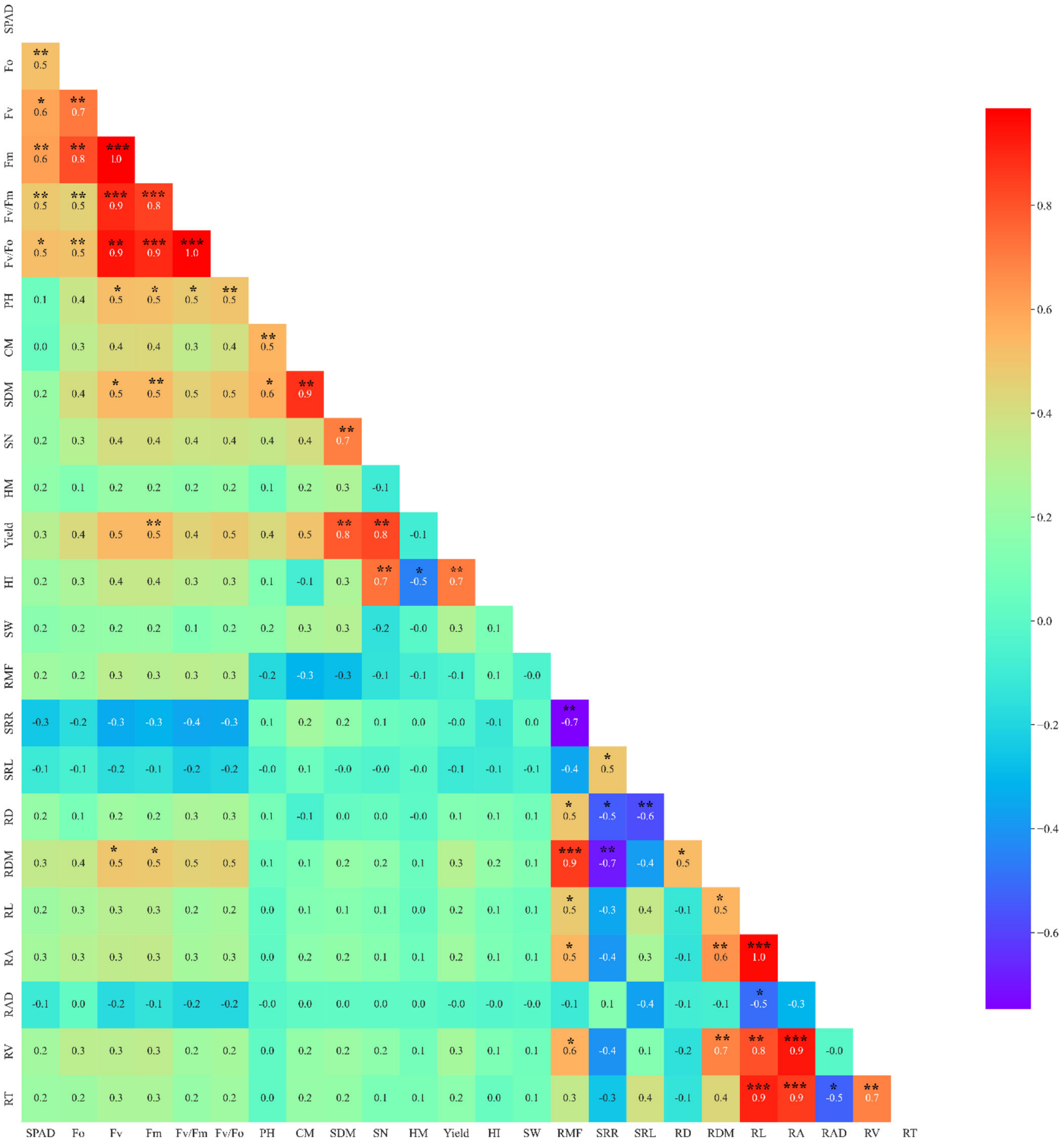
of their maximum and minimum yields under drought conditions, if only yield was used as the genotype selection criterion (Fig. 4(a)). In comparison, if the percent yield reduction (i.e. DTI) was used as a criterion, JUSTICE and BOLINA were classified as the best and poorest genotypes, as they had the highest and lowest drought-tolerant indices of 0.79 and 0.42, respectively (Fig. 4(b)). The superiority index was similar to GYT method in ranking genotypes, with the best genotypes of NORANDA, ROSKENS, and ORRIN by both indices (Fig. 4(c,d)). However, slight inconsistencies remained when genotypes with similar seed yields were ranked. For example, based on the GYT index, BOLINA outperformed RICHMOND (Fig. 4(d)); but this result was reversed according to the superiority index (Fig. 4(c)). In general, yield- and GYT-based methods showed that eastern genotypes were slightly better than western genotypes. But the opposite result was obtained when drought tolerance and superiority indices were used. This indicates that the GYT method could well identify the yield-ideal genotypes as it overall weighed the grain basic productivity (i.e. yield capacity under various environments) and stress-induced yield loss.

According to the which-won-what GYT biplot (Fig. 5(a)), NORANDA had better traits of yield*drought tolerance index, yield*chlorophyll, and yield*plant height than other genotypes. Similarly, SOURIS was best in yield*root average diameter and yield*root density, and ORE3541M was the best in yield*root dry mass, yield*Fv, yield*root length, yield*root volume, and yield*specific root length. The GYT method recommended that NORANDA was the best genotype and HIDALGO was the poorest under limited watering conditions (Fig. 5(b)).

DISCUSSION

The mechanism of oat tolerance to drought

As drought occurs more frequently and becomes more severe worldwide due to global climate change,[17] understanding the underlying mechanisms of traits in response to drought stress has important implications. In this study, the yield reduction ranged from 25 to 56% after plants subjecting to 15 days of drought stress at heading stage, and it was slightly lower than the yield reduction in previous studies, where the grain yield reductions of 69% and 76% were reported.[5,18] This was mainly due to the specific drought tolerance of different oat genotypes. In this study, western genotypes had slightly better drought tolerance than eastern genotypes (Fig. 4(b)). This may be attributed to the long-term meta-environmental differences between the eastern (high rainfall potential) and western Canada (low precipitation).[19,20] The western genotypes may have stronger root uptake capacity to adapt to the water-limiting conditions because they had an average of 7% longer roots and 8% higher fine roots under drought conditions. Previous studies also reported an increased root length, root surface area, and length of fine roots for tolerant genotypes compared to susceptible genotypes.[4] This is because an advanced root architecture enables plants to enhance water and nutrient uptake[21-23] through extensive ion-exchange processes.[24,25] A significant increase in root length per unit area and fine roots under water-deficient conditions (Table 1), indicates stronger drought tolerance with a larger specific surface area.[26] In this study, we also observed linear relationships between yield and grain number per plant, mean grain weight, leaf chlorophyll content, and harvest index, showing a strong influence of these traits on yield (Fig. 3). Zhao *et al.*[5] reported that genotype-specific source-sink



	SPAD	Fo	Fv	Fm	Fv/Fm	Fv/Fo	PH	CM	SDM	SN	HM	Yield	HI	SW	RMF	SRR	SRL	RD	RDM	RL	RA	RAD	RV	RT
SPAD																								
Fo	** 0.5																							
Fv	* 0.6	** 0.7																						
Fm	** 0.6	** 0.8	*** 1.0																					
Fv/Fm	** 0.5	** 0.5	*** 0.9	*** 0.8																				
Fv/Fo	* 0.5	** 0.5	** 0.9	*** 0.9	*** 1.0																			
PH	0.1	0.4	* 0.5	* 0.5	* 0.5	** 0.5																		
CM	0.0	0.3	0.4	0.4	0.3	0.4	** 0.5																	
SDM	0.2	0.4	* 0.5	** 0.5	0.5	0.5	* 0.6	** 0.9																
SN	0.2	0.3	0.4	0.4	0.4	0.4	0.4	0.4	** 0.7															
HM	0.2	0.1	0.2	0.2	0.2	0.2	0.1	0.2	0.3	-0.1														
Yield	0.3	0.4	0.5	** 0.5	0.4	0.5	0.4	0.5	** 0.8	** 0.8	-0.1													
HI	0.2	0.3	0.4	0.4	0.3	0.3	0.1	-0.1	0.3	** 0.7	* -0.5	** 0.7												
SW	0.2	0.2	0.2	0.2	0.1	0.2	0.2	0.3	0.3	-0.2	-0.0	0.3	0.1											
RMF	0.2	0.2	0.3	0.3	0.3	0.3	-0.2	-0.3	-0.3	-0.1	-0.1	-0.1	0.1	-0.0										
SRR	-0.3	-0.2	-0.3	-0.3	-0.4	-0.3	0.1	0.2	0.2	0.1	0.0	-0.0	-0.1	0.0	** -0.7									
SRL	-0.1	-0.1	-0.2	-0.1	-0.2	-0.2	-0.0	0.1	-0.0	-0.0	-0.0	-0.1	-0.1	-0.1	-0.4	* 0.5								
RD	0.2	0.1	0.2	0.2	0.3	0.3	0.1	-0.1	0.0	0.0	-0.0	0.1	0.1	0.1	* 0.5	* -0.5	** -0.6							
RDM	0.3	0.4	* 0.5	* 0.5	0.5	0.5	0.1	0.1	0.2	0.2	0.1	0.3	0.2	0.1	*** 0.9	** -0.7	-0.4	* 0.5						
RL	0.2	0.3	0.3	0.3	0.2	0.2	0.0	0.1	0.1	0.1	0.0	0.2	0.1	0.1	* 0.5	-0.3	0.4	-0.1	* 0.5					
RA	0.3	0.3	0.3	0.3	0.3	0.3	0.0	0.2	0.2	0.1	0.1	0.2	0.1	0.1	* 0.5	-0.4	0.3	-0.1	** 0.6	*** 1.0				
RAD	-0.1	0.0	-0.2	-0.1	-0.2	-0.2	-0.0	0.0	0.0	0.0	0.0	-0.0	-0.0	-0.0	-0.1	0.1	-0.4	-0.1	-0.1	* -0.5	-0.3			
RV	0.2	0.3	0.3	0.3	0.2	0.2	0.0	0.2	0.2	0.2	0.1	0.3	0.1	0.1	* 0.6	-0.4	0.1	-0.2	** 0.7	** 0.8	*** 0.9	-0.0		
RT	0.2	0.2	0.3	0.3	0.2	0.2	0.0	0.2	0.2	0.1	0.1	0.2	0.0	0.1	0.3	-0.3	0.4	-0.1	0.4	*** 0.9	*** 0.9	* -0.5	** 0.7	

Figure 3. The Pearson correlation between oat yield and yield-associated traits. The values in boxes present the square of correlation coefficient. SPAD, leaf chlorophyll content; PH, plant height; CM, culm mass; SDM, shoot dry mass, i.e. biomass; SN, grain number; HM, hull mass; HI, harvesting index; SW, mean grain weight; RMF, root mass fraction; SRR, shoot-to-root ratio; SRL, specific root length; RD, root density; RDM, root dry mass; RL, root length; RA, root area; RAD, root average diameter; RV, root volume; RT, root tips. *, **, and *** above the correlation coefficients indicate significant levels at $P \leq 0.05$, 0.01, and 0.001, respectively.

biomass adjustment was detrimental to oat yield under water-deficit stress. In general, great biomass accumulation through robust source activities, such as stronger photosynthesis and longer green leaf duration, is critical to reduce yield loss from early drought events. In response to late-season drought stress, stronger sink activity is required, including higher grain and spikelet numbers, lower floret or grain abortion rates, and greater allocation of carbohydrates to panicles. During the experiment, we observed that the green leaf duration of the drought-tolerant genotypes was 1–3 days longer than that of drought-sensitive genotypes, which was important for carbon assimilation and nutrient allocation to grains under drought

Table 2. Dataset for GYT (genotype by yield*trait) biplot in the drought environment

Cultivar	Y	SPAD*Y	Fo*Y	Fv*Y	PH*Y	SDM*Y	SN*Y	HM*Y	HI*Y	SW*Y	SRR*Y	SRL*Y	RD*Y	RDM*Y	RAD*Y	RL*Y	RV*Y	DTI*Y
NORANDA	1.14	1.18	1.10	0.40	0.88	0.82	0.92	0.25	1.29	1.08	0.85	0.21	0.87	0.35	1.20	0.06	0.43	1.18
ROSKENS	0.85	0.39	1.40	1.65	0.92	0.60	0.91	0.58	0.97	0.54	0.59	1.13	−0.06	0.28	0.52	1.03	0.97	0.78
ORRIN	0.89	1.23	1.25	0.05	0.86	0.81	0.80	0.59	0.92	0.83	0.90	−0.38	0.60	−0.23	1.41	−0.62	−0.26	1.06
AKINA	0.74	0.80	0.85	0.75	0.62	0.57	0.80	0.42	0.96	0.54	0.38	0.49	0.70	0.13	0.18	0.34	−0.01	0.89
CAMDEN	0.66	0.63	0.25	0.90	0.51	0.17	0.46	−0.35	1.13	0.95	0.00	0.67	0.25	0.18	0.38	0.88	0.65	9.05
ARBORG	0.77	0.83	0.70	−0.70	0.86	0.61	0.77	0.11	0.84	0.61	−0.22	−0.22	0.91	0.68	0.65	−0.04	0.36	8.55
SOURIS	0.80	0.94	0.25	−0.10	0.86	0.52	0.70	0.70	0.89	0.60	0.50	−0.64	0.18	−0.25	1.46	−0.83	−0.31	7.46
ORE3542M	0.41	0.26	0.80	−0.25	0.39	0.47	0.07	0.72	0.24	0.66	0.20	−0.05	−0.26	0.62	0.86	0.34	1.12	7.12
BOLINA	0.51	0.49	1.10	0.65	0.42	1.06	1.22	0.96	0.47	0.18	0.38	−0.08	0.18	0.87	0.72	0.15	0.88	9.77
RICHMOND	0.44	0.48	0.50	0.10	0.18	0.70	0.28	0.50	0.03	0.32	1.60	1.15	−0.22	−0.34	0.23	0.59	0.14	7.24
NICOLAS	0.30	0.24	0.10	−0.2	0.17	0.37	0.17	0.48	0.09	0.28	0.85	0.44	0.05	−0.02	0.31	0.15	0.08	4.37
ORE3541M	0.21	0.00	0.50	0.20	0.16	0.04	0.03	0.25	0.18	0.19	−0.69	0.06	−0.13	1.76	0.04	1.53	1.92	6.70
SYNEXTRA	0.25	0.40	0.30	0.65	0.39	0.21	0.11	−0.16	0.17	0.20	0.50	1.18	−0.64	−0.42	0.03	0.09	0.10	3.60
SUMMIT	0.25	0.13	−0.15	0.05	0.21	−0.01	−0.11	−0.06	0.34	0.49	−0.29	−0.36	0.35	0.24	0.24	−0.15	−0.03	1.67
NICE	0.24	0.11	0.10	−0.50	0.42	0.25	0.14	0.02	0.12	0.23	0.00	0.03	−0.25	−0.43	0.04	−0.20	−0.32	0.40
KOLOSSE	−0.01	0.16	0.20	−0.25	−0.11	0.24	−0.07	0.51	−0.31	−0.03	−0.16	−0.28	0.17	0.61	0.26	0.06	0.36	0.83
RUFFIAN	0.00	0.10	−0.25	0.10	−0.05	−0.09	−0.09	0.09	−0.07	−0.12	−0.35	−0.39	1.48	0.48	−0.10	−0.11	−0.37	0.20
LEGGETT	−0.15	−0.38	−0.70	−0.45	−0.02	−0.17	−0.15	−0.23	−0.23	−0.31	−0.33	−0.23	0.17	0.09	−0.15	−0.17	−0.07	−3.55
TRIACTOR	−0.31	−0.44	−0.30	0.00	−0.25	−0.33	−0.42	−0.17	−0.32	−0.04	−0.64	−0.39	0.09	0.69	−0.18	0.07	0.27	−3.26
KARA	−0.20	−0.01	−0.15	0.20	−0.29	−0.31	−0.16	−0.44	−0.17	−0.36	0.46	0.18	−0.42	−0.72	−0.35	−0.33	−0.57	−3.70
BULLET	−0.49	−0.51	−0.55	−0.40	−0.43	−0.40	−0.50	−0.05	−0.50	−0.31	−0.31	−0.31	0.48	0.08	−0.01	−0.32	−0.33	−5.51
MORRISON	−0.39	−0.19	−0.60	0.30	−0.31	−0.42	−0.11	−0.25	−0.29	−0.69	−0.64	−0.62	0.55	0.35	−0.27	−0.36	−0.33	−4.92
NORSEMAN	−0.50	−0.66	−0.35	−0.55	−0.44	−0.40	−0.47	−0.29	−0.55	−0.43	−0.83	−0.54	−0.27	0.12	−1.06	0.06	−0.40	−7.98
RIGODON	−0.61	−0.66	−0.55	−0.65	−0.57	−0.55	−0.57	−0.56	−0.66	−0.56	−0.03	1.52	−0.88	−0.78	−0.85	0.68	−0.03	−7.04
DANCER	−0.72	−0.75	−0.30	−0.05	−0.73	−0.73	−0.63	−0.68	−0.64	−0.61	−0.69	−0.56	−0.17	0.15	−0.56	−0.21	−0.21	−8.72
JUSTICE	−0.79	−0.79	−1.05	−0.55	−0.60	−0.62	−0.67	−0.04	−0.89	−0.88	−0.62	−0.71	0.22	−0.16	−0.60	−0.61	−0.69	−10.45
DIETER	−0.83	−0.75	−0.85	0.00	−0.75	−0.66	−0.70	−0.66	−0.75	−0.49	−0.06	−0.22	−0.61	−0.83	−0.78	−0.36	−0.79	−11.05
MORGAN	−1.12	−1.08	−1.05	−0.50	−1.11	−0.87	−0.87	−0.58	−1.04	−0.87	−0.64	−0.29	−1.00	−0.44	−0.82	−0.07	−0.06	−13.77
MINSTREL	−1.12	−1.08	−1.00	−0.65	−1.03	−0.94	−0.89	−0.95	−1.08	−0.93	−0.45	−0.57	−1.00	−0.87	−0.76	−0.74	−0.69	−16.00
HIDALGO	−1.22	−1.07	−1.15	−0.35	−1.17	−0.94	−0.97	−0.70	−1.15	−1.06	−0.25	−0.54	−1.03	−0.99	−0.83	−0.72	−0.78	−16.21

Note: Y, groat yield; SPAD, chlorophyll content; PH, plant height; SDM, aboveground biomass; SN, grain number; HM, hull mass; HI, harvest index; SW, mean grain weight; SRR, shoot-to-root ratio; SRL, specific root length; RD, root density; RDM, root dry mass; RAD, root average diameter; RL, root length; RV, root volume; DTI, drought-tolerance index.

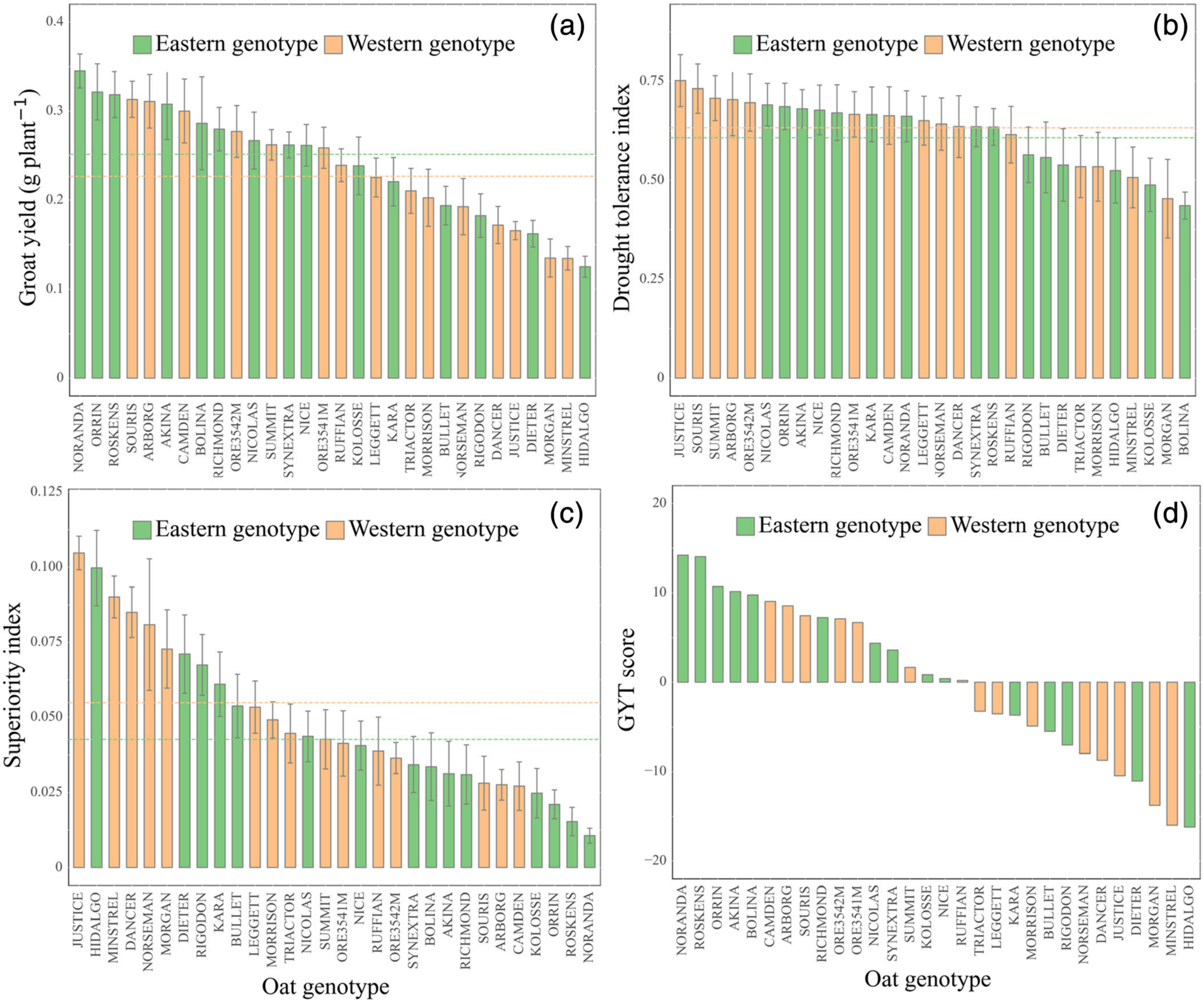


Figure 4. The four genotype selection methods. (a) The yield-based method, (b) the drought tolerance index-based method, (c) the superiority index-based method, and (d) the GYT (genotype by yield*trait) index-based method. The light green and orange dashed lines represent the average index values of eastern and western genotypes, respectively. The yield (a) was collected under drought conditions while the drought tolerance index (b) and superiority index (c) included yield data of both control and drought treatments, as shown in formulas in section materials and methods. The first three (a, b, and c) are single trait methods while the fourth (d) is multiple traits-based method.

conditions. This genetic improvement in drought tolerance extended the period of staying green, and the continuous uptake of nutrients and water through a viable root system is critical for stabilizing yield under extreme conditions.[27]

Traditional genotype selection *versus* GYT method

In agronomic practices, yield-based selection of crop genotypes has traditionally been used because pursuing high yields is the main priority for crop growers to maximize economic returns. In this study, NORANDA and ORRIN had the highest yield under water-deficit conditions (Fig. 4(a)), indicating that they are the best oat genotypes if only yield was considered as a selection criterion. However, the yield data is vulnerable because it is greatly influenced by genotype, environment, and their interactions.[3,5] For example, BOLINA produced the highest yield under well-watered conditions (Fig. 2), but its yield was reduced by more than 50% under limited watering conditions (Fig. 4(b)). In contrast, JUSTICE had greater yield stability, as its yield did not change after reduced watering, although its grain yield was much lower than the other genotypes (Fig. 2). This indicated that the yield-only-based selection method is not sufficient for crop breeding and agronomic production, as it may exclude useful candidate genotypes, especially during extremely dry weather seasons. Similar to the yield-based method, the superiority index could well reflect the oat productivity variation under adverse environments, but it appeared to underestimate the ability of plants to withstand drought, as it ranked JUSTICE as the most inferior genotype (Fig. 4(c)). According to the superiority index calculation procedure, this is attributed to the lower yield of JUSTICE under both control and dry conditions, which is far away from the optimal genotype on the Euclidean distance.

Although improving yield is the primary goal of breeding programmes, including key yield-associated traits and DTI is more valuable and practical than traditional yield-only based selection

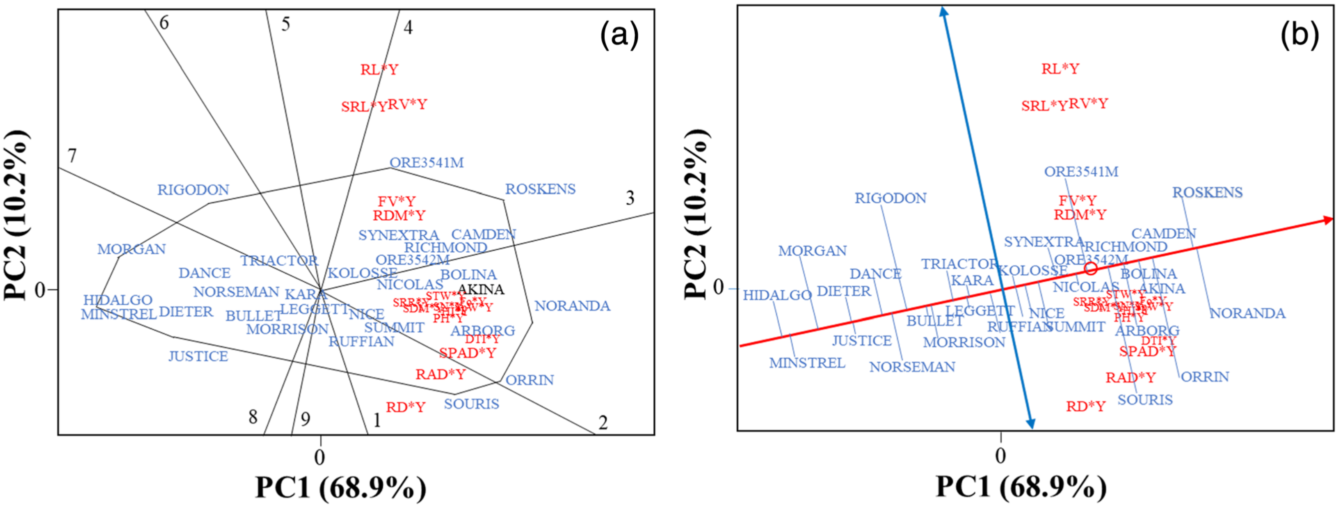


Figure 5. The GYT (genotype by yield*trait) biplot to graphically display the different genotype performances under drought conditions, including the which-won-where (a) and the average tester coordination (b) from the GYT biplot. The blue and red expressions in the biplots are oat genotypes and traits, respectively. The dataset was normalized before performing the biplot graphs, therefore, the transform = 0, scaling = 0, centring = 0 and SVP = 1 were selected. The abbreviations of traits are shown in Table 1. The small red circle represents the average placement of the yield–trait combinations and is referred to as the 'average tester'. The red line with a single arrow passes through the biplot origin and the average tester refers to as the 'average tester axis', which points to the higher level of combination between yield and related traits.

strategies when selecting genotypes for agronomic management, in the context of global climatic change.[28] In general, the seed mass accumulation is directly benefiting from biomass production and photo-assimilates translocation from source, e.g. plant leaf to the sink organs.[29] For example, sucrose produced in photosynthetic leaves is a major source of grain growth because it can be transported to developing grains during grain filling by the activity of sucrose, glucose, and fructose transporters, where it is eventually converted to starch and stored in grains.[30] The production of photo-assimilates also provided a carbon skeleton for the formation of other biochemicals, such as amino acids through reactions with nitrogen and sulphur nutrients. The root system architecture also needs to be considered during genotype selection, as roots form the interface between plant and soil, and the key function of roots is to extract nutrients and water needed for plant productivity.[31] Better drought-tolerant genotypes generally had larger root mass and lower shoot-to-root mass ratio (Table 1), and this mass reallocation between the source and sink organs is another important feature for genotype selection as it explains the specific drought resistance of different oat genotypes.[5,32] These findings underscore the importance of plant leaf and root traits for the GYT score calculation, because they can reflect the degree of damage to photo-assimilating and nutrient uptake organs by drought stress.[33] In this study, we measured chlorophyll content and root morphology, including Fo, Fv, and Fm values, and found that drought stress significantly affected these parameters (Table 1 and Fig. S1). Combining the significant differences in grain yield and drought tolerance among the 30 oat genotypes enabled the establishment of efficient GYT-based genotype selection criteria under water-limited conditions. We found that NORANDA and ROSKENS were the best two genotypes due to their high grain productivity under drought conditions, greater drought tolerance indices, better root structure and resilient photosynthesis capacity (Fig. 5). In contrast, HIDALGO and MINSTRELE were the worst genotypes under water-deficit conditions, with low yield and SPAD values, poor drought tolerance, and small root systems (Fig. S3). Unlike the other three methods, GYT-based genotypes ranking clearly distinguished those genotypes with similar grain yield but different drought tolerance, such as BOLINA *versus* RICHMOND. In this context, yield-index methods could only screen genotypes based on their yield differences from the optimal genotype. In contrast, the GYT-index method reflects not only the stress-tolerant ability but also other properties of an ideotype, such as strong photosynthesis (chlorophyll content) and water uptake capacity (root morphology), depending on the traits included in the modelling.[34] In this study, we used yield components, leaf and root traits, and crop DTI as inputs for the GYT-index calculation and determined that GYT index effectively ranked oat genotypes by balancing these agronomic attributes as a whole. It is worth noting that the oat plants in this study were grown in small cones, and the limited growing space may have resulted in phenotypic traits, especially root morphologic traits that were different from those under field conditions. Therefore, further field trials should be conducted to confirm the effectiveness of this GYT-based approach in various stressful settings.

CONCLUSIONS

In this study, we examined a variety of agronomic traits, including roots and leaf photosynthetic functional features. By combining a number of key phenotypic traits along with yield potential and drought tolerance, a GYT method was established to rank the genotypes for tolerance to increased drought events and to optimize yield potential. Our results indicated that the GYT method appeared to be an effective and informative tool for multi-trait genotyping due to its balanced high yielding, drought tolerance, and other desirable features. Therefore, it is necessary to further test this tool for oat genotype selection under a wide range of environmental conditions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest regarding the publication of this article.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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