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Use of spectral reflectance for indirect selection of yield potential and stability in Pacific Northwest winter wheat

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ABSTRACT

The use of canopy spectral reflectance as a high throughput selection method has been recommended to augment genetic gain from yield based selection in highly variable environments. The objectives of this study were to estimate genotypic correlations between grain yield and spectral reflectance indices (SRIs), and estimate heritability, expected response to selection, relative efficiency of indirect selection, and accuracy of yield predictive models in Pacific Northwest winter wheat (*Triticum aestivum* L.) under a range of moisture regimes. A diversity panel of 402 winter wheat genotypes (87 hard and 315 soft) was grown in rain-fed and irrigated conditions across the eastern Washington in 2012 and 2013. Canopy spectral reflectance measured at heading, milk, soft dough, and hard dough stages were used to derive several SRIs which generally had higher broad sense heritability (H^2) than yield *per se*. Grain yield and SRIs showed generally high genetic variability and response to selection in moist-cool rain-fed condition. Efficiency of indirect selection for yield using SRIs was high in drought environment and exceeded efficiency of yield-based selection in the soft winter subgroup. Normalized water band index (NWI) showed consistent response to selection across environments, higher genetic correlation with yield (0.51–0.80, $p < 0.001$), and highest indirect selection efficiency (up to 143%). A yield predictive model with one or more SRIs explained 41–82% of total variation in grain yield ($p < 0.001$). The repeatability of genotypic performance between years increased when selection was conducted based on both SRIs and grain yield compared to selection based on yield or SRI alone. The generally high heritability of SRIs and their significant genotypic correlation with grain yield highlight the possibility to improve yield and yield stability in winter wheat through remotely sensed phenotyping approaches.

1. Introduction

Drought stress is a major constraint in rain-fed wheat production across the US Pacific Northwest (PNW), including the states of Idaho, Oregon, and Washington. The eastern and south-central semiarid regions of the PNW often receive less than 350 mm precipitation. The wheat growing period in the region including the high precipitation zone of the Palouse (>450 mm annual precipitation) exhibits seasonal fluctuation in precipitation and temperature (Schillinger and Papendick, 2008). The variation in precipitation and thermal time cumulatively contribute to more than 70% of total yield variation in the region (Schillinger et al., 2012; Gizaw et al., 2016). Climate prediction models indicate that the region will likely experience more unprecedented warm winters with lack of snow-pack ensuing water shortages similar to the 2015 drought (Mote, 2003; Miles et al., 2010).

The winter wheat germplasm in the region has been continuously subjected to selection for yield, yield stability, end-use qualities, farming preferences, and disease resistance (Barrett and Kidwell, 1998; Chen, 2005; Schillinger and Papendick, 2008). Donaldson (1996) indicated that wheat cultivars adapted to the region contain significant variations for emergence, early canopy establishment, root growth and development, winter survival, osmotic adjustment, optimum maturity, and plant architecture. Barret and Kidwell (1998) attributed the broad and stratified genetic basis for these agronomic traits to the breeding effort in region that has been in place for more than a century. Similarly, the study population is known to have a genetic stratification that align with market class and breeding history. In particular, population structure analysis differentiated hard winter genotypes from club winter genotypes with only a slight overlap (Naruoka et al., 2015).

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Grain yield, which is a result of biological and environmental processes that occur during the complete cycle of the plant, exhibits a high level of genotype x environment interactions (GEI). Genetic progress from yield-based selection is generally low in environments that exhibit precipitation fluctuation and moisture deficit (Blum, 2006). The effect of GEI on crop yield depends on the severity, duration, and timing of the stress with respect to the affected developmental stages. In addition, factors such as variation in soil depth and ambient temperature across different croplands often confound the partitioning of variation into genotypic and environmental effects (Silvey, 1981). To address these challenges, plant breeders need to augment yield based selection with secondary traits that have inherent association with grain yield and higher heritability than yield *per se*.

Morph-physiological traits often have predictable norm of response to environmental variation and as a result, maintain high heritability across environments (Fischer et al., 2012). The study of these traits can help understand how yield potential changes in response to environmental variation, identify traits that stabilize genotypic performance, to conduct selection at early generations, and advance lines with desired characteristics for target environments (Lafitte et al., 2003). Indirect selection uses secondary traits that have inherent relationship with agronomic performance, selectable genetic variation, and predictable response to environmental variations (Passioura, 2012). This study is a part of broader research initiative to characterize the phenotypic and genetic basis of drought adaptation in Pacific Northwest winter wheat using emerging phenotyping platforms.

The drought stress intensity in the PNW, plant response to drought, and phenotypic association of secondary traits with grain yield were presented in the Gizaw et al. (2016). The major findings are summarized as follows: (i) more than 80% of total yield variation across the years and locations in the eastern Washington was explained by variation in precipitation and temperature; (ii) SRIs showed moderate to high phenotypic correlations with grain yield consistently across moisture regimes and subpopulations; (iii) variation in spike emergence and physiological maturity didn't have a net yield advantage under PNW drought conditions whereas longer vegetative period had a positive yield advantage under optimum conditions; (iv) SRIs showed strong association with stay green estimated from flag leaf senescence; and (v) the market classes of PNW winter wheat showed genotypic differentiation for agronomic and remotely sensed traits.

Similar results were reported in spring and winter wheat germplasm in low latitude environments (Aparicio et al., 2000; Babar et al., 2006a; Lopes and Reynolds, 2012). These reports altogether suggest the need to carefully determine which population, growth stage, and selection environment is most informative if SRIs are to be used efficiently in wheat breeding to augment selection for grain yield in diverse environments. Specific objectives of this particular research were the following: (i) Estimate genetic variability and heritability of SRIs, phenology, and grain yield across a range of precipitation zones in Washington. (ii) Evaluate genotypic correlations and relative efficiency of indirect selection. (iii) Develop predictive models for yield using selected in-season traits. (iv) Identify genotypes that have superior performance in optimum and stress environments.

2. Materials and method

2.1. Experimental population and field trial

The experimental design and phenotyping conditions were fully described in Gizaw et al., 2016. The study was conducted on two PNW winter wheat subpopulations: hard winter (n = 87), and soft winter (n = 315). Genotypes were selected from mapping populations, advanced breeding lines, and cultivars from PNW breeding programs targeted to Oregon, Washington, and Idaho. The hard red winter wheat cultivar 'Norwest 553′ (PI 655030) and the soft white winter cultivar 'Madsen' (PI 511673) were included as local checks. Madsen is known for its wide adaptation and disease resistance and has been grown in the PNW for over 20 years, whereas Norwest 553 has high yield potential, good disease resistance, and was the most commonly grown hard red cultivar in the PNW when the trial was initiated. Because both accessions have semi-dwarf plant height and photoperiod sensitivity, the variation across years and locations is expected to have low effect on their performance making them ideally suited to account for spatial variations with in each trial.

The study population was grown in three moisture regimes at the following Washington State University agronomy research farms: Central Ferry (46° 4′ N; 117° 8′ W), Pullman (46° 4′ N; 117° 5′ W), and Othello (46° 5′ N; 119° 2′ W) (Table 1). Central Ferry has a well-drained and moderately permeable Chard silt loam soil with water holding capacity ranging from 220 to 280 mm. Othello has a well-drained and moderately permeable Shano silt loam soil with 170–220 mm water holding capacity. The Palouse silt loam soil in Pullman is the most fertile and highly cultivated soil with deep profile, moderate permeability, and high water holding capacity. Planting of winter wheat in the study area is usually between late September and mid-October. The annual rainfall is highest in Pullman followed by Central Ferry and Othello (S. Table 1).

The population was planted in two treatments in Central Ferry and Othello: a rain-fed planting representing the drought condition and irrigated treatment representing the water optimum condition. In Pullman, the population was planted only in a rain-fed condition representing the moist-cool condition. The irrigated trials were conducted using solid-set sprinkler systems for 4–8 h, one or two times a week depending on the weather. Overhead sprinkler irrigation system is recommended in the region to minimize runoff. This system delivered approximately 600 mm of water over the growing season. Irrigation started on booting (Feekes 9) before any sign of stress was detected and continued until the onset of physiological maturity. In all treatments, a modified augmented design was used with two checks, the cultivar 'Madsen' (PI 511673) and 'Norwest 553′ (PI 655030) each replicated in 16–20 percent of the trial design (Federer and Raghavarao, 1975; Lin and Poushinsky, 1983).

Details of data collection were described in Gizaw et al., 2016. Heading date was recorded as the number of days from sowing until full exposure of spikes in 50% of the plot. Canopy reflectance was measured at multiple growth stages using the CROPSCAN multispectral radiometer (CROPSCAN, Inc. Rochester, USA) and used to derive various SRIs. Grain yield (kg/ha) was calculated from the grain weight per plot obtained from a Wintersteiger NurseryMaster small plot combine (Wintersteiger AG, Austria).

2.2. Data analysis

2.2.1. Variance component analysis

Variance components were estimated for each trait within and across treatments with a mixed linear model using the PROC mixed procedure (SAS, Cary, NC). Genotype was considered to have a random effect whereas blocks within trial, environment, and check varieties were considered to have fixed effects.

$$y_{ij} = \mu + {}_{\beta j}X_{ij} + \mathrm{b}i\mathrm{Z}_{ij} + \varepsilon_{ij}$$

where: y_i = the trait value for the i^{th} genotype in j^{th} trial; μ_j = mean value of the trait in the j^{th} trial; β_j = random-effect coefficient in j^{th} trial; X_{ij} = random-effect regressor for i^{th} genotype in j^{th} trial; b_j = fixed effect coefficient for block in j^{th} trial; Z_j = fixed effect

Table 1
Genetic correlation (±SE) between grain yield and different vegetation indices in Pacific Northwest winter wheat in drought, irrigated, and high precipitation conditions.

Traits[a]	Hard			Soft		
	Drought	Irrigated	Moist-cool rain-fed	Drought	Irrigated	Moist-cool rain-fed
GNDVI	0.54 ± 0.07	0.56 ± 0.06	0.67 ± 0.15	0.64 ± 0.05	0.45 ± 0.13	0.40 ± 0.21
NCPI	−0.51 ± 0.11	−0.42 ± 0.13	−0.49 ± 0.06	−0.66 ± 0.03	−0.44 ± 0.04	−0.37 ± 0.15
NDVI	0.56 ± 0.10	0.52 ± 0.03	0.56 ± 0.15	0.70 ± 0.04	0.43 ± 0.12	0.39 ± 0.21
NWI	0.57 ± 0.12	0.57 ± 0.12	0.60 ± 0.08	0.80 ± 0.06	0.52 ± 0.16	0.51 ± 0.18
PRI	0.35 ± 0.10	0.23 ± 0.09	0.52 ± 0.05	0.41 ± 0.13	0.25 ± 0.15	0.24 ± 0.19
SR	0.53 ± 0.04	0.58 ± 0.05	0.65 ± 0.11	0.66 ± 0.06	0.46 ± 0.13	0.40 ± 0.16

[a] *GNDVI* Green normalized difference vegetation index, *NCPI* Normalized chlorophyll-pigment ratio index, *NDVI* Normalized difference vegetation index, *NWI* Normalized water index, *PRI* Photochemical reflectance index, *SR* Simple ratio.

Table 2
Broad sense heritability of spectral reflectance and grain yield in Pacific Northwest hard and soft winter wheat in drought, irrigated, and moist-cool rain-fed conditions.

Method[a]	Trait[b]	Hard			Soft		
		Drought	Irrigated	Moist-cool rain-fed	Drought	Irrigated	Moist-cool rain-fed
Mean	Grain yield	0.26	0.49	0.69	0.25	0.40	0.61
	GNDVI	0.60	0.69	0.83	0.86	0.79	0.94
	NCPI	0.65	0.29	0.88	0.84	0.48	0.89
	NDVI	0.61	0.42	0.90	0.85	0.77	0.93
	NWI	0.40	0.82	0.65	0.81	0.92	0.86
	PRI	0.64	0.46	0.64	0.88	0.62	0.76
	SR	0.56	0.83	0.73	0.89	0.92	0.94
AUVIC	GNDVI	0.56	0.36	0.73	0.63	0.59	0.69
	NCPI	0.56	0.50	0.82	0.31	0.26	0.75
	NDVI	0.55	0.25	0.66	0.51	0.41	0.49
	NWI	0.49	0.35	0.41	0.41	0.65	0.67
	PRI	0.67	0.14	0.46	0.50	0.19	0.32
	SR	0.51	0.40	0.72	0.64	0.75	0.63

[a] Mean and area under vegetation index curve (AUVIC) were calculated from spectral reflectance indices measured across growth stages.

regressor of blocks in jth trial and ε_{ij} = the error for observation of ith genotype in jth trial.

2.2.2. Genetic correlation of traits

Genotypic correlation (r_G) among trait values traits was calculated according to Kashiani and Saleh (2010) as follows:

$rG = \frac{COVGxy}{\sqrt{\sigma 2Gx * \sigma 2Gy}}$ where COVgxy is genotypic covariance of trait x and yield; σ2Gxandσ2Gy are the genotypic variances of trait x and yield respectively (all variance estimates were derived from the mixed model).

Broad sense heritability H^2 was estimated for each trait from the variance components estimates (Fehr, 1987) as follows:

$$H^2 = \sigma^2G/[(\sigma^2G + (\sigma^2GE/e) + (\sigma^2/e)]$$

where $\sigma 2_G$ is variance of genotype, $\sigma^2{}_{GE}$ is variance of genotype-by-environment interaction; e is number of environment; and σ^2 is within environment error variance (heritability was calculated within each moisture regime)

2.2.3. Response to selection and relative efficiency of indirect selection

Direct response to selection (Rx) is the genetic improvement of a trait in response to selection upon that trait itself whereas correlated response (CRx) is the genetic improvement of a trait in response to selection of an inherently associated trait. These parameters were estimated as follows:

$Rx = K * \sigma 2Gx * Hx$

$CRx = K * rG * Hy * \sigma 2Gx$ where K is selection intensity, r_G is genetic correlation between the two traits, H is the positive square root of broad sense heritability of selected trait and $\sigma 2G_x$ is genetic variance of the target trait.

Relative efficiency of indirect selection (E) is calculated as the ratio of CRx and Rx:

$$E = CRx/Rx\frac{rGHy}{Hx}$$

where CRx is the correlated response of yield when trait y is selected, Rx is response of yield form yield based selection, rG is genetic correlation between the two traits, Hy and Hx are square root of broad sense heritability for the secondary trait and yield, respectively.

3. Results

3.1. Genetic correlation

The studied SRIs showed statistically significant genetic correlations with grain yield ($p < 0.001$). The correlation between grain yield and NWI was generally higher within each soil moisture regime (0.51–0.80) than SRIs derived from combination of VIS and NIR light ranges (0.39–0.70) (Table 1). From the SRIs derived in VIS light range, NCPI showed moderate to high negative genetic correlation with grain yield (−0.37 to −0.66), whereas PRI had low to moderate genetic correlation (0.23–0.52). In the hard winter subgroup, genetic correlation between yield and SRIs ranged from 0.23 to 0.67 with the higher values estimated under moist-cool rain-fed condition. The estimates for soft winter wheat were slightly higher under drought (0.41–0.80) and lower under irrigated and moist cool conditions (0.24–0.51) compared to the hard winter subgroup.

3.2. Variance component and heritability

Overall, heritability for grain yield was low in dry environment moderate in irrigated, and high in high precipitation condition (Table 2). The effects of genotype (G), environment

Table 3
Estimated response to direct selection of spectral reflectance indices (unit) and grain yield (kg/ha) in Pacific Northwest winter wheat.

Trait[a]	Hard			Soft		
	Drought	Irrigated	Moist-coolrain-fed	Drought	Irrigated	Moist-coolrain-fed
GNDVI	0.04	0.03	0.06	0.05	0.03	0.04
NCPI	0.08	0.01	0.10	0.08	0.02	0.05
NDVI	0.07	0.02	0.09	0.07	0.03	0.06
NWI	0.01	0.01	0.01	0.01	0.01	0.01
PRI	0.01	0.00	0.02	0.01	0.01	0.01
SR	0.79	1.02	1.19	1.17	1.15	0.97
Grain yield	0.22	0.30	1.40	0.35	0.51	0.70

[a] *GNDVI* Green normalized difference vegetation index, *NCPI* Normalized chlorophyll-pigment ratio index, *NDVI* Normalized difference vegetation index, *NWI* Normalized water index, *PRI* Photochemical reflectance index, *SR* Simple ratio.

Table 4
Correlated response of grain yield (kg/ha) from indirect selection using spectral reflectance indices (unit) in Pacific Northwest winter wheat.

Trait[a]	Hard			Soft		
	Drought	Irrigated	Moist-coolrain-fed	Drought	Irrigated	Moist-coolrain-fed
GNDVI	0.18	0.20	1.03	0.42	0.33	0.35
NCPI	−0.17	−0.10	−0.78	−0.42	−0.25	−0.31
NDVI	0.19	0.15	0.90	0.45	0.30	0.34
NWI	0.15	0.22	0.81	0.50	0.40	0.43
PRI	0.12	0.07	0.71	0.27	0.16	0.19
SR	0.17	0.23	0.94	0.44	0.36	0.35
Grain yield[b]	0.22	0.30	1.40	0.35	0.51	0.70

[a] *GNDVI* Green normalized difference vegetation index, *NCPI* Normalized chlorophyll-pigment ratio index, *NDVI* Normalized difference vegetation index, *NWI* Normalized water index, *PRI* Photochemical reflectance index, *SR* Simple ratio.

[b] The response of grain yield to direct selection.

(E) and genotype × environment interaction (GEI) on grain yield were significant ($p < 0.05$) (data not shown). The low heritability in dry environment was associated with very low G:GEI ratio (<0.13) whereas the G:GEI ratio was moderate in irrigated condition (0.34–0.50) and high in the moist-cool rain-fed condition (0.84–1.13).

The studied SRIs had moderate to strong heritability that exceeded heritability of yield in all environments (Table 2). The effects of G, E, and GEI were significant for all indices ($p < 0.05$) (data not shown). The effect of genotype x growth stage interaction (GGsI) was significant within and across trials ($p < 0.05$). Overall, using SRIs averaged over multiple measurements between heading and hard dough stages improved the genetic variance relative to growth stage specific measurements (data not shown). In irrigated environment, the heritability of NDVI, GNDVI, PRI, and NCPI were consistently low, whereas NWI and SR showed high heritability (Table 2). Comparatively, PRI and NWI were strongly influenced by GGsI and GEI.

3.3. *Response to direct selection for grain yield and spectral reflectance indices*

Grain yield showed the highest response to direct selection in high precipitation conditions followed by the irrigated condition (Table 3). The yield response to selection in drought and irrigated conditions was slightly higher in the soft winter than in the hard winter germplasm base. Conversely, grain yield in the high precipitation condition showed higher selection response in hard winter than in the soft winter wheat. The gain in NWI was consistent across environments and subpopulations. Indices derived from VIS range (PRI and NCPI) or combination of VIS and NIR light ranges (GNDVI, NDVI, and SR) showed variable response across subgroups.

3.4. *Correlated response of grain yield and efficiency of indirect selection*

Selection of SRIs in the moist-cool rained condition for hard winter and in drought condition for soft winter resulted in the highest correlated response for grain yield (Table 4). In hard winter, vegetation based SRIs (GNDVI, NDVI, NCPI, and SR) resulted in higher correlated response of grain yield than stress related indices (NCPI, NWI, and PRI). In the soft winter subgroup, NWI resulted in higher correlated response in all water regimes.

In both subpopulations, indirect selection efficiency for grain yield using SRIs was higher in drought condition than the other environments (Table 5). In the hard winter subgroup, selection efficiency was highest for NDVI in drought conditions (86%), SR in irrigated (77%), and GNDVI in high precipitation conditions (74%). In the soft winter subgroup, NWI gave the highest correlated response in all treatments (61–143%).

3.5. *Predictive model for yield and yield stability*

A yield predictive model that contains one or more SRIs explained 56–71% of grain yield in the hard winter subgroup and 42–72% of yield variation in the soft winter subgroup (Fig. 1). Each vegetation index included in the model contributes at least 2% of the variation in grain yield in the multivariable model.

3.6. *Selection efficiency of environments*

Table 6 presents the relative merit of each environment in giving maximum correlated response of grain yield in a different environment. Even though direct selection in each environment was usually the most efficient for all traits, indirect selection in the high precipitation condition had greatest efficiency relative to irrigated and drought conditions. Selection of NDVI and PRI was more efficient in the high precipitation and drought conditions, respectively, than direct selection of these traits in irrigated conditions (170 and 253% respectively).

Table 5
Efficiency of indirect selection for grain yield using of spectral reflectance indices in Pacific Northwest winter wheat.

Trait[a]	Hard			Soft		
	Drought	Irrigated	Moist-coolrain-fed	Drought	Irrigated	Moist-coolrain-fed
GNDVI	0.82	0.67	0.74	1.20	0.65	0.50
NCPI	0.77	0.33	0.56	1.20	0.50	0.44
NDVI	0.86	0.50	0.64	1.29	0.59	0.49
NWI	0.68	0.73	0.58	1.43	0.78	0.61
PRI	0.55	0.23	0.51	0.77	0.31	0.27
SR	0.77	0.77	0.67	1.26	0.70	0.50

[a] *GNDVI* Green normalized difference vegetation index, *NCPI* Normalized chlorophyll-pigment ratio index, *NDVI* Normalized difference vegetation index, *NWI* Normalized water index, *PRI* Photochemical reflectance index, *SR* Simple ratio.

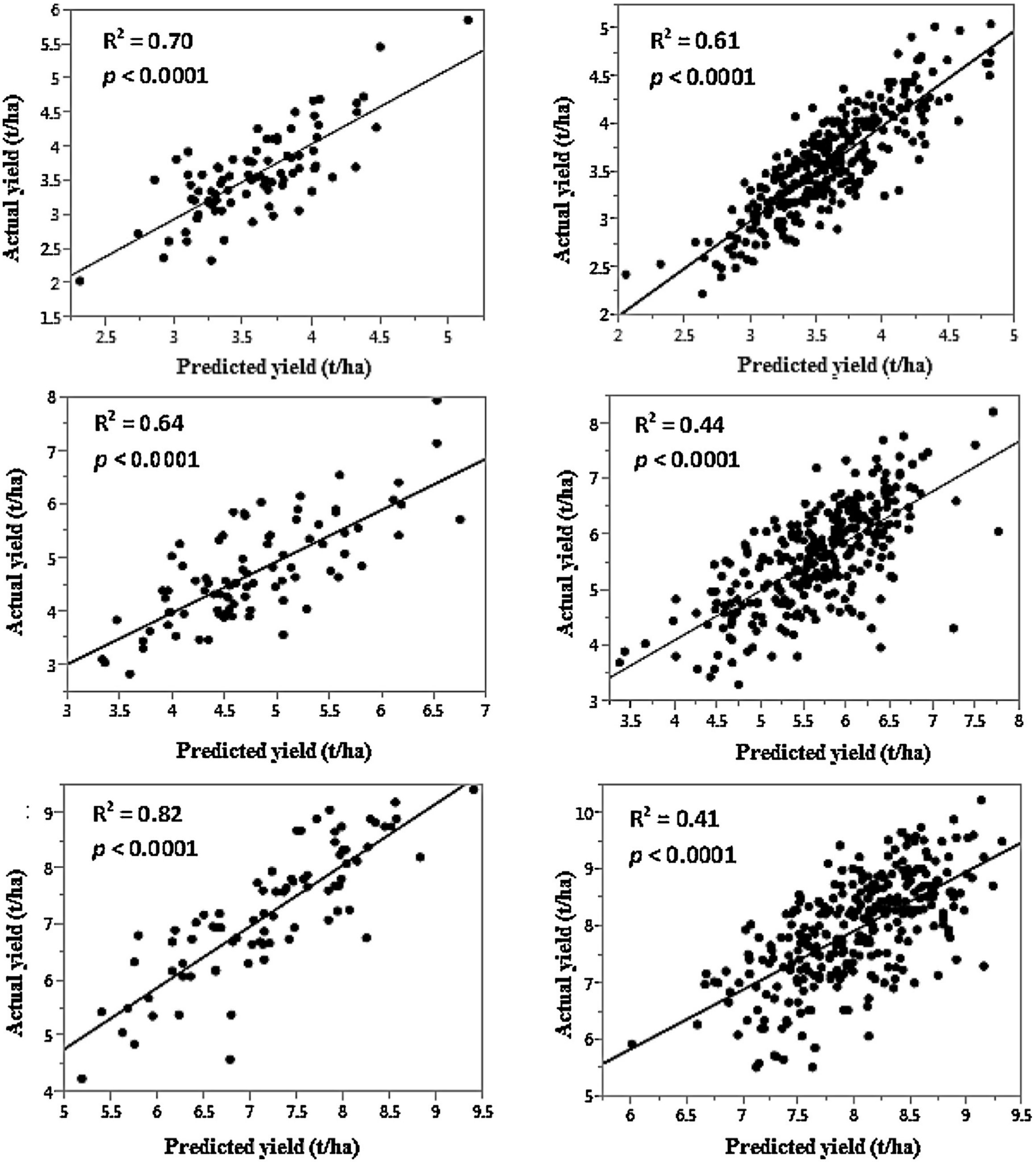

Fig. 1. Actual yield (Y-axis) *versus* predicted yield (X-axis) using SRI indices in PNW winter wheat: From top to bottom are drought, irrigated, and moist-cool rain-fed conditions. On the left is hard winter wheat and on the right is soft winter wheat.

In environments where indirect selection efficiency is moderate or strong, integrating SRI and yield-based selection resulted in 6% higher repeatability of genotypic performance than yield-based selection alone and 16% higher repeatability than SRI-based selec-

Table 6
Comparison of Pacific Northwest selection environments for indirect selection efficiency of grain yield and spectral reflectance indices. Prediction environment refers to environment of direct phenotyping and selection environment refers to the target environment.

Trait[a]	Prediction environment	Selection Environment		
		Drought	Irrigated	Moist-coolrain-fed
GNDVI	Drought	–	0.43	0.65
	Irrigated	0.60	–	0.88
	High Precipitation	0.48	0.46	–
NCPI	Drought	–	0.48	0.74
	Irrigated	0.74	–	0.82
	High Precipitation	0.56	0.40	–
NDVI	Drought	–	0.35	0.81
	Irrigated	0.68	–	1.21
	High Precipitation	0.42	0.33	–
NWI	Drought	–	0.38	0.36
	Irrigated	0.28	–	0.50
	High Precipitation	0.25	0.46	–
PRI	Drought	–	0.07	0.66
	Irrigated	2.57	–	1.70
	High Precipitation	0.73	0.05	–
SR	Drought	–	0.56	0.56
	Irrigated	0.53	–	0.64
	High Precipitation	0.48	0.58	–
Grain yield	Drought	–	0.36	0.41
	Irrigated	0.35	–	0.53
	High Precipitation	0.30	0.41	–

[a] *GNDVI* Green normalized difference vegetation index, *NCPI* Normalized chlorophyll-pigment ratio index, *NDVI* Normalized difference vegetation index, *NWI* Normalized water index, *PRI* Photochemical reflectance index, *SR* Simple ratio.

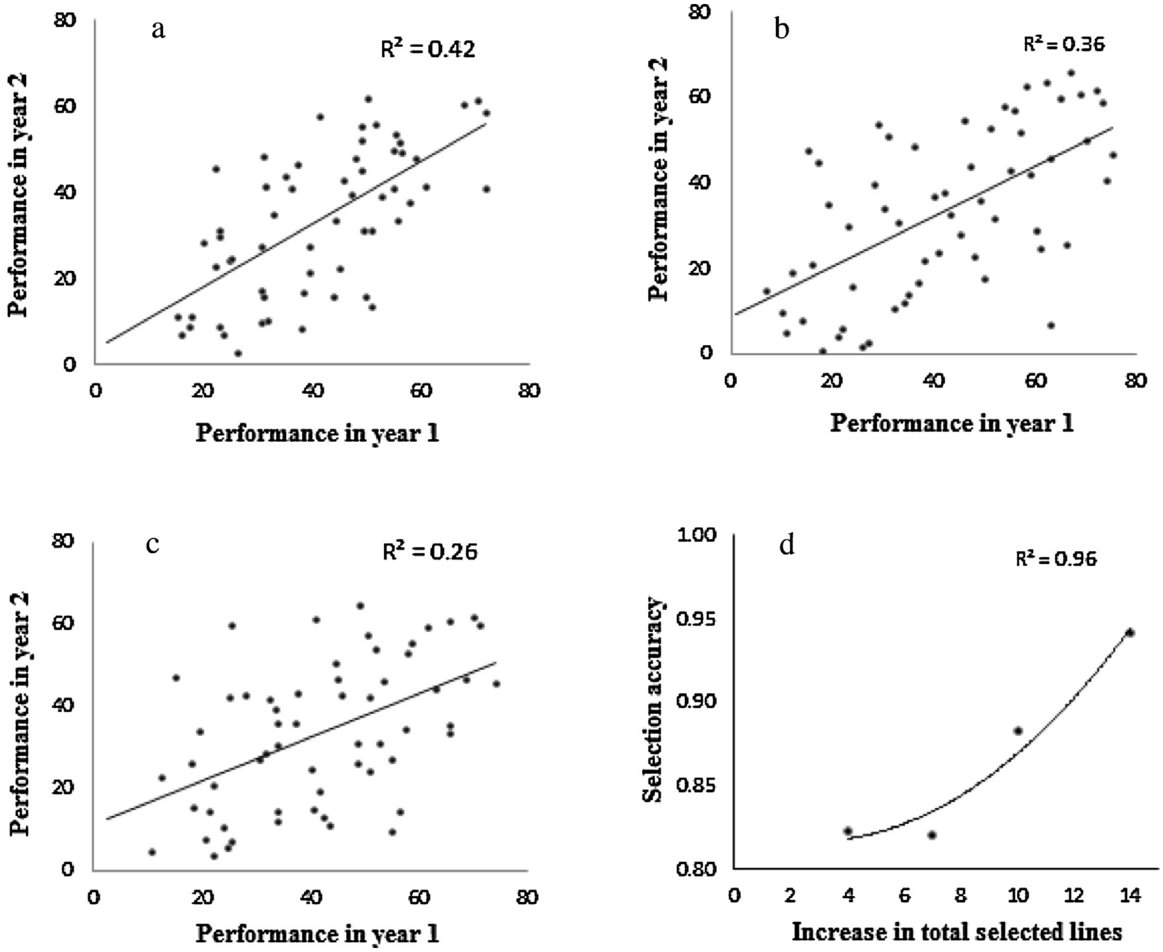

Fig. 2. Estimated repeatability of genotypic performance between years in Pacific Northwest winter wheat: a. genotypic performance from SRI-yield integrated selection; b. genotypic performance from yield-based selection; c. genotypic performance from SRI-based selection; and d. improvement in efficiency of indirect selection (Y-axis) with lowering the selection intensity (X-axis) in hard winter subgroup.

tion alone (Fig. 2a–c). We also found that setting a lower cutoff for SRIs led to identification of nearly all the high yielding genotypes that could be identified by direct selection (Fig. 2d).

3.7. Identification of genotypes for superior yield potential and drought tolerance

Twenty three genotypes were identified to have higher yield potential as well as drought tolerance. A total of 119 genotypes were identified to have high yield potential, yet low drought tolerance. Sixteen genotypes were identified to have high drought tolerance, but low yield potential. The subsets of these genotypes along with their stress tolerance index are presented in S. Table 2a and b.

4. Discussion

Genetic correlation of two traits indicates the proportion of phenotypic value attributed to shared genetic basis. The precise estimation of this inherent association requires a genetically diverse population that accounts for sampling error bias in gene frequency (Borhren et al., 1961). As such, the study populations in our experiment represented the most current winter wheat cultivars and representative samples of genetic materials from major breeding programs in the PNW. The genetic correlations between grain yield and SRIs were consistently significant across subgroups and environments indicating the dependability of these estimates. Similar results were also reported in spring wheat under irrigated conditions (Babar et al., 2006a,b) and in winter wheat under rain-fed conditions (Prasad et al., 2007) in low latitude mega environments. Despite the difference in environmental factors and genetic composition, consistent results suggest the possibility of using these proxy measurements to understand the genetic and physiological basis of yield. The consistently moderate to strong genetic correlation of SRIs to grain yield in the drought and near optimum conditions of the Pacific Northwest also indicates the potential use of an indirect selection approach to identify high yielding and drought tolerant genotypes.

Differences in the strength of genetic correlations were observed across the different moisture regimes and subpopulations. In the soft winter wheat subgroup, grain yield was more strongly correlated with SRIs in drought conditions than in irrigated and high precipitation conditions. As plants attain maximum leaf area and pigment accumulation in irrigated conditions, indices derived merely from VIS saturates will not precisely correspond to variation in grain yield (Babar et al., 2006a). This limitation is clearly reflected in the generally low genotypic correlation of grain yield with PRI and NCPI. On the other hand, the indices derived from the NIR range (NWI) and combination of the VIS and NIR range (GNDVI, NDVI, and SR) showed higher consistency. The combined use of SRIs at multiple growth stages resulted in higher genetic correlation relative to growth stage-specific SRIs. Babar et al. (2006a) and Prasad et al. (2007) reported similar results in different wheat populations and recommended using the average of SRIs between heading and grain-fill. The combined use of multiple measurements throughout the growing season allows us to capture the variations of morph-physiological attributes that are pertinent to plant health and grain yield (Babar et al., 2006b).

The SRIs had generally higher heritability than grain yield. The disparity between heritability of grain yield and SRIs was highest in drought conditions possibly because grain yield experienced stronger GEI than SRIs, because the population has low genetic variance for yield, or a combination of these two. The low G:GEI ratio asserts that strong GEI effect in moisture stressed environments is the primary challenge to increasing genetic gain in grain yield from multi-location and multi-year selection. Conversely, the higher G:GEI ratio in high precipitation conditions suggests higher potential to increase genetic gain through selection in this environment. The effect of genotype x growth stage interaction on SRIs was in general mild under drought conditions and under high precipitation conditions in the hard winter subgroup.

Indirect selection for secondary traits is a preferred selection approach when the secondary trait has higher heritability and genetically correlated with the target trait. The relatively higher heritability of SRIs and their moderate to strong genetic correlation to grain yield indicates their potential use in improving genetic gain from indirect selection. The low GGsI on SRIs corresponded to higher genetic correlation between SRIs and grain yield estimates. This is consistent with the assertion by Banziger and Lafitte (1997) that genetic correlation between secondary traits and grain yield increases in stressed conditions. In the hard winter subgroup, the efficiency of indirect selection didn't exceed direct selection for grain yield in all conditions. The fairly small size of the hard winter subgroup may have inadequate sample of variation in order to estimate these genetic correlations. In the soft winter wheat subgroup, the indirect selection efficiencies for all indices except PRI exceeded efficiency of yield-based selection under drought conditions. The highest indirect selection efficiency was obtained by selecting GNDVI and NWI in the hard and soft subgroups, respectively.

In addition to genetic variability, selection environment is an important factor to evaluate genetic gain and efficiency of alternative selection approaches (Manneveux and Ribaut, 2006). High indirect selection efficiency of secondary traits is often reported in drought conditions (Banziger and Lafitte, 1997). Secondary traits that showed higher indirect selection efficiency than direct selection for yield *per se* under drought conditions will be prime targets to improve genetic gain in yield and drought tolerance. While such findings support the notion that SRIs are more useful as indirect selection tools in stressed conditions, high selection efficiency under drought can be attributed to wide disparity between heritability of grain yield and SRI.

In order to bolster the actual genetic gain, selection environments should be characterized to identify the most effective election environment in relation to GEI and correlated response of traits across environments. In this study, the high precipitation condition was found to be most efficient selection environment for grain yield. In cases where selection environment is different from breeding target environment, it is essential to evaluate the selection efficiency of respective environments. In our study, selection of yield and most SRIs under high precipitation gave the highest correlated response in drought and irrigated conditions (Table 6). Selection under irrigated conditions resulted in the least correlated response in rain-fed conditions. The indirect selection efficiency for NDVI in the high precipitation environment and PRI in the drought environment was higher than direct selection for these indices in the irrigated environment.

Spectral reflectance can be used in plant breeding, not just as a standalone indirect selection criterion, but also as a component in an integrated selection approach. As demonstrated in Fig. 2a–c using the hard winter subgroup, integrated selection of grain yield and SRIs increased repeatability of genotypic performance across multiple trials. We used SRIs to identify high yielding and drought tolerant genotypes in Pacific Northwest winter wheat mega-environments. Conducting SRI-based selection at 25% selection intensity before harvest enabled us to select nearly all the high yielding lines that could be selected at 10% selection intensity using direct selection for grain yield.

When determining selection efficiency, we also consider factors other than rate of genetic gain such as phenotyping speed, cost, and scalability (Manneveux and Ribaut, 2006). The remotely sensed phenotyping platforms allow us to screen a larger set of germplasm than yield-based selection. To this effect, the authors found it reasonable to use lower selection intensity for SRI-based selection so that most superior genotypes that could be advanced through yield-based selection could be selected in the SRI-based selection as well. Lowering the selection intensity for SRIs from 10% to 25% increased the indirect selection efficiency substantially (>0.94). In fact, selection at differential cutoffs for different traits is commonly practiced in index selection models (Lafitte et al., 2003). As demonstrated in the high repeatability of integrated selection model (Fig. 2a–c), the additional lines selected for their high SRI could improve overall yield stability despite their moderate performance in grain yield.

5. Conclusions

This study demonstrated that the use of SRIs as indirect selection criteria increases the genetic gain in Pacific Northwest winter wheat. The highest selection efficiency obtained under drought conditions indicates that indirect selection will have more practical advantage in stressed conditions. The SRI-based selection in soft winter wheat was more efficient than selection of grain yield *per se*. In environments where the indirect selection efficiency was moderate to high, the use of SRIs is still pertinent to increase stability of genotypic performance using a multi-trait (index) selection approach.

Our study also showed that the efficiency of indirect selection can be further improved using differential selection intensity in order to select all genotypes that could be discarded when selection is carried out at a more stringent cutoff point. The indices derived based on VIS and NIR (GNDVI, NDVI, and SR) showed high selection efficiency in hard winter wheat whereas the NIR-based index (NWI) showed the highest genetic correlation and selection efficiency in soft winter wheat. This difference indicates that the hard and soft winter wheat germplasm might have different genetic composition and subsequently different target traits for drought adaption and yield potential. Selection using vegetation related indices (VIS and VIS-NIR) is more likely to improve the traits related to aboveground biomass and pigment composition whereas selection using NWI (NIR) is more likely to improve the plant hydration status and root access to soil moisture. The higher heritability and selection efficiency of NCPI relative to PRI makes it a better option to study the composition and dynamics of photosynthetic and stress responsive pigments in the PNW germplasm. In general, the results of this study highlight the possibility of using these traits to facilitate winter wheat adaptation breeding in Mediterranean-like climates.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2016.06.022.

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