Combined selection for productivity and resilience through modified stress tolerance indices in a HUW-234 X HUW-468 derived wheat (*Triticum aestivum* L.) RIL mapping population for heat stress

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Abstract

Stress indices are a set of quantitative estimators that elucidate stress response by yield data from single or multi-environment evaluations. A major disadvantage of using such indices is the reported lack of correspondence in rankings across indices and their failure to delineate overlapping responses in terms of yields under stress. In the present study, HUW-234 x HUW-468 derived wheat RIL mapping population was used to validate the usefulness of such a modified index. The correlation coefficient between the index score and their original index values were negative for SSI (Stress Susceptibility Index) and TOL (Tolerance Index) and positive for MP (Mean Productivity), GMP (Geometric Mean Productivity) and STI (Stress Tolerance Index). Based on index scores, two new indices namely YPSI (Yield Production Index) and YSSI (Yield Stress Score Index) were created by combining score indices. Using these indices, the RILs could be effectively classified into four stress response classes. Most of the genotypes fall in Class II, III and IV. As such, it is highly imperative to identify highly resilient (Class III) and productive genotypes (Class II) for planned crossing. Based on the results of present and earlier studies, it is proposed that the new indices YPSI and YSSI can be effectively used for evaluating large genotype sets in diverse environments for stress response.

Key words: Wheat, heat stress, RIL population, stress tolerance indices, index scores, YPSI, YSSI

INTRODUCTION

Wheat (*Triticum spp.*) is one of the important food crops of the world with a significant contribution to the global food security imperatives and the second most important food crop in India after rice (Reddy and Babariya, 2020). Among cereals, it is the most traded crop, with 10 per cent of total production going to international markets (Marathe and MacPherson, 2001) and is the most widely grown of all the cereals, with a growing area spanning the equator to latitudes of more than 60°N and 50°S, and altitudes of up to 3,000 m above sea level. With the global population expected to touch 9 billion by 2050, the wheat demand is expected to increase by 32 per cent in the year 2050, with projections up to 880 MMT (Weigand, 2011). In terms of absolute quantity, wheat is the leading source of protein in human food, with a protein content of about 13 per cent, which is comparatively higher than other major cereals. However, wheat protein is low in essential amino acids. An annual increase of at least 1.6 per cent in grain

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yield is required in the coming years in order to fulfill the demand. With global production of more than 750 million tons, wheat (Triticum aestivum L.) is the world’s most significant food crop for direct consumption (FAO, 2017). Wheat is grown on more land area than any other food crop with a cropped area of about 220.4 million hectares, accounting for about 30 per cent of the global cereal area and providing food to 36 per cent of the global population. India recorded production of more than 100 million tons in 2019 which contributes to ~36 per cent of the national food basket (FAO, 2019). The major wheat producing states are Uttar Pradesh, Punjab, Haryana, Madhya Pradesh, Rajasthan, Bihar, Maharashtra, Gujarat, Karnataka, West Bengal, Uttarakhand, Himachal Pradesh and Jammu & Kashmir. These states contribute about 99.5 per cent of total wheat production in the country.

High temperature severely implicates seed germination, seedling emergence and other physiological parameters in wheat (Tewolde et al., 2006, Khajuria et al., 2016). It also causes reduction of grain weight and deterioration in grain quality, if heat stress occurs during the grain-filling stage mainly through its effect on photosynthetic availability and remobilisation as well as the starch synthesis and deposition to the wheat grain (Bhullar and Jenner, 1985). In arid, semi-arid, tropical and subtropical regions of the world, heat stress severely impacts wheat seed yields (Rehman et al., 2009). Heat stress effects in wheat are invariably manifested as a reduction in grain size, plant height, grain growth duration, kernel number and kernel weight (Viswanathan and Khanna-Chopra, 2001).

The major difficulty in breeding for heat stress tolerance is the creation of stress conditions in experimental set up and poor correspondence with actual field conditions. In fact the translation of greenhouse and laboratory observations to a myriad of diverse patterns and processes observed in the field is a huge challenge, even in the case of experiments where a seemingly fair amount of control is expected (Poorter et al., 2016). Even, in the case of experiments where similar traits are studied under different screening systems, the correspondence is not fairly straightforward. In production breeding, yield is the primary breeding objective and has been improved by using yield per se and yield components based on correlated response. One major problem that is encountered by researchers while dealing with the yield data is that yield under stress per se as well as yield differences under non-stress and stress conditions (\(Y_s-Y_p\)) cannot effectively discriminate the genotypes into tolerant and susceptible as well cannot account for the range of response exhibited by genotypes under stress. Plant breeders have primarily focussed on selecting genotypes that exhibit higher yield under non-stress conditions followed by testing under stress conditions of various severities (mild/severe) and applying stress at various stages (early season, intermittent and terminal stress) on the assumption that a genotype with high yield potential will perform comparably well under stressful environments (Blum, 2005). There is substantial experimental support for the argument that yield under optimal conditions corresponds well with yield under mild stress, however, a higher resilience, even with a lower yield, under severe stress may be more desirable (Panthuwan et al., 2002).

In the field experiments, usually the classification of genotypes is based on the premise that the tolerance and susceptibility response are quite distinguishable. However, invariably, the genotypic responses are never so distinct and extreme, but overlapping. Moreover, differential genotypic responses in form of varying degrees of resilience and productivity are a result of different underlying physiological and biochemical mechanisms. As outlined by Fernandez (1992) and Thiry et al. (2016) the genotypic response under stress and non-stress conditions can be broadly grouped into the following four classes: namely Class A (representing genotypes that express uniform superiority in both stress and non-stress condition. These genotypes are invariably rare and have both resilience and productivity), Class B (representing genotypes that express good performance only in non-stress and not under stress conditions. These genotypes have high productivity under non-stress conditions but do not have resilience), Class C (representing genotypes having higher yield only under stress i.e., they possess resilience but are not productive), and Class D (representing genotypes that express poor yield performance in both environments and lack both productivity and resilience).

Stress indices are quantitative measures that characterize stress response (here high temperature) by yield data from one or several environments based on timing, duration and intensity of stress (Sofi et al., 2018). Such an index is more readily useable than raw yield data. Since heat stress response under field conditions is a yield based trait, selection could vary depending on which index is chosen by the breeder. In cases, where reduction in yield (\(Y_s-Y_p\)) due to heat stress is used for selecting cultivars with resistance to heat stress, there is a likelihood of selecting low yielding cultivars with a small yield differential. As pointed out by Thiry et al. (2016) and Sofi et al. (2017a), a major practical bottleneck of using these indices is the observed lack of correspondence in rankings across indices and their failure to delineate the overlapping responses. Moreover, there have been contrasting reports about their practical utility in identifying optimally yielding genotypes (Ramirez-Vallejo and Kelly, 1998, Sareen et al., 2012). The selection based on a combination of different indices may provide a more useful alternative criterion for improving stress adaptation of cowpea. However, there are not yet any accurate screening indices that can be used in breeding programmes to select genotypes for abiotic stress adaptation and high yield. The indices per se have certain basic shortcomings (Fernandez, 1992, Thiry et al., 2016 and Sofi et al., 2017b) that necessitate the use of new indices for reliable estimation of differential genotypic
response under stress environments. Therefore the present study was undertaken to test the hypothesis that the modified index is equally effective across different crops. We used a HUW-234 x HUW-468 wheat RIL mapping population comprising 160 RILs and two parents to further establish the usefulness of such a modified index in crop breeding programmes aimed at identifying wheat genotypes resilient to heat stress.

MATERIALS AND METHODS
The present study was undertaken in Rabi. 2018 at an experimental farm of the Faculty of Agriculture at Wadura (34° 17' North and 74° 33 E at an altitude of 1594 metres above sea level) and Division Genetics and Plant Breeding, Faculty of Agriculture, SKUAST-J Chattha (32°39' North and 74°58' East at an altitude of 332 meters above sea level). The minimum and maximum temperature during the experimental period in Wadura experimental site were 14.87 and 28.97 degrees Celsius, the minimum and maximum relative humidity were 55.68 and 80.14 per cent and the total rainfall recorded was 336.2 mm. The Chattha experimental site was used as a heat stress site while as Wadura site was used as an ambient temperature site for estimation of various stress tolerance indices based on mean yields at the two sites. The plant material used in the present study comprised 164 genotypes including 160 bi-parental RIL's derived from a cross of HUW-234 x HUW-468 and four checks namely Shalimar Wheat-1, Shalimar Wheat-2, HUW-234 and HUW-468. Shalimar Wheat-1 and Shalimar Wheat-2 are the varieties released by SKUAST-Kashmir, while as, HUW-234 and HUW-468 are the parents of the RIL population. HUW-234 (HU12*2 / CPAN 1666) is a wheat variety released by Banaras Hindu University (BHU), Varanasi in 1986 as Malvya-234 for late sown irrigated conditions. HUW-468 (CPAN 1962//TONI//LIRA/PRL) is also released by BHU, Varanasi in 1999 as Malvya-468 for timely sown irrigated conditions. HUW234 has shown substantial heat tolerance while HUW-468 is a heat susceptible genotype (Joshi et al., 2007).

The material was evaluated in an augmented block design (Federer, 1956), comprising two kinds of treatments, the checks or the standard treatments and new or augmented treatments (Federer, 1956). In this design, the checks are assumed as fixed effects whereas the new entries as random effects. The new entries are usually not replicated especially when dealing with large germplasm sets, but the checks are replicated to estimate error. The checks and new entries are randomly distributed among a set of blocks assumed to be homogenous. This design can accommodate both replicated as well as un-replicated entries and is highly useful in testing a huge number of test entries/accessions when the replication is not practically possible, the amount of seed is very limited, or in the case of unequal plot sizes. It saves time and money without compromising on the precision of critical comparisons among treatments.

For all the genotypes (parents and RILs), seed yield was calculated on a plot basis. Various drought tolerance indices were calculated based on the values of seed yield per plant under non-stress and heat stress conditions to discriminate genotypes on the basis of high temperature response in terms of grain yield. Based on established experimental evidences, the following five stress tolerance indices were used. The calculations were done as follows:

| Index                              | Formula                                                                 | Reference           |
|------------------------------------|-------------------------------------------------------------------------|---------------------|
| Stress susceptibility index (SSI)   | \(1- \left( \frac{Y_{\text{NS}}}{Y_{\text{S}}} \right) \) / \(1- \left( \frac{X_{\text{S}}}{X_{\text{NS}}} \right) \) | Fisher and Maurer (1978) |
| Tolerance index (TOL)              | \(Y_{\text{NS}} - Y_{\text{S}}\)                                       | Rosille and Hamblin (1981) |
| Mean productivity (MP)             | \(\left( \frac{Y_{\text{S}} + Y_{\text{NS}}} {2} \right) \)            | Rosille and Hamblin (1981) |
| Geometric mean productivity (GMP)   | \(\sqrt{\left( \frac{Y_{\text{NS}} \times Y_{\text{S}}} {2} \right)}\) | Fernandez (1992)    |
| Stress Tolerance Index (STI)       | \(\left( \frac{Y_{\text{NS}} \times Y_{\text{S}}} {X_{\text{NS}}} \right)\) | Fernandez (1992)    |

Where \(Y_{\text{S}}\) and \(Y_{\text{NS}}\) are mean yields of genotypes under stress and non-stress conditions respectively and \(X_{\text{S}}\) and \(X_{\text{NS}}\) are the mean of yield of all genotypes under stress and non-stress conditions.

Linear regression was calculated between indices and seed yield under non-stress and heat stress conditions. Since the direction of various indices used is not in line with the seed yield under different screening systems, a major problem accruing in genotypic evaluations for stress response is the ambiguity regarding the reliable genotypic response to stress using the yield per se and the five stress indices (SSI, TOL, MP, GMP and STI). In order to overcome such ambiguity, Thiry et al. (2016) proposed two new indices defined as YPSI (Yield Potential Score Index) and YSSI (Yield Stress Score Index) that determine the yield potential and resilience capacity of genotypes respectively, Thiry et al. (2016) and Sofi et al. (2017a) outlined the discriminatory power of the new indices in terms of the yield decrease of the genotypes under stress within a population. Both the studies emphasised that the combined use of the five indices (SSI, TOL, MP, GMP and STI), and new indices (YPSI and YSSI) are highly effective in understanding the basis of any yield limitations under particular stress. Following Thiry et al. (2016) these five indices were divided into two classes viz., Class 1 (SSI and TOL) and Class 2 (MP, GMP and...
The plant material used in the present study comprised 164 genotypes including 160 bi-parental RIL's derived from a cross of HUW-234 x HUW-468 and four checks namely Shalimar Wheat-1, Shalimar Wheat-2, HUW-234 and HUW-468. Shalimar Wheat-1 and Shalimar Wheat-2 are the varieties released by SKUAST-Kashmir, while as, HUW-234 and HUW-468 are the parents of the RIL population. HUW-234 (HU12*2/CPAN 1666) is a wheat variety released by Banaras Hindu University (BHU), Varanasi in 1986 as Malvya-234 for late sown irrigated conditions. HUW-468 (CPAN 1962/TONI//LIRA/PRL) is also released by BHU, Varanasi in 1999 as Malvya-468 for timely sown irrigated conditions. HUW234 has shown substantial heat tolerance while HUW-468 is a heat susceptible genotype (Joshi et al., 2007).

The material was evaluated in an augmented block design (Federer, 1956), comprising two kinds of treatments, the checks or the standard treatments and new or augmented treatments (Federer, 1956). In this design, the checks are assumed as STI) based on the premise that the first class tends to identify genotypes based on resilience and productivity, respectively. The scoring scale for each index is based on deriving the range from minimum and maximum values from the original index. This range is further divided into ten parts and each part has a score from 1 to 10 in a way that each part represents 10, 20, or 100 per cent of the range value. In addition to this, the values of TOL and SSI were inverted, so as to obtain a higher value with the original equation will receive a lower score in all cases that allows the two classes of indices to have the same scale, where a high score will always mean a 'good' genotype and a lower score a poor genotype (Thiry et al., 2016). The index scores were then combined and tested against yield under non-stress and stress conditions to elucidate differential genotypic response in terms of adaptability to stress and/or non-stress environments. The new score indices were calculated as follows

| Index                                      | Formula                                      | Reference         |
|--------------------------------------------|----------------------------------------------|-------------------|
| Yield susceptibility score index (YSSI)    | \( \frac{(STI_i + SSI_i)}{2} \)             | Thiry et al. (2016) |
| Yield production score index (YPSI)        | \( \frac{(MP_i + STI_i) - (SSI_i + TOL_i)}{2} \) | Thiry et al. (2016) |

Where STIs, SSI, MPs, TOLs are the index scores of the Stress tolerance index, Stress susceptibility index, Mean productivity and Tolerance index, respectively.

The genotypes were classified into four classes as outlined in the previous section. Genotypes possessing higher values of YPSI and YSSI possess both resilience and productivity. Those possessing higher values of YPSI but lower values of YSSI possess only productivity under optimal conditions but undergo severe yield reductions under heat stress. Genotypes possessing higher values of YSSI but lower or negative values of YPSI possess only resilience to heat stress but are not so productive under optimal conditions. Similarly, genotypes possessing lower values of both YPSI and YSSI are neither productive nor resilient.

**RESULTS AND DISCUSSION**

Initially, five indices namely SSI, TOL, MP, GMP and STI were used for understanding genotypic response under heat stress. Invariably, in most of the studies, these indices show variable rankings that necessitate the need
to use a more relevant index (Thiry et al., 2016, Sofi et al., 2017a). In order to identify the best combination of indices linear regression and the coefficient of determination of the different indices v/s yield was performed under non-stress and heat stress environments, calculated on 164 genotypes (Fig. 1) which clearly indicated that no single index, per se, can clearly discriminate the high yielding genotypes, independently. This observation conforms to the result reported by Khayatnezhad et al.(2010) and Thiry et al. (2016) in wheat, Sofi et al. (2017a) in common bean and Musharib Gull et al. (2019) in cowpea. The indices SSI and TOL usually indicate susceptibility as higher values of these indices stand for increased susceptibility to stress while MP, GMP and STI indicate tolerance as higher values are indicative of greater tolerance. In each class of index (susceptibility and tolerance), GMP and STI showed the closest relationship (Fig. 1) with yield under heat stress (R= 0.565 and 0.562, respectively). In contrast, MP and TOL showed a close relationship with yield in a non-stress environment (R=0.852 and 0.845 respectively). Similar results have been reported by Thiry et al. (2016) and Sofi et al. (2017a). The results of the present study substantiate the premise that the combination of the score indices from each class would improve the relationship between the indices per se and grain yield.

In this study it was first tested the score indices against their original value from each index. The correlation coefficient between the score indices and the original indices calculated on yield data from the 164 genotypes evaluated under ambient and heat stress conditions, revealed that the correlation between the stress susceptibility index score (SSIs) and the tolerance index score (TOLs) values and their original index values (SSI and TOL) was highly significant and negative (ranging from −0.948 to −0.983). This is obviously due to the fact that the score scale was inverted in order to create a scale showing resilience instead of susceptibility. In contrast, the correlation between the original values for MP, GMP and STI and the score indices MPs, GMPs and STIs were highly significant and positive (0.966 to 0.984) (Table 1). The high correlation demonstrates that the score indices can be used effectively as compared to their original index value as suggested by Thiry et al. (2016). An interesting observation from the correlation of index scores and original indices, in this study as well as the earlier ones reported by Thiry et al. (2016), Sofi et al. (2017a) and Asmat Ara (2019) is that within each class the values are almost same and substantiate the premise that SSI and TOL can be assigned to class 1 and, MP, GMP and STI, can be assigned to class 2. In fact, these two classes were used to build two new indices that would represent two different characteristics of plant response viz., resilience capacity (YSSI) and production capacity (YPSI), respectively.

The new indices namely YPSI and YSSI were calculated by combining indices from each class to overcome the ambiguity in using individual indices and inconvenience in combining indices per se. We created score indices using the approach as already outlined in the methodology. The two new indices (YPSI and YSSI) as proposed by Thiry et al. (2016) were based on the various combinations of score indices. The effectiveness of modified indices was experimentally demonstrated in wheat and common bean genotypes (Thiry et al., 2016, Sofi et al., 2017a and Asmat Ara, 2019) and came up with strong experimental support for using new indices for evaluation of germplasm sets of any scale. Combined into YPSI (yield potential score index) and YSSI (yield stress score index), we could identify genotypes that could fall into four classes. The Class I genotypes are resilient and productive, but are very rare, and are characterised by higher positive values of both YPSI and YSSI. Class II genotypes are productive but not resilient and are characterised by higher positive values of YPSI but invariably lower values of YSSI. They produce better yields in productive environments but undergo severe reduction under stress. Similarly, Class III genotypes are resilient but not productive and are characterised by higher positive values of YPSI but invariably lower or negative values of YSSI. They produce

### Table 1. Pearson correlation coefficient between the score indices (SSIs, TOLs, MPs, GMPs and STIs) and their original indices (SSI, TOL, MP, GMP and STI)

| Trait | SSI | TOL | MP | GMP | STI |
|-------|-----|-----|----|-----|-----|
| Class I |     |     |    |     |     |
| SSI   | −0.983 | −0.864 | −0.864 | 0.074 | 0.075 |
| TOLs  | −0.864 | −0.948 | −0.948 | −0.272 | −0.275 |
| Class II |     |     |    |     |     |
| MPs   | 0.860 | 0.966 | 0.966 | 0.314 | 0.307 |
| GMPs  | −0.071 | 0.327 | 0.327 | 0.982 | 0.975 |
| STIs  | −0.053 | 0.336 | 0.336 | 0.978 | 0.984 |

Stress susceptibility index (SSI), Tolerance index (TOL), Mean productivity (MP), Geometric mean productivity (GMP), Stress Tolerance Index (STI)
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Fig. 1. Linear regression and coefficient of determination ($R^2$) between yields under stress and non-stress and score indices.

- $R^2 = 0.427$
- $R^2 = 0.488$
- $R^2 = 0.130$
- $R^2 = 0.845$
- $R^2 = 0.852$
- $R^2 = 0.173$
- $R^2 = 0.457$
- $R^2 = 0.565$
- $R^2 = 0.562$
- $R^2 = 0.446$

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Fig. 2. Linear regression and coefficient of determination ($R^2$) between yield under non-stress and YPSI

$R^2 = 0.883$

Fig. 3. Linear regression and coefficient of determination ($R^2$) between yield under heat stress and YSSI

$R^2 = 0.951$
lower yields in productive environments but undergo less reduction under stress. The Class IV genotypes are neither resilient nor productive and possess lower values of YSSI and invariably negative values of YPSI. The reliability of using these modified indices can be further projected on the observation that the regression analysis revealed very high values of coefficient of determination (Fig. 2 and 3) for yield under non-stress and YPSI (0.883) and yield under heat stress and YSSI (0.951). This substantiates our hypothesis that new proposed indices can be used for better genotypic discrimination into various response classes.

In the present study a number of genotypes could be effectively classified into four stress response classes (Table 2). Class I included only three RILs viz., A-2648, A-2614 and A-186. Class II included 50 RILs. Similarly, Class III had 45 RILs including HUW-234. Interestingly the heat tolerant parent was most appropriately also grouped into this class. A large number of RILs (66) were grouped into Class IV. These class differentiations that become obvious using these new indices could be very useful from a plant breeding point of view. Invariably genotypes having both resilience and productive potential are rare and hard to identify as also revealed in the present study that out of 162 genotypes only three such potential genotypes were identified. Most of the genotypes fall in Class II, III and IV. As such, it is highly imperative to identify highly resilient (Class III) and productive genotypes (Class II) for planned crossing. Contrasting genotypes in terms of resilience or productivity could provide an understanding of the possible role of morphological, biochemical and physiological adjustments that a genotype puts in place under stress and non-stress environments, which requires detailed studies on morphological, biochemical and physiological parameters determining differential genotypic response to stress. The ability of genotypes to exhibit higher yield under stress can be either due to stress tolerance, or good yield performance under non-stress or a combination of both and may be a result of various underlying processes that can be elaborated by using various biochemical, physiological and biomass partitioning traits (Sofi et al., 2017b). In fact, Thiry et al. (2016) in their study outlined that genotypes belonging to different response classes may have comparable per se yields under stress but may have different yields under potential non-stress conditions. However, such genotypes may undergo smaller reductions in yield under stress resulting in higher resilience, which can be identified by a higher YSSI value. Therefore, the score indices can be effectively used for understanding differential genotypic plasticity to stress in terms of YPSI and YPSI values rather than per se yield values. An interesting observation from Table 2 shows that some RILs had comparable values of YSSI and YPSI indicating that these genotypes had similar capacities of productivity and resilience. Also, different genotypes share comparable values of YSSI indicating comparable resilience but almost opposite values of YPSI indicating a lower productivity potential. Similarly, different genotypes share comparable values of YPSI indicating comparable productivity potential but almost opposite values of YSSI indicating a lower resilience to stress.

Table 2. Classification of genotypes into four classes based on resilience, susceptibility and productivity

| Class | Genotypes *(YSSI and YPSI values)* |
|-------|------------------------------------|
| Class I (Resilient and Productive) | A-2648 (-7, 4.5), A-2614 (-6, 2.5), A-186 (5.5, 5) |
| Class II (Productive but not Resilient) | A-2596 (-6, 1.5), A-176 (4), A-2516 (-4, 4.5), A-2522 (-4, 4), A-190 (-3.5, 3.5), A-2510 (-3.5, 3.5), A-189 (-3.5, 3.5), A-2520 (-3, 3.5), A-2621 (-3, 3.5), A-191 (-2.5, 2.5), A-193 (-2.5, 2.5), A-2513 (-2.5, 2.5), A-2523 (-2.5, 2.5), A-165 (-2.5, 2.5), A-178 (-2.5, 2.5), A-2518 (-2.5, 2.5), A-2548 (-2.5, 2.5), A-2592 (-2.5, 2.5), A-2617 (-2.5, 2.5), A-2618 (-2.5, 2.5), A-2643 (-2.5, 2.5) |
| Class III (Resilient but not Productive) | HUW-234 (-8.5, 6.5), A-2554 (-7.5, 6.5), A-2608 (-7, 6.5), A-2612 (-7, 6.5), A-2509 (-6.5, 6.5), A-2537 (-6.5, 6.5), A-2547 (-6.5, 6.5), A-2566 (-6, 6.5), A-2566 (-6, 6.5), A-2572 (-6, 6.5), A-2599 (-6, 6.5), A-2625 (-6, 6.5), A-2644 (-6, 6.5), A-2647 (-6, 6.5), A-2512 (-5.5, 6.5), A-2529 (-5.5, 6.5), A-2536 (-5.5, 6.5), A-2556 (-5.5, 6.5), A-2563 (-5.5, 6.5), A-2642 (-5.5, 6.5), A-2645 (-5.5) |
| Class IV (Neither Resilient nor Productive) | A-2531 (-3.5, 2), A-209 (-3, 2.5), A-2574 (-2, 2.5), A-207 (-2, 2.5), A-163 (-2, 2.5), A-166 (-1, 4), A-173 (-1.5, 4), A-174 (-1.5, 4), A-2530 (-2, 3.5), A-2624 (-1, 2.5), A-167 (-1, 2.5), A-170 (-2, 2.5), A-172 (-2, 2.5), A-182 (-2, 2.5), A-195 (-3.5, 4), A-197 (-5.5, 4), A-198 (-2.5, 2.5), A-199 (-3.5, 4), A-207 (-3.5, 3), A-209 (-3, 2.5), A-2505 (-1.5, 4), A-2507 (-1.5, 4), A-2528 (-1, 3.5), A-2533 (-4.5, 4), A-2535 (-1, 3.5), A-2541 (-1, 4), A-2569 (-2.5, 4), A-2651 (-1, 3), A-2588 (-1.5, 4), A-2555 (-3.5, 3.5) |

* Values in parentheses are YSSI and YPSI values for class I and IV, YPSI values for class II and YSSI values for class III

Table 3. Mean CTD and seed growth rate of identified genotypes in various classes

| Class | CTD (°C) | Seed growth rate (mg/day) |
|-------|----------|--------------------------|
|       | Non-stress | Heat stress | Non-stress | Heat stress |
| I     | 5.30      | 9.30        | 67.90      | 67.72       |
| II    | 4.18      | 8.71        | 63.93      | 59.16       |
| III   | 3.84      | 9.13        | 47.70      | 69.95       |
| IV    | 5.37      | 9.05        | 46.92      | 58.28       |

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The pattern of variation of two physiological traits pertaining to stress tolerance viz. canopy temperature depression that defines the ability of a plant to manoeuvre evaporative demand and the seed growth rate that determines the speed of photosynthate remobilisation after flowering (Table 3). Both the traits have been found to be effective traits for screening genotypes under stress (Musharib Gull et al., 2018, Sofi et al., 2019). In class I (both productivity and resilience), CTD was higher viz., 5.30 and 9.30 degrees under non-stress and heat stress conditions respectively. In Class III (resilience but not productivity), CTD was lower under non-stress (3.84 °C) but comparatively higher under heat stress conditions (9.13 °C). In the other two classes, the differences could not be made out on the basis of CTD. In terms of seed growth rate (SGR), the values were comparable in Class I under non-stress and heat stress conditions (67.90 and 67.72 mg/day). In class II that bears productive genotypes SGR was higher under non-stress (63.93 mg/day) as compared to heat stress conditions (59.16 mg/day). In Class III that bears resilient genotypes, the mean SGR was higher under heat stress (65.95 mg/day) as compared to non-stress conditions (47.70 mg/day). In the case of poor genotypes (neither productive nor resilient), pooled under class IV, the corresponding values were lower than Class I under non-stress and heat stress conditions (46.92 and 58.28 mg/day). SGR is a phenology based index used to understand the stress response in terms of biomass partitioning in relation to phenological stages different growing conditions. Ramirez Vallejo and Kelly (1998) and Musharib Gull et al. (2018) used these indices in common bean and cowpea and found that the SGR was positively correlated with seeds per pod and seed number. Sofi et al. (2017) also used SGR in common beans and reported that SGR was positively correlated with grain yield under stress conditions. Similar observations were made in cauliflower for curd yield under heat stress in terms of relative sink strength (Kage et al., 2004). SGR is more important under stress as the relative growth rate is limited more by the utilization rather than the generation of photosynthates. The higher SGR values in resilient genotypes are also attributed to faster remobilisation on account of the reduced time taken to seed fill under stress, while as in productive genotypes, the genotypes maintain a higher SGR over a relatively extended seed fill period resulting in higher yields. The implication of SGR in seed yield is graphically presented in Fig. 4. Under heat stress, when the seed fill duration is contracted from GHI to DEF, the genotypes with higher SGR will produce higher yield (ACFD), while those with lower values of SGR, will have lower yields spanning rectangle (ABED). On a similar premise, under optimal conditions, when
seed fill duration is extended to GHI, the genotypes with higher SGR will produce higher yield (AG/G), while those with lower values of SGR, will have lower yields spanning rectangle (ABHG).

Plant breeders, by and large, focus on grain yield as a target trait for genetic enhancement for heat stress. Using yield per se or yield reductions under stress is invariably misleading and warrants the use of certain indices based on either simple mathematical relationships of stress and non-stress yields, relating yields under stress with phenology, using multiple regression where stress yields can be explained on the basis of various explanatory variables ranging from phenology to physiology based on their established influence on yield under stress. The proposed modified index as proposed by Thiry et al. (2016) have been validated in the present study using a RIL mapping population in wheat having diverse parents for various stress conditions in crops like wheat, common bean and cowpea. As such, it is proposed that these indices should be routinely used for identifying genotypes having productive potential as well as resilience to heat stress in wheat breeding programmes.

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