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A comparative ideotype, yield component and cultivation value analysis for spring wheat adaptation in Finland

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In this study Mixed structural covariance, Path and Cultivation Value analyses and the CERES-Wheat crop model were used to evaluate vegetation and yield component variation affecting yield potential between different high-latitude (> 60° N lat.) and mid-European (< 60° N lat.) spring wheat (*Triticum aestivum* L.) genotypes currently cultivated in southern Finland. Path modeling results from this study suggest that especially grains/ear, harvest index (HI) and maximum 1000 kernel weight were significant factors defining the highest yield potential. Mixed and Cultivation value modeling results suggest that when compared with genotypes introduced for cultivation before 1990s, modern spring wheat genotypes have a significantly higher yielding capacity, current high yielding mid-European genotypes even exceeding the 5 t ha^{-1} non-potential baseline yield level (y_b). Because of a forthcoming climate change, the new high yielding wheat genotypes have to adapt for elevated temperatures and atmospheric CO_2 growing conditions in northern latitudes. The optimized ideotype profiles derived from the generic high-latitude and mid-European genotypes are presented in the results. High-latitude and mid-European ideotype profiles with factors estimating the effects of concurrent elevated CO_2 and temperature levels with photoperiodical daylength effects can be utilized when designing future high yielding ideotypes adapted to future growing conditions. The CERES-Wheat ideotype modeling results imply, that with new high yielding mid-European ideotypes, the non-potential baseline yield (y_b) would be on average 5150 kg ha^{-1} level (+ 108 %) vs. new high-latitude ideotypes (y_b 4770 kg ha^{-1}, 100%) grown under the elevated $CO_{2(700ppm)}$×temperature $_{(+3°C)}$ growing conditions projected by the year 2100 climate change scenario in southern Finland.

Key words: ideotype profile, generic genotype, yield component, spring wheat, grain yield, climate change, cultivation value, adaptation strategy, CERES-Wheat model, Finland

Introduction

Donald (1968) defined the concept of a spring wheat ideotype as the optimal wheat genotype with a maximum potential for grain yield production under optimal growing conditions. A crop ideotype in cereal breeding can be described as a plant model system, which is expected to yield greater quantity or quality of grain, oil or other useful product when developed as a cultivar.

In agronomic studies the Donald's original ideotype concept has been reviewed by Sedgley (1991) and by Reynolds et al. (1994) for yield potential estimations in modern wheat cultivars. According to Sedgley (1991) Donald's ideotype concept explains both the optimal resource allocation and translocation of assimilates maximizing crop yield and the relationships between yield, harvest index (HI) and morphological characters in monoculture and variety mixture growing environments. Later on Donald and Hamblin (1983) expanded the Donald's ideotype concept with additional climatic, edaphic, disease, pest and stress ideotype concepts. Sedgley (1991) evaluated the two antagonist components in Donald's ideotype, the optimal communal ideotype for cereals maximizing yield potential with uniculm growth habit without side tillers, short stem and narrow erect leaves and the adversary competitive ideotype with freely tillering and tall stature with large leaves.

The Donald's ideotype concept have been widely studied and reviewed for a variety of crops and traits, e.g. in plant canopy and leaf architecture modeling (Carvalho et al. 1978), in ideotype-based breeding strategies for wheat with genotype×environment (G×E) covariances (Sedgley 1991, de la Vega et al. 2002), in crop modeling studies (Boote et al. 2001) and in phenotypic plasticity studies for wheat yields (Sadras et al. 2009). According to

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Sadras et al. (2009) high yield and low plasticity for yield were coupled with early anthesis, long anthesis duration and low plasticity of post-anthesis development with wheat genotypes grown in Mexico. In Finland Peltonen et al. (1993) applied the Cultivation value model (Weizensorten und Backqualität 1990) to estimate the cultivation scoring and ranking values with adaptation plasticity, cultivation certainty and baking quality components for current high yielding wheat genotypes. In this study the Cultivation value model was evaluated for high-latitude (HiL) and mid-European (MidE) ideotype profiles (ItPrf).

The benefits of applying both statistical and dynamic, mechanistic crop models for Donald's ideotype evaluation have been reviewed by Boote et al. (2001) and de la Vega et al. (2002). Crop models used in plant breeding should be both dynamic varying over edaphic and weather conditions and mechanistic simulating physiological processes like phenological development, source-sink relationships and translocation of assimilates. According to Boote et al. (2001) crop models simulate genetic improvement and variability within a species by evaluating intracultivar variation and how crop models can be used to hypothesize ideotypes for specific growing environments. In this study the CERES-Wheat/DSSAT dynamic crop model (Ritchie & Otter 1985, Jones et al. 2003) was used to define genetic coefficients for MidE (Laurila 1995) and HiL (Laurila 2001) ideotype profiles. The genetic coefficients in the CERES-Wheat model control both wheat phenological development and grain yield components.

Statistical structural and clustering analysis and modeling have been extensively applied in biometrics and biometrical analysis to detect interacting and indirect covariances, trends and underlying variables in the experimental data. The techniques commonly used are Mixed Structural Covariance Analysis (Littel et al. 1996), Path coefficient analysis (Wright 1923) and Principal Component Analysis (PCA, de la Vega et al. 2002, Reynolds et al. 2007).

In Finland Öfversten and Nikander (1996) applied the Mixed Covariance Analysis for the analysis of current high-latitude spring wheat genotypes. Peltonen-Sainio et al. (2009) studied spring wheat yield trends and sustainability in Finland using the MTT Agrifood Research Finland 1970−2005 official variety trial data. The Mixed structural covariance technique was used to divide the yield trends in variety trials into two intracultivar G×E covariance components: genetic improvements and environmental changes. According to Peltonen-Sainio et al. (2009) the yield trends of future wheat genotypes will constantly increase during global climate change (IPCC 2007) because of the increasing demand for food and biofuel production. Cereal theoretical maximum yield capacity is limited by environmental and vegetation stresses during growing season (Passioura 2006, Rajala et al. 2009). These stress factors result in reduced non-potential baseline yield levels (y_b, kg ha^{-1}) for cereals in actual non-optimal field growing conditions. In this study the Mixed Analysis was applied for evaluating the factors affecting non-potential baseline yield levels (y_b) between HiL and MidE wheat genotypes.

The Path coefficient analysis, using standardized regression coefficients, has been widely applied for structural analysis in population genetics to detect underlying covariance and indirect, interacting factors (Dewey and Lu 1959, Li 1974). In this study Path coefficient analysis was applied to identify significant direct and indirect effect factors affecting yield potential with HiL ideotypes.

In Finland, spring wheat production in high-latitude northern agriculture regions is limited by a short growing season, which reduces the light intensity and temperature available for crop growth (Saarikko 1999). Kontturi (1979) reported a photoperiodical threshold daylength of 18 hours for high-latitude genotypes adapted to Finnish long day growing conditions. Daylengths below the threshold delay vegetative phase from sowing to heading. In generative phase from heading to full maturity, the thermal time controls the phenological development.

The ideotype analysis for Finnish growing conditions with G×E interactions has been reviewed by Peltonen-Sainio (1992) and Mäkelä et al. (1996) for spring wheat, barley and oat genotypes grown under long day growing conditions. Aula and Talvitie (1995) studied yield production with high latitude rye (*Secale cereale* L.) and wheat genotypes using organic and conventional cultivation practices.

Currently only few crop modeling results are available for the identification of the most important factors affecting wheat non-potential baseline yield levels currently and in the 2050−2100 period with elevated temperature and atmospheric CO_2 levels in Finland (Saarikko 1999, Laurila 1995,2001). In Finland the FINSKEN climate change scenario (Saarikko et al. 1996, Saarikko 1999, Carter 2004) estimated that atmospheric CO_2 concentration with seasonal variation will increase from the current mean ambient 377 ppm to 523 ppm and the mean temperature will increase by 2.4 °C by the year 2050 and respectively to 733 ppm and by +4.4 °C by the end of 2100.

Previous Finnish crop simulation results (Laurila 1995, 2001), field and Open Top Chamber (OTC) crop physiological experimental results (Hakala 1998, Hakala et al. 2005) for a high-latitude spring wheat cultivar (cv. 'Polkka') indicated, that the concurrent elevated atmospheric CO_2 concentration (700 ppm) and elevated diurnal temperature (+ 3 °C) will increase the yield potential of the HiL wheat genotypes by 1−6% (by 9−13% for a mid-European cv. 'Nandu') by 2100 in southern Finland. The sole elevated temperature effect had a decreasing effect on wheat yield potential by accelerating the cereal phenological development especially in the generative phase (Hakala 1998, Hakala et al. 2005).

The overall objective of the present study was the identification and evaluation of high-latitude (HiL, growing latitude > 60° N) and mid-European (MidE, < 60° N) ideotype profiles ($ItPrf_{HiL,MidE}$) adapted for future growing conditions with elevated CO_2 and temperature levels in southern Finland by deriving generic HiL and MidE spring wheat genotypes validated in this modeling study.

The specific objectives of the present study consisted of following modeling and analysis procedures: (i) evaluating factors affecting non-potential baseline grain yield levels (y_b) between HiL and MidE springs wheat genotypes in soil type, cultivation practices and decade of introduction to cultivation categories (ii) identifying the most important vegetation parameters and yield components affecting the yield capacity of HiL and MidE wheat ideotypes, (iii) evaluating the genotype×environmental (G×E) covariances (Eq. 1) and source-sink interactions affecting grain yield potential between high yielding wheat ideotypes, and finally (iv) assessing implications for future adaptation strategies in southern Finland using high yielding spring wheat ideotypes.

Materials and methods

Data sources

Table 1 illustrates different data sources applied in this study with different modeling phases (I−IV, Fig. 1), experimental years, Mixed structural categories for HiL and MidE genotypes (Table 2) and references for datasets. The definitions and abbreviations applied in this study are presented in Table 10 (Appendix 1). During modeling process different datasets were combined and consolidated for different analyses (Fig. 1).

Dataset I (Table 1) provided the primary field experimental data for HiL and MidE spring wheat modeling methods applied in this study. Dataset I was extracted from the 1978−2007 MTT Agricultural Research Centre Official variety trial data, containing yield data for spring wheat genotypes currently cultivated in Finland (Järvi et al. 1997, Kangas et al. 2006, 2008).

Dataset II provided averaged yield estimates for MidE wheat genotypes using the European wheat genotype database (ECP/GR). Dataset III provided the baseline yield (y_b kg ha^{-1}) estimates for HiL and MidE spring wheat cultivars using the Finnish agricultural remote sensing large area results in 1996−2006 (Laurila et al. 2010a, 2010b). Experimental sites were located in southern Finland and in Etelä-Pohjanmaa Agricultural Advisory Centre in growing zones I−IV. Baseline yield estimates (y_b) for spring what genotypes were compared with averaged MTT official variety trial results and with annual Ministry of Agriculture Finland stratum sampling estimates for crop inventory. With datasets IV and V, crop physiological experiments and simulation studies were used to evaluate the effects of elevated atmospheric CO_2 and elevated temperature levels on yield potential and phenological development of HiL and MidE spring wheat genotypes. The SILMU I (The Finnish Research Program for Climate Change, 1992−1994) data was extracted from Open Top Chamber experiments (Hakala 1998, Hakala et al. 1999, Laurila 2001). The SILMU II data was extracted from greenhouse and pot experiments (Saarikko et al. 1996, Saarikko 1999). Dataset VI provided the averaged yield levels for rye and HiL spring wheat genotypes with organic and ecological cultivation practices (1989−1993) from the MTT Satakunta Research station (Aula and Talvitie 1995). With dataset VII, the HiL and MidE spring wheat data from the Pöytyä and Helsinki University experimental sites was used to evaluate the Cultivation value model (Peltonen 2010). Datasets VIII (Rajala et al. 2009) and IX (unpublished data) provided detailed morphological, yield quality and yield component data for HiL spring wheat genotypes.

Table 1. Spring wheat data sources and field experiments.

Dataset (Modeling phase, Fig. 1)	Dataset	Experiment years, Mixed categories[3]	References
I,(I)	Spring wheat official variety trial data (MTT Agrifood Research Finland), Estimation of Cultivation value (C$_{Val}$)	1978-2007, (HiL/MidE) Old$_{,70,80}$	Järvi et al. 1997, Kangas et al. 2006, 2008, Peltonen 2010
II, (I)	The European Wheat Database (European Cooperative Programme for Crop Genetic Resources Networks ECP/GR	1978-2010, (HiL/MidE) Old$_{,70,80}$	http://genbank.vurv.cz/ewdb/
III ,(I)	Finnish agricultural remote sensing field experiments 1996-2006 with actual field condition measurements btw. MTT official variety trials vs. Ministry of Agriculture Finland stratum estimates	1996-2006, (HiL/MidE) Old$_{80,}$ New$_{90}$	Laurila et al. 2010a, 2010b
IV,(I)	SILMU I Experimental data from Open Top Chamber experiments with elevated CO$_2$ and temperature levels[2]	1992-1994, (HiL/MidE) Old$_{80,}$ New$_{90}$	Hakala 1998, Hakala et al. 1999, 2005, Laurila 1995, 2001
V,(I)	SILMU II Experimental data with field, greenhouse and pot experiments.	1994-1996 (HiL/MidE) Old$_{80,}$ New$_{90}$	Saarikko et al. 1996, Saarikko 1999. Data prov. by Dr. R. Saarikko
VI ,(I)	The rye and spring wheat experiments for organic and ecological cultivation, MTT Agrifood Res. Finland (Ylistaro, Satakunta)	1989-1993, (HiL) Old$_{,70,80,}$New$_{90}$	Aula and Talvitie 1995
VII ,(II)	Cultivation value estimation dataset	2009-2010, (HiL/MidE) Old$_{80,}$ New$_{90}$	Peltonen 2010, Dr. Jari Peltonen, Helsinki Univ. Exp. site and Pöytyä Exp. Site
VIII ,(III)	Spring wheat yield component and quality factor data.	1996-1998, (HiL) Old$_{,70,80}$ New$_{90}$	Rajala et al. 2009. Data provided by Dr. Ari Rajala (MTT Agrifood Res. Finland)
IX ,(III)	Spring wheat data containing yield component and morphological characteristics for 20 spring wheat genotypes (Helsinki Univ., Dept of Crop Husbandry)	1988, HiL$_{Old,70,80}$	Unpub. data provided by Dr. R. Karjalainen and Ms. Sci. T. Kangasmäki (MTT Agrifood Res. Finland).

[1] Modeling phases (I-IV) are described in Fig. 1. [2] The Finnish Program for Climate Change (SILMU 1992-1996, Kuusisto et al. 1996). [3] Mixed categories in Table 2.

Modeling process and system analysis

The detailed modeling process and system analysis (Ritchey 1996, IIASA 2010) applied in this study, is illustrated in Figure 1 describing the analysis methodology in phases I−IV, each phase using different experimental datasets (I−IX, Table 1). The detailed modeling process consisted of following phases.

1. In phase Ia1 previous crop modeling results (Laurila 1995, Laurila 2001) with the CERES-Wheat/DSSAT dynamic crop model (Ritchie & Otter 1985, Jones et al. 2003) were used to calibrate and define the genetic coefficients (PHINT, P1V, P1D, P5, G1,G2,G3) for generic HiL (using cv. 'Polkka') and MidE (using cv. 'Nandu') genotypes using the MTT Agrifood Research Finland Official Variety Trial dataset 1978−2007 (Dataset I, Table 1). Genetic coefficients for generic spring wheat genotypes were used in defining the future HiL and MidE ideotype profiles. The CERES-Wheat genetic coefficients controlling spring wheat phenological development (PHINT with leaf appearance rate and phyllochron interval, P1V affecting vernalization, P1D affecting photoperiodism and P5 affecting grain filling duration) and yield components (G1 defining the grains per ear component, G2 defining the 1000 seed weight and G3 defining spike number with lateral tiller production) are given in Table 10 (Appendix 1).

2. In phases Ia2-Ic the HiL vs. MidE structural contrast categories for spring wheat genotypes were defined and analyzed by using the combined I−VI dataset (1978−2010, Table 2).

3. In phase Id the latitudal contrasts (HiL > 60° N lat. vs. MidE genotypes < 60° N lat.) with corresponding baseline yield estimates (y_b, kg ha^{-1}) were estimated by using datasets I−VI (Tables 3-5).

4. In phase Ie the decade of introduction to cultivation contrast (Old_{70} vs. Old_{80} vs. New_{90}) with baseline yield estimates (y_b) were estimated by using datasets I−VI (Tables 3–5).

5. In phase If the cultivation practices contrast (conventional vs. organic cultivation) with baseline yield estimates (y_b) were estimated (dataset VI, Tables 3, 4).

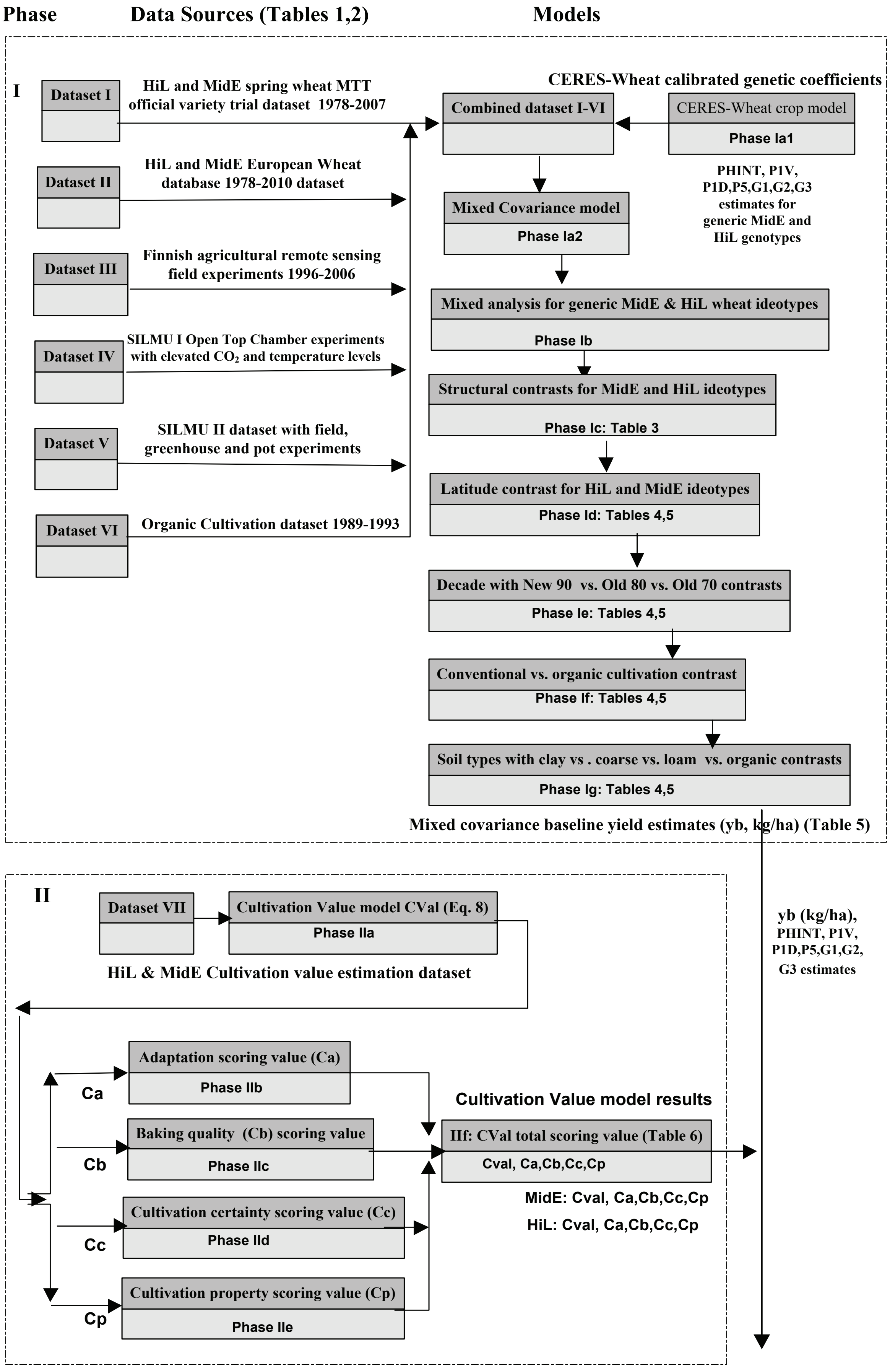
6. In phase Ig the soil type contrast (coarse type soils vs. fine type soils vs. organic type soils) with baseline yield estimates (y_b) were estimated (datasets I−VI, Tables 3, 4).

7. In phases IIa−IIf the Cultivation Value model (Weizensorten und Backqualität 1990, Peltonen et al. 1993) using dataset VII was used to estimate the total cultivation scoring value profiles (C_{ValTot}) for HiL and MidE high yielding generic wheat genotypes in Finland (Table 5).

8. In phases IIIa−IIIb Principal Component Analysis (PCA) and correlation analyses were used with datasets VIII−IX to identify significant PCA factor loadings and correlations for vegetation parameters (p_v) and yield components (p_y) with HiL ideotypes (Tables 6−8).

9. Phases IIIc−IIIe yielded, using Path coefficient analysis (Wright 1923, Dewey and Lu 1959, Li 1974) and datasets VIII−IX, significant direct and indirect effect factors affecting yield potential with HiL ideotypes. In Path-models (I−IV, Table 6) significant direct effect factors were expressed as Path-coefficients for vegetation parameters ($p_{v,}$ Table 7) and yield components ($p_{y,}$ Table 8) respectively. Correlation coefficients were used to measure indirect effects. Coefficient of determination (R^2, Eq. 7) and error residual factors (U, Eq. 6) were used to evaluate Path coefficient models I−IV.

10. In phase IV, based on results from previous phases (I−III), high yielding ideotype profiles ($ItPrf_{HiL(New90)}$, $ItPrf_{MidE(New90)}$, Eq. 10) for generic HiL and MidE genotypes adapted for future growing conditions in southern Finland were calibrated and validated.


Phase
Data Sources (Tables 1,2)
Models
I
Dataset I
HiL and MidE spring wheat MTT official variety trial dataset 1978-2007
Dataset II
HiL and MidE European Wheat database 1978-2010 dataset
Dataset III
Finnish agricultural remote sensing field experiments 1996-2006
Dataset IV
SILMU I Open Top Chamber experiments with elevated CO₂ and temperature levels
Dataset V
SILMU II dataset with field, greenhouse and pot experiments
Dataset VI
Organic Cultivation dataset 1989-1993
CERES-Wheat calibrated genetic coefficients
Combined dataset I-VI
CERES-Wheat crop model
Phase Ia1
PHINT, P1V, P1D,P5,G1,G2,G3 estimates for generic MidE and HiL genotypes
Mixed Covariance model
Phase Ia2
Mixed analysis for generic MidE & HiL wheat ideotypes
Phase Ib
Structural contrasts for MidE and HiL ideotypes
Phase Ic: Table 3
Latitude contrast for HiL and MidE ideotypes
Phase Id: Tables 4,5
Decade with New 90 vs. Old 80 vs. Old 70 contrasts
Phase Ie: Tables 4,5
Conventional vs. organic cultivation contrast
Phase If: Tables 4,5
Soil types with clay vs . coarse vs. loam vs. organic contrasts
Phase Ig: Tables 4,5
Mixed covariance baseline yield estimates (yb, kg/ha) (Table 5)
II
Dataset VII
Cultivation Value model CVal (Eq. 8)
Phase IIa
HiL & MidE Cultivation value estimation dataset
Adaptation scoring value (Ca)
Phase IIb
Ca
Baking quality (Cb) scoring value
Phase IIc
Cb
Cultivation certainty scoring value (Cc)
Phase IId
Cc
Cultivation property scoring value (Cp)
Phase IIe
Cp
Cultivation Value model results
IIf: CVal total scoring value (Table 6)
Cval, Ca,Cb,Cc,Cp
MidE: Cval, Ca,Cb,Cc,Cp
HiL: Cval, Ca,Cb,Cc,Cp
yb (kg/ha), PHINT, P1V, P1D,P5,G1,G2, G3 estimates

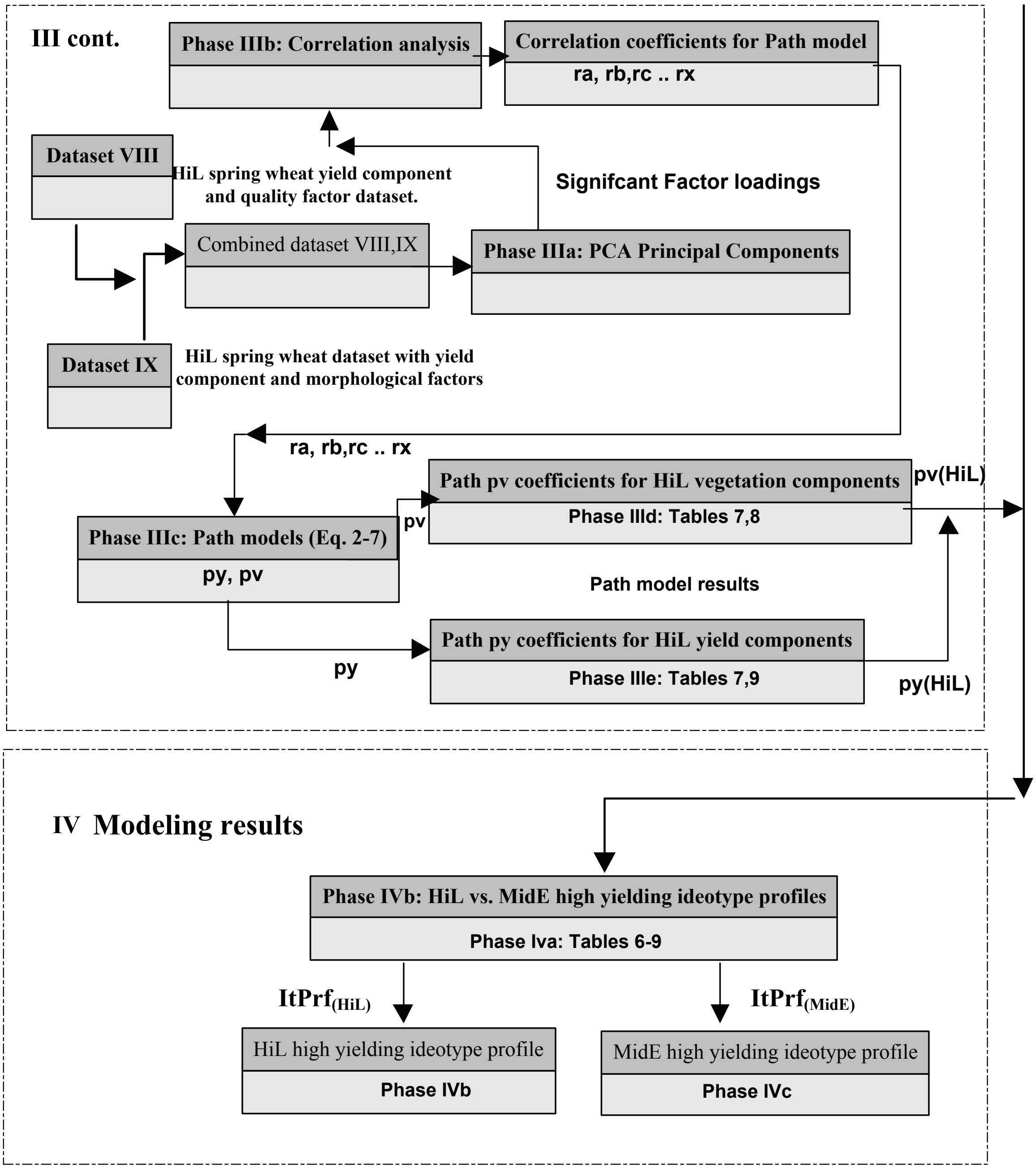


Fig. 1. Modeling process diagram with phases I-IV for identifying generic ItPrf(HiL) and ItPrf(MidE) ideotype profiles, data sources are given in Table 1 (Ritchey 1996, IIASA 2010).

Soil type variation in the experimental sites

The detailed soil classifications in experimental areas in southern Finland (experimental datasets I–IX, Table 1) with corresponding growing zones (I–IV) is reviewed by Laurila et al. (2010a,b). The Ylistaro, Lapua, Ilmajoki and Seinäjoki experimental sites were located near the Gulf of Bothnia on sandy clay type soils. Respectively Helsinki, Porvoo and Kirkkonummi experimental sites were located close to the Baltic Sea. Jokioinen and Mellilä sites were located mainly on clay type soils. Currently a growing zone classification of four growing zones (I–IV) is applied for the high-latitude genotypes (HiL) currently cultivated in southern Finland: Zone 1 - Southern and SW-Finland (Lat. < 61° N), Zone 2 - Southern Finland (Lat: 61° N < 62° N), Zone 3 - Southern Finland (Lat: < 62° N), Zones 3–4, Northern Finland (Lat: > 62° N). The zonal classification is based on Effective Temperature Sum (ETS) expressed as cumulative degree-days [dd] with a threshold temperature (Tb) of 5 °C (Kontturi 1979, Saarikko 1999).

Statistical analysis

SAS™ statistical software (SAS, 1990) was used for Mixed Structural Covariance analysis (Phase I, Fig. 1), Cultivation value (Cval) model (Phase II), Principal component (PCA), correlation and Path coefficient analysis (Phase III, SAS REG and GLM procedures). Least squares (LSQ) algorithm was applied in the linear model fitting with SAS REG and GLM (General Linear Model) procedures. Mixed, Cval and Path models were used to detect spring wheat inter- and intracultivar G×E covariances and underlying variables interacting with wheat grain yield potential (Eq. 1, Falconer and Mackay 1996, Boote et al. 2001).

$$\mathrm{V}p = \mathrm{V}g + \mathrm{V}e + 2Cov(ge) \tag{1}$$

where V_p – phenotype variation, V_g - genotype variation, V_e – environmental variation,
$Cov_{(ge)}$ - genotype G×E environmental covariance variation in broad sense

According to Falconer and Mackay (1996) the phenotypic variance (V_p) of a plant genotype can be divided into genetic (V_g) and environmental variance (V_g). The ratio V_g / V_p is defined as a degree of genetic determination or heritability in broad sense (Eq.1). The environmental sensitivity of a genotype, measuring the interaction between genetic and environmental variances can be estimated by including a covariance component $Cov_{(ge)}$.

The SAS Univariate procedure was used with the experimental data (Table 1) to test the normal distribution of both the dependent (non-potential grain yield, y_b kg ha^{-1}) and independent yield and vegetation components by using Kolmogorov and Shapiro-Wilk test statistics (data not shown).

Mixed Structural Covariance analysis

Mixed structural covariance analysis using SAS Mixed procedure (Littel et al. 1996) was used in this study (Phase I, Fig. 1) to model ideotype baseline yield levels (y_b, kg ha^{-1}) for different HiL and MidE wheat genotypes. The baseline grain yield (y_b) was used as a response variable in the Mixed-model. Datasets I-VI (Table 1) containing long time series (1978-2010) were used in Mixed analysis to estimate baseline yield estimates (y_b) on (i) structural contrast category levels (Tables 2,4) and (ii) on genotype level (Tables 3,5).

Table 2. Structural contrast categories of wheat genotypes (Mixed-model, Littel et al. 1996)

Category	Genotype structural contrast categories (Mixed-model)
i	Latitude structural contrasts: HiL (> 60° N lat.) vs. MidE genotypes (< 60° N lat., Tables 3,4)
ii	Decade of introduction to cultivation structural contrasts: $(\mathrm{HiL/MidE})_{\mathrm{New90}}$ vs. $(\mathrm{HiL/MidE})_{\mathrm{Old80}}$ vs. $(\mathrm{HiL/MidE})_{\mathrm{Old70}}$ (Tables 3,4)
iii	Cultivation practices structural contrasts: conventional vs. organic practices (including ecological cultivation practices applied in Finland, Table 4)
iv	Soil structural contrasts: coarse type soils vs. fine type soils vs. vs. organic type soils (Table 4)

In Table 2, Mixed structural contrast categories applied in this study for wheat genotypes are displayed: (i) the latitude structural contrast comparison between HiL vs. MidE latitudes, (ii) the decade of introduction to cultivation contrast between genotypes introduced for cultivation before 1970 $(\mathrm{HiL/MidE})_{\mathrm{Old70}}$ vs. 1980 $(\mathrm{HiL/MidE})_{\mathrm{Old80}}$ vs. after 1990 $(\mathrm{HiL/MidE})_{\mathrm{New90}}$, (iii) cultivation practices contrast between conventional vs. organic cultivation (including ecological cultivation practices applied in Finland), (iv) the different soil type contrast comparison (coarse, fine and organic soil types).

The spring wheat genotypes evaluated in the Mixed-model analysis are displayed in Table 3.

High-latitude genotypes from Finland, Sweden and Norway and mid-European genotypes from Netherlands, Germany, UK, Tscheck and Serbia were classified into cultivation contrast categories based on cultivation latitude (HiL vs. MidE) and decade of introduction to cultivation (1970,1980,1990).

Table 3. Spring wheat genotypes in (I) latitude and (II) decade of introduction to cultivation contrast categories (Littel et al. 1996).[1]

Mixed Structural Contrast category		Genotype, origin, breeder reference, year of introduction to cultivation
I Latitude	II Decade	
High-latitude genotypes (> 60° N lat.)	$\mathrm{HiL}_{\mathrm{Old70}}$	Finland: Apu (Ref.), Heta, Kruunu ($\mathrm{C}_{\mathrm{val}}$ Ref.), Ruso, Sebastian, Taava, Tähti, Tapio, Ulla Sweden: Drabant (Ref.)
	$\mathrm{HiL}_{\mathrm{Old80}}$	Finland: Aino (Ref. Bor[3]), Luja Sweden: Polkka (Ref., SW), Dragon, Kadett, Norway: Reno (Ref. Norsk Kornforedling 1987), Runar, Norrona
	$\mathrm{HiL}_{\mathrm{New90}}$	Finland: Mahti (Ref., Bor[3], 1994), Anniina (Boreal), Kadrilj, Kruunu (Bor[3]), Laari, Manu, Marble (Boreal), Wellamo (Boreal) Norway: Bastian (Ref.) Sweden: Tjalve (Ref., SW 1993), Zebra (SW), Bjarne (SW), Landjet, Sport, Vinjett, Satu
Mid-European Genotypes (< 60° N lat.)	$\mathrm{MidE}_{\mathrm{Old80}}$	Netherlands: Matador (Ref., Dept. of Plant Brd. Agric. Univ., Wageningen), Pasteur (Zelder B.V)
	$\mathrm{MidE}_{\mathrm{New90}}$	Germany: Nandu (Ref.) [2], Amaretto, Attis, Epos, Mieka, Monsun, Munk, Picolo(Saaten Union), Triso, Sella, Trappe (DEU060, Bor[3]) UK: Azurite (www.hgca.com) Tscheck Republic.: Quarna (Ref.), Bombona Netherlands: Jondolar (Ref.) Serbia: Marina (Ref.)

[1] Ref. – Reference genotype/cultivar in the Mixed analysis (Table 10). Countries: Nl.- Netherlands, [2] Saatzuchtwirtschaft F. von Lochow-Petkus GmbH [3] Bor – Boreal plant breeding, Finland, SW – Svalöf-Weibull

Correlation, PCA and Path analyses for High-latitude (HiL) vegetation and yield components

After the Mixed covariance and Cultivation value analysis, the combined VIII−IX dataset was analyzed with correlation, PCA (Principal Component Analysis) and Path coefficient analysis (phase IIIa, Fig. 1) to identify significant vegetation (p_v) and yield (p_y) components affecting $\mathrm{HiL}_{\mathrm{Old70}}$, $\mathrm{HiL}_{\mathrm{Old80}}$ and $\mathrm{HiL}_{\mathrm{New90}}$ genotype yield potential (Tables 2,3). Correlation coefficients were used in Path-models (I−IV, Eq. 5) to construct standardized Path regression equations (Table 6).

Path analysis

The Path coefficient theory was originally presented by Wright (1923) and later revised for wheat seed production analysis by Dewey and Lu (1959). Li (1974) applied Path coefficient analysis for population genetics and Falconer & Mackay (1996) for quantitative genetics (Eq. 1). Later on, Path coefficient analysis was applied in yield component analysis for spring wheat mutants (Siddiqui et al. 1980) and for spring wheat genotypes (Reynolds et al. 2007).

In this study, Path coefficient analysis was calculated according to methodology presented by Dewey and Lu (1959) and Li (1974). Path-coefficients, which are standardized regression-coefficients, can be derived from general linear regression equation (Eq. 2). Path-coefficients were calculated using the SAS stepwise regression (REG) and GLM (General Linear Model) procedures (SAS 1990).

$$\mathrm{Y} = \mathrm{b0} + \mathrm{b1} * \mathrm{A} + \mathrm{b2} * \mathrm{B} + ..\mathrm{bx} * \mathrm{X} + \varepsilon \tag{2}$$

where Y = dependent variable, (y_b, baseline grain yield, kg ha^{-1}, 15% moisture content), b_0 = model intercept, $b_{1,}$ b_2 b_x = regression coefficients for independent variables A, B and X, ε= error residual variation (=0)

Equation 2 can be standardized by using standard deviations (s_y, s_a, s_b, s_x) for dependent (Y) and independent variables (A, B..X) (Eq. 3).

$$\mathrm{Y} = \mathrm{b0} + [\mathrm{b1} * (\mathrm{Sa}/\mathrm{Sy})) * \mathrm{A}] + [\mathrm{b2} * (\mathrm{Sb}/\mathrm{Sy})) * \mathrm{B}] + \ldots [\mathrm{bx} * (\mathrm{Sx}/\mathrm{Sy})) * \mathrm{X} \tag{3}$$

where s_y, s_a, s_b, s_x = standard deviations (SD) for variables Y, A, B, X

Equation 3 can be simplified into Equation 4 using Path-coefficients, which measure the direct effects on dependent variable (Y).

$$\mathrm{Y} = \mathrm{b0} + \mathrm{pa} * \mathrm{A} + \mathrm{pb} * \mathrm{B} + ..\mathrm{px} * \mathrm{X} \tag{4}$$

where $p_{a,}$ $p_{b,}$ $p_{x=}$ Path-coefficients, $p_a = b_1*(S_a/S_y)$, $p_b = b_1*(S_b/S_y)$, $p_{x=}$ $b_x*(S_x/S_y)$

The standardized Path-model (Eq. 5) can be derived from Equation 4 by adding correlation coefficients (r_i) between independent and dependent variables (Phase III, Fig. 1). Correlation coefficients measure indirect effects on dependent variable (Y). The standardized Path-model equations for high-latitude ideotypes are presented in Table 6.

$$\mathrm{Y} = \mathrm{pa} * \mathrm{ra} * \mathrm{A} + \mathrm{pb} * \mathrm{rb} * \mathrm{B}..\mathrm{pc} * \mathrm{rc} * \mathrm{X} \tag{5}$$

where r_a, r_b, r_x = correlation coefficients for dependent variables A, B, X

The residual-factor (U) estimates the unexplained variance estimated by the Path model (Eq. 6). U-factor is calculated by summing Path-coefficients (p_i) and subtracting the sum from 1 according to Equation 6. The U-factors for HiL genotypes are presented in Table 6.

$$\mathrm{U} = 1 - \sum_{(\mathrm{i}=1)}^{\mathrm{k}} (\mathrm{pi}) \tag{6}$$

where U= residual factor, ${}^{k}\Sigma_{(b=1)}$ (pi) = Sum of Path-coefficients p_i , index i =1..k.

The total variance, explained by the Path-model, can be measured as R^2(Y)-values (R-square, coefficient of determination) for the dependent variable. R^2 values (Eq. 7) can be derived by summing the multiplication product of correlation and Path-coefficients for independent variables (A,B..X). R^2 estimates for HiL genotypes are presented in Table 6.

$$\mathrm{R}^2(\mathrm{Y}) = \sum_{(\mathrm{i}=1)}^{\mathrm{n}} [(\mathrm{pa} * \mathrm{ra}) + (\mathrm{pb} * \mathrm{rb}) \ldots (\mathrm{px} * \mathrm{rx})] \tag{7}$$

where R_i=correlation coefficient, p_i=path-coefficient, A, B..X=independent variables, index i =1..n

Wheat Cultivation value model

A regression based German ranking and scoring Cultivation value model (Weizensorten und Backqualität 1990), previously applied for Finnish spring wheat varieties (Peltonen et al. 1993, Peltonen 2010) was applied in this study (Phase II, Fig. 1) to estimate the cultivation values of spring wheat genotypes currently cultivated in southern Finland in growing zones I–III (Dataset VII, Table 1). The cultivation value was expressed as a total scoring value ($C_{Val\text{-}Tot}$) in current highest yielding wheat genotypes, which are cultivated in growing zones I–III in southern Finland (Eq. 8). Cv. 'Kruunu' ($\mathrm{HiL}_{\mathrm{Old70}}$) was used as a control and reference genotype (Ref.) in the model.

$$CValTot = Ca + Cc + Cp + Cb \tag{8}$$

where C_{ValTot} – Cultivation total scoring value of a genotype in growing zones I–III, C_a – Adaptation plasticity scoring value inside cultivation zone (I–III), C_c – Cultivation certainty scoring value, C_p – Cultivation property scoring value, C_b – Baking quality scoring value.

In the Cultivation value model, a three class classification was applied for wheat genotypes (i) Elite wheat class, (ii) Quality wheat class and (iii) Other wheat class (Peltonen et al. 1993, Table 5). The genotypes used in the scoring model were 'Quarna' ($\mathrm{MidE}_{\mathrm{New90}}$), 'Amaretto' ($\mathrm{MidE}_{\mathrm{New90}}$), 'Epos' ($\mathrm{MidE}_{\mathrm{New90}}$), 'Wellamo' ($\mathrm{HiL}_{\mathrm{New90}}$), 'Zebra' ($\mathrm{HiL}_{\mathrm{New90}}$), 'Marble' ($\mathrm{HiL}_{\mathrm{New90}}$) from the Elite wheat class, 'Kruunu' ($\mathrm{HiL}_{\mathrm{Old70}}$), 'Anniina' ($\mathrm{HiL}_{\mathrm{New90}}$) and 'Bjarne' in the Quality wheat class and 'Trappe' ($\mathrm{MidE}_{\mathrm{New90}}$) in the Other wheat class (Table 1, Peltonen 2010). The corresponding genotypes in latitudal and decade of introduction to cultivation contrasts are presented in Table 3.

The adaptation plasticity scoring value (C_a) in growing zones I–III consisted of growing days (d) and relative yield in growing zones I-III (cv. 'Kruunu' as a control = 100). The cultivation certainty scoring value (C_c) consisted of grain yield (kg ha^{-1}) and relative yield expressed as a three category classification: (i) the low final grain yield (median 4 t ha^{-1}), (ii) the medium final grain yield (median 5 t ha^{-1}), and (iii) the high final grain yield (median 6 t ha^{-1}). The cultivation property scoring value (C_p) consisted of grain yield accumulation/growing day ratio (kg DM d^{-1}), the nitrogen amount in grains (N kg ha^{-1}), denoting the efficiency of a genotype to utilize nitrogen fertilization, the 1000 kernel weight (g), the grain protein content (%) and the falling number reduction (s) with late harvest. The baking quality scoring value (C_b) consisted of the flour volume yield (%), the flour water retention capacity (%), the falling number (s), the Farinograph dough water absorption (%) and the bread loaf volume (ml).

CERES-Wheat dynamic crop model with calibrated genetic coefficients

The calibrated CERES-Wheat genetic coefficients (Ritchie & Otter 1985, Jones et al. 2003) were used in defining the optimized ideotype profiles ($\text{ItPrf}_{\text{HiL,New90}}$, $\text{ItPrf}_{\text{MidE,New90}}$) for future generic HiL (using cv. 'Polkka' as a reference cultivar, ref.) and MidE (cv. 'Nandu', ref.) genotypes in the New_{90} Mixed contrast category (Laurila 1995, 2001). The CERES-Wheat genetic coefficients controlling both spring wheat phenological development (PHINT with leaf appearance rate and phyllochron interval [dd] , P1V affecting vernalization, P1D affecting photoperiodism and P5 affecting grain filling duration) and yield components (G1 - the grains per ear component, G2 - the 1000 seed weight and G3 - spike number with lateral tiller production) are given in Table 10.

The RMSD (Root Mean Square Difference, Eq. 9) algorithm was used to calibrate both the CERES-Wheat genetic coefficients controlling spring wheat phenological development and yield components for generic HiL and MidE genotypes in Finland (Laurila 1995, Laurila 2001). The RMSD minimized the difference (RMSD_{YLD}, t ha^{-1}) between the observed and modeled baseline yield levels (y_b) and phenological anthesis ($\text{RMSD}_{\text{ANTH}}$) and full maturity ($\text{RMSD}_{\text{FMAT}}$) development phases for generic HiL and MidE genotypes. Dataset I (Table 1, Fig. 1, Phase Ia1) derived from the MTT Agrifood Official Variety Trial dataset (1978−2007) for spring wheat genotypes was used in the calibration process (Kangas et al. 2006, 2008).

$$RMSD = \sqrt[2]{\sum_{i=1}^{n} \frac{d^2}{n-1}} \tag{9}$$

where d - difference (observed – simulated) in days (DOY – Day of Year) from sowing to anthesis ($\text{RMSD}_{\text{ANTH}}$) and sowing to full maturity ($\text{RMSD}_{\text{FMAT}}$) in the calibration of phenological coefficients (PHINT, P1V, P5) or d is also the yield difference (RMSD_{YLD} observed-simulated, t ha^{-1}) in the calibration of yield coefficient components (G1, G2 and G3). Parameter n is the number of experimental sites x years (35 total) in the MTT Agrifood Research Finland Official Variety Trial dataset (1978−2007).

Results

Variation in vegetation, leaf area and dry weight components

There was a large variation between HiL and MidE genotypes in datasets I-IX (Table 1) with vegetation, leaf area and dry weight components.Especially in dataset IX, the highest yielding HiL cv. 'Kadett' ($\text{HiL}_{\text{Old80}}$) had also the highest number of side tillers in June before anthesis. The lowest yielding cv. 'Tähti' ($\text{HiL}_{\text{Old70}}$) had the minimum number of leaves/main stem in June. There was a large variation between HiL genotypes both in June and July in flag leaf area, second highest leaf area, flag leaf dry weight, second highest leaf dry weight in the main tiller and above ground biomass. Flag leaf area in the main tiller varied between 1620 mm^2 and 2145 mm^2 in vegetative phase in June and later in July in generative phase between 1236 mm^2 ('Luja', $\text{HiL}_{\text{Old80}}$) and 2398 mm^2. The second highest leaf area in the main tiller varied between 1204 mm^2 (cv. 'Luja', $\text{HiL}_{\text{Old80}}$) and 1579 mm^2 (cv. 'Ulla', $\text{HiL}_{\text{Old70}}$) in June and in July between 1295 mm^2 and 1876 mm^2. Respectively the Leaf Area Index (LAI) with fully developed flag leaves reached the LAI maximum value (LAI_{max}) ranging on average between 4 and 5 during pre-heading and anthesis. Peltonen-Sainio et al. (2005) marked the fully developed flag leaves as the L_7 leaf development phase.

The dry weights of flag leaves in the main tiller varied between 38.8 mg (cv. 'Tapio', $\text{HiL}_{\text{Old70}}$) and 68.6 mg (cv. 'Kadett', $\text{HiL}_{\text{Old80}}$). The dry weights of the second leaves in the main tiller varied between 26.2 mg and 37.6 mg in the vegetative phase in June and between 27.4 mg and 68.8 mg in generative phase in July. The total above ground dry weights of plants varied between 288.6 mg (cv. 'Drabant', $\text{HiL}_{\text{Old70}}$) and 449.8 mg (cv. 'Tapio', $\text{HiL}_{\text{Old70}}$) in vegetative phase and between 964.9 mg (cv. 'Line 48') and 1829 mg (cv. 'Drabant', $\text{HiL}_{\text{Old70}}$) in generative phase.

Mixed contrast category results for baseline yield (y_b) estimations

The modeled mean baseline yield (y_b) for a generic genotype over all contrast categories was 4014 kg ha^{-1} (SD 245 kg ha^{-1}, Table 4, Fig 1., Phase I). In the decade contrast category, the modeled baseline yield levels (y_b) were 3880 kg ha^{-1} for the HiL$_{Old70}$ and 4010 kg ha^{-1} for the HiL$_{Old80}$ generic genotypes and 4340 kg ha^{-1} for the MidE $_{Old80}$ category. With genotypes introduced into cultivation in the 1990s (New90) the baseline yield levels were 4650 kg ha^{-1} for HiL and 5060 kg ha^{-1} for MidE genotypes.

The conventional vs. organic cultivation category results in cultivation practices contrast suggest (Dataset VI), that genotypes cultivated with conventional practices (4269 kg ha^{-1}) had ca. 600 kg ha^{-1} higher yielding capacity compared with genotypes cultivated with organic methods (3640 kg ha^{-1}). The soil type contrast indicates, that clay type soils produced higher baseline yields (4100 kg ha^{-1}) when compared with coarse (3850 kg ha^{-1}) and loam soil types (3702 kg ha^{-1}).

Table 4. Hierarchical Mixed-model baseline yield estimates (y_b, kg ha^{-1}) in different contrast categories (I–III).

I Latitude contrast	II Cultivation type, soil type, decade of introduction contrast	III genotype contrast	Baseline Mixed estimate (y_b kg ha^{-1}) (SD)	Mixed estimation error (kg ha^{-1}) 1)
MidE & HiL	Average all 2)	Generic Ideotype mean	4014 (245)	94.8
	Cultivation type 3)	Generic Conventional	4269	17.9
		Generic Organic	3640	52.5
	Soil type	Coarse soils	3856	27.5
		Silt & Loam soils	3702	120.5
		Clay soils	4101	41.0
		Organic soils	3640	52.5
MidE	MidE 1980 4)	Old 80	4375	28.2
	MidE 1990 4)	New90	5057	108.5
HiL	HiL 1970	Old 70	3886	19.2
	HiL 1980 3)	Old 80	4014	35.4
	HiL 1990 4)	New90	4652	59.6

1) All levels significant on 0.1% error level (***).2) Over all MidE and HiL contrast categories.
3) Organic and conventional dataset VI (Table 1, Aula and Talvitie 1995). 4) Includes dataset II.

Mixed and Cultivation value modeling results for generic HiL and MidE genotype evaluation

Mixed modeling results on genotype level (Table 5) using datasets I-VI (Fig 1., Phase I) imply a general higher baseline yield (y_b) level for a generic MidE genotype (4922 kg ha^{-1}, SD 283 kg ha^{-1}) vs. a generic HiL genotype (4532 kg ha^{-1}, SD 573 kg ha^{-1}). A general increasing yield trend can be observed from both MidE $_{New90}$ and HiL$_{New90}$ categories.

In the MidE$_{New90}$ contrast category genotypes 'Amaretto', 'Azurite', 'Bombona', 'Epos', 'Jondolar', 'Marina', 'Monsun', 'Picolo', 'Sella', 'Triso' exceeded the 5 t ha^{-1} baseline yield level and cv. 'Trappe' obtained the highest baseline grain yield level (6.2 t ha^{-1}). In the HiL$_{new90}$ contrast category genotypes 'Kadrilj', 'Zebra' and 'Mahti' exceeded the 5 t ha^{-1} level.

Generic HiL and MidE genotypes derived from the Mixed and Cultivation value analyses

Table 5 presents the generic HiL and MidE genotypes with Mixed baseline yield estimates ($y_{b,}$ kg ha^{-1}) and Cultivation total scoring values (C_{ValTot}, Eq. 8, Fig 1., Phase II, Table 1, dataset VII).

Table 5. Mixed model baseline yield estimates (y_b, kg ha^{-1}), observed mean yield values from datasets I–VII and Cultivation scoring value (C_{Val}) profiles on genotype level. [1]

Generic latitude type	Mixed contrast category	Genotype (Table 3) [8]	Cultivation value (C_{Val}) rating (Peltonen 2010, Eq. 8)						Mixed baseline yield (y_b) [X, ±SD, kg ha^{-1}] [7]
			C_{Val} sub class[1]	C_a [2] (d)	C_c [3] Observed yield [kg ha^{-1}] [7]	C_p [4] [kg DMd^{-1} ha^{-1} / N kg ha^{-1}]	C_b [5]	C_{Val} Tot Score 6)	
MidE	$\text{MidE}_{\text{New90}}$	Quarna	Elite	23 104	22 4743	39 46/109	39	123 Max MidE	4620
		Amaretto		23 107	36 5645	34 53/104	28	121	5474
		Epos		22 109	32 5302	34 49/106	33	121	5224
		Trappe	Other	22 110	27 5976	30 55/104	24	103	6241 Max. MidE
		Nandu Ref.		-	-	-	-	-	4371
	$\text{MidE}_{\text{Old80}}$	Matador		-	-	-	-	-	4079
		Pasteur		-	-	-	-	-	4387
MidE	$\text{MidE}_{\text{Old80}}$	Pasteur Ref.	Other						4375±371
MidE [9]	**$\text{MidE}_{\text{New90}}$** ±SD	**Nandu Ref.**	**Other**	**23** ±1.2	**29** ±3.6	**34.2** ±1.8	**31.2** ±3.6	**117.4** ±7.57	**4755±282**
MidE	Generic Latitude type	Mid-E. mean							4922±554
HiL	$\text{HiL}_{\text{New90}}$	Zebra	Elite	25 106	28 5057	34 48/100	32	119	5053
		Marble		25 107	28 5120	33 48/101	31	117	Max HiL
		Wellamo		27 106	29 5119	31 49/107	32	119 MaxHiL	-
		Bjarne	Quality	23 104	19 4556	28 44/99	37	107	-
		Anniina		23 101	21 4627	30 46/108	36	110	4387
		Kruunu Ref.		24 104	24 4910	33 47/97	30	111	4689
		Tjalve Ref .	Other	-	-	-	-	-	4652
HiL	$\text{HiL}_{\text{Old70}}$	Apu	Other	-	-	-	-	-	3886±341
HiL	$\text{HiL}_{\text{Old80}}$	Polkka Ref.	Other	-	-	-	-	-	4014±297
HiL [9]	**$\text{HiL}_{\text{New90}}$** ±SD	**Tjalve Ref.**	**Other**	**24.4** ±1.7	**24.2** ±4.3	**31** ±2.1	**23** ±2.3	**112.8** ±5.1	**4616±564**
HiL	Generic Latitude type	HiL mean							4532±573

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[1] C_{Val} – Cultivation scoring value profile on a genotype level in Zones I-III (Classes: Elite, Quality, Other, Eq. 8, cv. Kruunu Ref.) [2] C_a – adaptation plasticity scoring value with growing days (d) from sowing to full maturity [3] C_c – cultivation certainty scoring value with final grain yield (kg ha^{-1}) [4] C_p – cultivation properties scoring value containing grain yield accumulation/growing day ratio (kg DM/d) and the nitrogen amount in grains (N kg ha^{-1}) [5] C_b – baking quality scoring value [6] C_{ValTot} – Cultivation total scoring value of a genotype (Eq. 8) in growing zones I–III. [7] Observed mean yields from dataset VII (Fig. 1), [8] Ref. - Reference genotype. [9] Generic reference genotype in the Mixed New_{90} contrast category.

The C_{ValTot} scoring value consisted of cultivation properties (C_p), adaptation plasticity (C_a), baking quality (C_b) and cultivation certainty (C_c) subcomponents (Peltonen 2010). Especially cv. 'Quarna' (Elite and $MidE_{New90}$ classes) obtained the highest Cultivation total scoring value (C_{ValTot} 123), the C_a, C_c and C_p components were 23, 22 39. The Mixed mean baseline yield estimate was (y_b) 4620 kg ha^{-1} vs. 4743 kg ha^{-1} observed mean yield level.

With cv. 'Quarna' the grain yield accumulation/growing day ratio was 46 kg DM d^{-1} ha^{-1} and the nitrogen amount in grains was 109 N kg ha^{-1} and the mean growing days from sowing to full maturity were 104 d. The cv. 'Wellamo' obtained 119 and cv. 'Marble' 117 in total scoring (C_{ValTot}), both cv. 'Wellamo' and 'Marble' yielded above 5 t ha^{-1} average yield levels. The reference genotype 'Kruunu' (HiL_{New90}, Quality class) obtained 111 in total scoring.

Especially HiL and MidE generic reference genotypes in the Mixed New_{90} contrast category ($MidE_{New90}$ and HiL_{New90}, Table 5) were utilized when defining the ideotype profiles ($Itprf_{MidE,HiL}$ Eq. 10) in conjunction with the CERES-Wheat crop model. The HiL_{New90} generic genotype factors (y_b, [kg ha^{-1}±SD], C_p, C_a, C_b, C_c, C_{ValTot}) were (4616±564, 24.4±1.7, 24.2±4.3, 31.0±2.1, 23.0±2.3, 112.8±5.1) and the corresponding factors for the $MidE_{New90}$ generic genotype were (4755±282, 23.0±1.2, 29.0±3.6, 34.2±1.8, 31.2±3.6,117.4±7.57).

Path coefficient analysis results with yield (p_y) and vegetation (p_v) components

Table 6 presents Path coefficient modeling results (Models I–IV) for HiL ideotypes using datasets VIII and IX (Fig 1., Phase III) with estimates for correlation coefficients (r), values for coefficient of determination (R^2) and U residual factors (Eq. 2–7). With Path models I–III and using vegetation components (p_v) as independent variables, R^2 values were relatively low (I:0.219, II:0.08, III: 0.351).

Table 6. Path models (I-IV) for baseline grain yield values (y_b, kg ha^{-1}) with Path (p) and correlation (r) coefficients.1)

Path - Model	y_b for a generic HiL ideotype X, (SD) (kg ha^{-1})	Linear regression for baseline y_b (kg ha^{-1}) $=b_0+b_1*x1+b_2*x2+ .. b_n*x$ (Eq. 2)	Standardized Path Model for baseline grain yield (p=Path- and r=correlation coefficients (Eq. 5) y_b = pa * ra *A + pb* rb *B .. pc * rc*X	R^2 for grain yield kg ha^{-1} 15% moist. cont.) (Eq. 7) 2)	p_v 2) p_y 3)	R^2 (U) 4)
I (pv) 5)	3105.0 (342.3)	3443.71 – 0.32*(Fla$_{June}$) + 0.29*(Fla$_{July}$) – 0.37*(FlDw$_{June}$) + l0.44*(FlDw$_{July}$)	p*r(Fla$_{June}$) + p*r(Fla$_{July}$)+ p*r(FlDw$_{June}$) + p*r(FlDw$_{July}$)	(-0.14*0.046) + (0.25*0.38)+ (-0.l02*-0.003) + (+0.31*0.414) = 0.2190	-0.140 2) +0.250 -0.l02 +0.310	0.2190 (0.682)
II (pv) 5)	3860.7 (192.0)	3522.9+0.38*(2LfA$_{June}$) + 0.14*(2LfA$_{June}$) - 0.14*(2LfDw$_{June}$) – 0.27 (2Lf Dw$_{July}$)	p*r(2LfA$_{June}$) + p*r(2LfA$_{June}$)+ p*r(2LfDw$_{June}$) + p*r(2Lf Dw$_{July}$)	(0.397*0.209)+ (0.15*0.034)+ (-0.142*0.038) +(-0.296*-0.055)= 0.085	+0.397 2) +0.150 -0.142 -0.296	0.085 (0.891)
III (pv) 5)	3158.7 (304.4)	2820.5-0.11 (FlDW$_{June}$) -0.068*(2LfDW$_{June}$) -0.49*(FlDW$_{July}$) +0.68*(2LfDW$_{July}$)	P*r(FlDW$_{June}$)+ P*r(2LfDW$_{June}$)+ P*r(FlDW$_{July}$)+ P*r(2LfDW$_{July}$)	(-0.124*-0.003)+ (-0.077*0.038)- (-0.538*0.414)+ (0.788*-0.055)= 0.351	-0.124 2) -0.077 -0.538 +0.788	0.351 (0.951)
IV (py) 6)	3461.0 (90.6)	-129.25 + 35.59*(1000gw) +90.31*(GrSpk$_{Aug.}$) – 128.15*(SpkEar$_{Aug.}$) + 15.24*(EarLng$_{Aug.}$)	p*r(1000 gw) + p*r(GrEar$_{Aug.}$)+ p*r(SpkEar$_{Aug.}$)+ p*r(EarLng$_{Aug.}$)+ p*r(EarStem$_{Aug.}$)	(0.679*0.39) + (0.581*0.42) + (-0.306*-0.33)+ (0.281*0.38) + (0.562* -0.048)= 0.7098	+0.679 3) +0.581 -0.306 +0.281 +0.562	0.7098 (0.797)
Mean	3396.4(232)					

1) Abbreviations: Fla–Flag leaf area (L_7, mm^2), FlDw–Flag leaf dry weight (mg), 2Lf–Second uppermost leaf, 1000gw–1000 grain weight (g), Dw–Dry weight, GrEar–Grains/Ear, SpkEar–Spikelets/Ear, EarLng–Ear Length, mm), EarStem - Head bearing stalks m^{-2}. 2) p_v - Vegetation parameter Path coefficients (Eq. 5, Table 7) 3) p_y - Yield component Path coefficients (Eq. 5, Table 8). 4) U - Residual-factor (Eq. 6), R^{2-} R-square, total variance explained by the model (Eq. 7) 5) p_v- vegetation components as independent variables (Models I–III) 6) p_y - yield components as independent variables (Model IV)

Correspondingly with Path model IV and using yield components (p_y) as independent variables, R^2 was high (0.709). The Path-model dependent variable, baseline grain yield (y_b) estimate was for a generic HiL ideotype with Model I: 3105.0 kg ha^{-1} (SD 342.3 kg ha^{-1}), Model II: 3860.7 (192.0), Model III: 3158.7 (304.4) and Model IV: 3461.0 (90.6). The overall mean HiL grain yield estimate (y_b) was 3396 kg ha^{-1} (SD 232 kg ha^{-1}).

Vegetation Path-coefficient (p_v) estimations and leaf area and dry weight variation

The vegetation Path coefficients (p_v) results for HiL genotypes (models I-III, Table 7, Fig 1., Phase III) indicate, that significant vegetation components (p_v) on final grain yield (y_b) and 1000 kernel weight were number of leaves/plant in June (0.477, SD 0.18), both flag leaf area (0.386, SD 0.17, L_7 leaf development phase, Peltonen-Sainio et al., 2005) and flag leaf dry weight in July (0.611, SD 0.24) and dry weights of whole plants in June (0.505, SD 0.24). The number of side tillers in June, the length of main stem in June, July and August and the second highest leaf area in July had significant direct effects on final 1000 kernel weight.

Table 7. HiL vegetation Path-coefficients (p_v) and PCA factor loadings vs. baseline grain yield (y_b, kg ha^{-1}) and vs. 1000 grain weight (g).

Vegetation parameter	p_v vs. baseline grain yield (y_b, kg ha^{-1}) (SD) 1)	p_v vs. 1000 grain weight (g) (SD) 1)	PCA factor loadings (2 factor solution)
Side tillers in June	0.200 (0.187)	0.584 (0.113)	+0.558
Number of leaves in June	0.477 (0.183)	0.131 (0.110)	+0.377
The length of main stem in June, July, August	0.070, 0.360, 0.570	0.640, 0.703, 0.316	+0.873,+0.804, +0.783
Flag leaf area (mm^2, L_7) phase in June and July 2)	0.153 (0.050), 0.386 (0.176)	0.012 (0.080), 0.131 (0.233)	+0.324,+0.661
Second leaf area (mm^2) in June and July	0.226 (0.166) 0.042 (0.073)	0.088 (0.061), 0.541 (0.110)	+0.681, -
Flag leaf dry weight (mg) in June and July	0.139 (0.063) 0.611 (0.243)	0.393 (0.103) 0.141 (0.175)	+0.345,+0.369
Second leaf dry weight (mg) in June and July	0.216 (0.080) 0.237 (0.170)	0.108 (0.121) 0.259 (0.175)	+0.703 , -
Dry weight of rest of plant (mg) in June and July	0.512 (0.050) 0.205 (0.134)	0.251 (0.207) 0.085 (0.327)	+0.784, -
Dry weight of whole plant (excluding root bm.) in June and July	0.505 (0.244) 0.231 (0.525)	0.339 (0.281) 0.339 (0.477)	+0.827, -
Dry weight of straw biomass (mg) in August	0.062 (0.052)	0.341 (0.071)	+0.504

1) Standard deviation (SD) denotes variance with different Path-model combinations from models I-III (Table 6)

2) L_7 leaf development phase (Peltonen-Sainio et al., 2005)

Yield component Path-coefficient (p_y) estimations

In table 8, the Path-model IV (Fig 1., Phase III) indicated a strong direct connection with HiL yield component Path-coefficients (p_y) between final baseline grain yield (y_b) and 1000 grain weight (0.679) and Harvest Index (HI, 0.480). In addition, model IV had a high overall coefficient of determination (R^2 0.709, Table 6). Grains/head (0.581), head bearing stalks (0.562) and head length (0.281) had also strong positive effect on final grain yield determination in grain filling phase after anthesis.

Table 8. HiL yield component Path-coefficients (p_y) and PCA factor loadings vs. baseline grain yield (y_b) and vs. 1000 grain weight (g)

Yield component	P_y vs. baseline grain yield (y_b, kg ha^{-1})	P_y vs. 1000 grain weight (g)	PCA factor loadings (2 factor solution)
1000 grain weight (g)	0.679	-	+0.554
Harvest Index (HI)	0.480	0.338	-
Grains/head	0.581	0.791	+0.347
Head bearing stalks m^{-2}	0.562	0.644	+0.618
Main head length (mm)	0.281	0.061	+0.383
Spikelets/head	-0.306	0.219	-

The high p_y yield component factor (0.581) between grains/head and final grain yield confirms the positive direct effect. This was also noted with vegetative parameters, especially with flag leaf area and dry weights with high p_v values in generative phase in July.

The Principal Component Analysis (PCA) analysis results (phase IIIa, Fig.1) with high positive PCA factor loadings for vegetation (Table 7) and yield components (Table 8) indicated, that especially head bearing stalks m^{-2}, the length of main stem and the plant above ground dry weight were significant factors affecting both final grain yield and 1000 grain weight determination with HiL genotypes.

Ideotype profiles (ItPrf) for generic HiL and MidE spring wheat genotypes

Table 9 illustrates the CERES-Wheat phenological (PHINT, P1V, P1D and P5) and yield component coefficient (G1, G2 and G3) calibration results for HiL and MidE generic genotypes using the RMSD algorithm (Root Mean Square Difference , Eq. 9, Laurila 2001). The average anthesis difference ($RMSD_{ANTH}$) was 2.99 d assuming that the anthesis is reached on average ca. 5 days after wheat heading, the full maturity difference ($RMSD_{FMAT}$) was 5.86 d and the baseline yield levels (y_b) difference was 1.79 t ha^{-1} ($RMSD_{YLD}$) pooled over all soil types derived from the MTT Agrifood Research Official Variety Trial dataset (1978–2007, Dataset I, Table 1, Kangas et al. 2006, 2008).

The calibrated genetic coefficients (PHINT, P1V, P5, G1, G2, G3) were for a generic HiL genotype (60.0, 0.10, 1.0, 10.0, 5.0, 1.0, 1.5) and respectively for a generic MidE genotype (60.0, 0.10, 1.0, 9.0, 4.0, 3.0, 2.0).

Table 9. The CERES-Wheat (Jones *et al.* 2003) calibrated yield component coefficients (G1, G2 and G3) and phenological coefficients (PHINT, P1V, P1D and P5) for HiL (*cv.* Polkka ref., Laurila, 2001) and for MidE (*cv.* Nandu ref., Laurila, 1995) genotypes.

Generic genotype	Soil type	$RMSD_{YLD}$ (t ha^{-1}) [1]	G1	G2	G3
MidE (*cv.* Nandu ref.)	All soil data pooled	-	4.0	3.0	2.0
HiL (*cv.* Polkka ref.)	Sand (coarse and fine)	1.7478	0.50	5.00	5.00
	Heavy clay	1.8323	1.00	8.50	1.00
	Mixed clays	1.7245	1.00	8.50	1.00
	Silt, Silt loam	1.4080	1.00	6.00	1.00
	Organic soil (Peat, Mould)	0.2892	2.00	2.30	2.00
	All soil data pooled	1.7980	5.00	1.00	1.50

Generic genotype & Phenology	$RMSD_{ANTH}$ (d) [2]	$RMSD_{FMAT}$ (d) [3]	PHINT (dd)	P1V	P1D	P5
HiL (*cv.* Polkka ref.)	2.99	5.86	60.0	0.10	1.00	10.0
MidE (*cv.* Nandu ref.)	-	-	60.0	0.10	1.00	9.0

[1] RMSDYLD = RMSD for grain yield (t ha^{-1}). [2] $RMSD_{ANTH}$ = RMSD for anthesis (d), the anthesis is reached ca. 5 days after heading, [3] $RMSD_{FMAT}$ =RMSD for full maturity (d).

The combined statistical Mixed Covariance, Cultivation value (Table 5) results and modeling results from the dynamic CERES-Wheat crop model on wheat non-potential baseline yield (y_b kg ha^{-1}, Table 9) were synthesized as generic ItPrf$_{HiL,New90}$ and ItPrf$_{MidE,New90}$ ideotype profiles in the New90 Mixed contrast category including genotypes introduced into cultivation in the 1990s or later (Fig 1., Phase IV).

The statistical modeling results yielding generic HiL and MidE genotypes (Table 5) and results from the CERES-Wheat crop model with phenological and yield component factors (Table 9) were combined as ItPrf$_{HiL,New90}$ and ItPrf$_{MidE,New90}$ ideotype profiles (Eq. 10). The elevated atmospheric CO$_2$ concentration (700 ppm) combined with +3 °C mean diurnal temperature change factors on wheat non-potential baseline yield (y_b kg ha^{-1}) were included in ItPrf$_{HiL,New90}$ and ItPrf$_{MidE,New90}$ ideotype profiles simulating the year 2100 climate change scenario in southern Finland (Carter 2004).

$$\begin{aligned}&\mathrm{ItPrf(HiL/MidE(New90))} = (\mathrm{yb} \pm \mathrm{SD}, \Delta\mathrm{yb(CO2{,}700ppm)}\ [\mathrm{min.} - \mathrm{max.}, \%],\\ &\Delta\mathrm{yb}(\Delta\mathrm{T}, +3^{\circ}\mathrm{C})[\mathrm{min.} - \mathrm{max.}, \%], \Delta\mathrm{yb(CO2, TempCov)}[\mathrm{min.} - \mathrm{max.}, \%], \mathrm{PHINT},\\ &\mathrm{P1V, P5, G1, G2, G3, Ca\ , Cp\ \ , Cb\ , CValTot})\end{aligned} \tag{10}$$

where (i) y_b±SD is the mean non-potential baseline grain yield level (kg ha^{-1}) without the $y_{b(CO2,TempCov)}$ covariance effect (ii) the $y_{b(CO2,700ppm)}$ factor estimates the change range (min.-max., %) on baseline yield (y_b kg ha^{-1}) with doubled atmospheric CO$_2$ concentration (700 ppm), (iii) the $y_{b(\Delta T,+3ºC)}$ factor estimates the change range (min.-max.,%) on y_b with +3 ºC mean diurnal temperature change (ΔT) and (iv) the covariance factor $y_{b(CO2,TempCov)}$ estimates the change range (min.-max.,%) on y_b with concurrent doubled CO$_2$ concentration and with +3ºC mean diurnal temperature change in the ItPrf$_{HiL,New90}$ and ItPrf$_{MidE,New90}$ profiles (Laurila 1995, 2001, Hakala 1988, Saarikko 1999, Carter 2004).

The $\Delta y_{b(CO2,700ppm),}$ $\Delta y_{b(}\Delta T_{,+3ºC)}$ and the covariant $\Delta y_{b(CO2,TempCov)}$ factors in the ideotype profiles were excluded from the non-potential baseline yield estimates (y_b, Eq. 10). The covariant $\Delta y_{b(CO2,TempCov)}$ factor simulating the concurrent elevated CO$_2$ and temperature effects in conjunction with the HiL and MidE non-potential baseline yield estimates (y_b) are reviewed in the discussion section. The optimized ideotype profile for a generic HiL$_{New90}$ ideotype (ItPrf$_{HiL,New90}$) with parameters (y_b±SD [kg ha^{-1}], $\Delta y_{b(CO2,700ppm)}$ [min.-max.,%], $\Delta y_{b(\Delta T,+3°C)}$ [min.-max.,%], $\Delta y_{b(CO2,TempCov)}$ [min.-max., %], PHINT [dd], P1V, P5, G1, G2, G3, C_a, C_p, C_b, C_{ValTot}, Eq. 10) was (4616±564, 1.12-1.42 , 0.72-0.83, 1.01-1.06, 60.0, 0.10, 1.0, 10.0, 5.0, 1.0, 1.5, 24.4, 24.2, 31, 23, 112.8). The optimized ideotype profile (ItPrf$_{MidE,New90}$) for a generic MidE$_{New90}$ ideotype was (4755±282, 1.49–1.72, 0.59–0.62, 1.04–1.13, 60.0, 0.10, 1.0, 9.0, 4.0, 3.0, 2.0, 23, 29, 34.2, 31.2, 117.4).

Discussion

Spring wheat yield trends in Finland

According to Mela and Suvanto (1987), HiL$_{Old70}$ and HiL$_{Old80}$ spring wheat genotypes increased the average baseline yield (y_b) levels by +0.34%/year in Finland during the period 1956−1985 due to improved plant breeding and other cultivation techniques. A general trend of breaking the averaged 5 t ha^{-1} baseline barrier (y_b) over the years with MidE$_{New90}$ genotypes introduced into cultivation after the 1990s is noticeable in the MTT Agrifood Research Finland 1978−2007 official variety trial data (Dataset I). Recently Peltonen-Sainio et al. (2009) concluded using the Finnish MTT official variety trial (1970-2005) data and FAOSTAT data (1960−2005) that the yield trends of future wheat genotypes will constantly increase in Finland and on global scale during climate change because of the increasing demand for global food production. In practical cultivation in southern Finland, the average yield levels have been rising steadily from the old 3 t ha^{-1} average level above 5 t ha^{-1} in southern Finland by using new HiL$_{New90}$ and MidE$_{New90}$ genotypes, incorporated with new fertilizer and pesticide practices (Kangas et al. 2008, Peltonen 2010). The increase of sowing seed density from 600 seeds m^{-2} to 700 seeds m^{-2} has increased the yield levels by 1 t ha^{-1}. Peltonen (2010) reported promising high yield results in southern Finland using new spring wheat cultivars from the MidE$_{New90}$ category (e.g. cv. 'Quarna', 'Amaretto', 'Trappe', 'Piccolo', 'Triso', 'Jondolar') and from the HiL$_{New90}$ category from Borealis (cv. 'Marble', 'Wellamo') and cv. 'Zebra' from Svalöf-Weibull.

Optimum vegetation and yield components for high yielding wheat ideotypes

Path coefficient analysis using datasets VIII and IX identified several significant vegetation (p_v) and yield components (p_y) with direct effects for HiL wheat ideotypes with maximum yield capacity. The overall mean y_b estimate (Models I−IV) for a generic HiL ideotype was 3589 kg ha^{-1} (SD 338.7 kg ha^{-1}). Following HiL vegetation (p_v) components with corresponding threshold values for high yield capacity were significant: sowing seed density (>700 seeds m^{-2}), emerged seedlings m^{-2} (> 600 seeds m^{-2}), maximum side tillers/plant in June (> 2), maximum number of leaves/plant in July (> 5), maximum flag leaf and second highest leaf areas (>1800 mm^2 and >1600 mm^2) in July, maximum flag leaf and second highest leaf dry weights (> 57 mg and > 46 mg) and maximum plant whole dry weight (> 1390 mg) in August.

The highest yielding cv. 'Kadett' in the HiL$_{\text{Old80}}$ category had the highest flag leaf dry weight in June in datasets VIII and IX. This indicated an effective photosynthetic mechanism and high assimilation capacity in vegetative phase in June. In July, in generative phase, the dry weights of flag and the second highest leaves had decreased from June values as the senescence of leaves already had started.

With HiL yield components (p_y) especially grains/ear (> 30), 1000 kernel weight (> 40 g), harvest index (HI>39), spikelets/ear (>12) and ear bearing stems m^{-2} (> 647) were significant. Peltonen-Sainio et al. (2005) reported that in Finnish growing conditions grains/ear component is one of the most important factors defining the ideotype final grain yield. The current cereal genotypes contain ca. 25 grains per ear on average. In our field results (Datasets VIII−IX), the average grains/ear was higher (42.3, SD 5.3) suggesting above average baseline yield levels for HiL genotypes. Theoretically, there are ca. 160 grain primordiums in the wheat ear (Slafer and Savin 1994). According to Peltonen-Sainio et al. (2005) there is a critical cereal flowering period ("window of opportunity for yield") in Finnish long-day growing conditions, which defines the critical yield component grains/ear number. This period starts on average three weeks before heading, and lasts ca. two weeks (< 50 on Zadoks growth scale, Zadoks et al. 1984) with wheat flower differentiation setting the final grain number in head (Sinclair and Jamieson 2008). In our study the average 1000 kernel weight was below average 32.8 (SD 2.6) when compared with the average 37 g in MTT spring wheat variety trials (Dataset I, Kangas et al. 2006, 2008). Respectively the ear bearing stems m^{-2} was above average 647.7 (SD 63.2) vs. 500 stems m^{-2} in MTT trials.

Genotype×environmental (G×E) variation and covariances

The Mixed model soil type contrast results expressing the genotype×environmental (G×E) covariance indicated, that clay type soils produced higher baseline yields (y_b 4100 kg ha^{-1}) than coarse (y_b 3850 kg ha^{-1}) and loam soil types (y_b 3700 kg ha^{-1}) when using the same cultivars. This was due to the frequent drought periods during growing season on coarse and loam type soils reducing the cereal yield potential (Järvi et al. 1997, Kangas et al. 2008). Recently, Rajala et al. (2009) studied in Finland the effects of water limitation and fertilizer availability on development of yield components. The greenhouse experiment results, using cv. 'Amaretto' (MidE$_{\text{New90}}$) with different water treatments, indicated that especially plants per unit land area, spikes per plant, grains per spikelet, and single grain weight (SGW) were significant components affecting final grain yield when water and nitrogen availability were limiting factors.

The Mixed modeling results using conventional vs. organic cultivation practices with the same cultivars in the experiments suggested, that genotypes using conventional cultivation practices (y_b 4270 kg ha^{-1}), with herbicide introduction and chemical fertilizers, had ca. 600 kg ha^{-1} higher yield capacity compared with genotypes using organic cultivation practices (y_b 3640 kg ha^{-1}). According to Aula and Talvitie (1995) growing period from sowing to full maturity is ca. 1−2 days longer in organic cultivation in Finland compared with conventional cultivation practices.

Source-sink variation and adaptation between ideotypes

Inter- and intracultivar source-sink variation with high yielding wheat genotypes has been reviewed by Slafer & Savin (1994) and by Reynolds et al. (2007). Previous studies have indicated a significant morphological variation in leaf angle, leaf weight and leaf area duration between wheat genotypes (Austin et al. 1980). Ledent (1979) and Gent & Kiyomoto (1985) reported the crucial roles of wheat flag leaf (L_7) and the second highest leaf on yield formation. Peltonen-Sainio et al. (2005) and Peltonen-Sainio & Rajala (2007) studied detailed cereal leaf development order (L_1-L_7) starting from the emergence of cotyledon leaf (L_1) from coleoptile following consecutive phases until the flag leaf ($L_{7,}$ highest leaf) emerged below the head. In Finnish long day growing conditions cereals differentiate six or seven leaves in the main stem.

The Mixed structural covariance and Path coefficient results detected several direct and indirect factors affecting the final grain yield with HiL and MidE genotypes. Results indicated a strong intracultivar source-sink correlation between source (e.g. flag leaf area during L_7 leaf and LAI_{max} development phases) and sink components (e.g. grains/ear, final grain kernel size in the head and harvest index) in the HiL_{Old70}, HiL_{Old80} and HiL_{new90} contrast categories. These modeling results are consistent with the PCA and Path coefficient analysis results published by Reynolds et al. (2007) reviewing source-sink traits and interactions with yield, biomass and radiation use efficiency (RUE) for wheat genotypes with high yield capacity. Reynolds et al. (2007) stated that source-sink imbalance and sink strength are still critical yield limiting factors in wheat genotypes.

When analyzing the Mixed HiL_{Old70} - HiL_{Old80} vs. HiL_{new90} contrast categories, the highest yielding late cv. 'Kadett' (HiL_{Old80}, 4071 kg ha^{-1}), relatively late cv. 'Ruso' (HiL_{Old70}, 3611 kg ha^{-1}) and early cv. 'Apu' (HiL_{Old70}, 3978 kg ha^{-1}) were clearly inferior in yielding capacity compared with the most common wheat in cultivation, cv. 'Tjalve' (HiL_{new90}, 4563 kg ha^{-1}). Also the 1000 grain weight and protein content were superior with cv. 'Tjalve' (38.7 g, 13.2%) compared with cv. 'Kadett' (37.7 g, 9.2%), cv. 'Ruso' (36.8 g, 10.3%), cv. 'Apu' (30.6 g, 9.8%).

According to the Path coefficient results, the high yielding genotypes especially in the HiL category expressed the source-sink covariances in a well balanced and optimal combination (Eq. 1). The cv. 'Kadett', with highest sink capacity (grain yield and dry matter accumulation) in the HiL_{Old80} category, also had a high source capacity (e.g. flag leaf area and dry weight). With lowest yielding cultivar Tähti (HiL_{Old70}), the source-sink imbalance and inadequate translocation of assimilates were potentially yield limiting factors (Reynolds et al. 2007, Sinclair and Jamieson 2008).

The Cultivation scoring value (C_{ValTot}) results indicated that mid-European genotypes belonging to the Elite and $MidE_{New90}$ classes obtained the highest total scoring sums. Especially cv. 'Quarna' (C_a 23, C_b 39, C_c 22, C_p 39) obtained the highest C_{ValTot} value (123) in $MidE_{New90}$ and Elite classes. Respectively, cv. 'Marble' (C_a 25, C_b 31, C_c 28, C_p 33) obtained the highest total scoring value (117) in the HiL_{New90} and Elite classes. The mid-European genotype 'Trappe' ($MidE_{New90}$, Other class) with a relatively low Cultivation Value profile (C_a 22,C_b 34, C_c 27, C_p 24, C_{ValTot} 103), produced the highest grain yield level (6 t ha^{-1}). The Mixed baseline estimate (y_b) for cv. 'Trappe' was 6240 kg ha^{-1}. Cv. 'Quarna' yielded 4730 kg ha^{-1}. In the ($HiL_{New90,}$ Elite) category, the highest yielding cultivar was cv. 'Marble' (5120 kg ha^{-1}).

In the C_a component (adaptation plasticity), cv. 'Wellamo' (HiL_{New90}, Elite class) had the highest adaptation plasticity value (C_a 27). The growing period from sowing to full maturity was longer in the $MidE_{New90}$ category. Cv. Trappe had the longest growing period from sowing to full maturity (110 d). The C_a values and the growing days were for cv. 'Trappe', 'Quarna' and 'Marble' (22/110 d, 23/104 d, 25/107 d).

The Cultivation certainty (C_c) component results indicated that the final grain yield levels with high yielding cultivars were higher in the $MidE_{New90}$ category than in the HiL_{New90} category. The highest cultivation certainty (C_c 36) was with cv. 'Amaretto' (HiL_{New90}, Elite).

When analyzing the variation between high yielding cultivars in the Cultivation properties component (C_p), the accumulated grain yield/growing day ratio (DM d^{-1} ha^{-1}) and the nitrogen amount in grains (N kg ha^{-1}) were significant. The C_p values, the grain yield accumulation/growing day ratio and the nitrogen amount in grains were for cv. 'Trappe', 'Quarna' and 'Marble' (30/55/104, 39/46/109 and 33/48/101). Cv. 'Quarna' had the highest C_p value (39), highest baking quality (C_q 39) and the highest nitrogen amount in grains (109). Cv. 'Trappe' had the highest grain yield accumulation/growing day ratio (55) and the longest growing period enabling an effective translocation system from the source (flag leaf and second highest leaf) to the sink organs (head and grains) during grain filling phase, therefore contributing to the high final grain yield level.

Implications from the ideotype profile analysis for generic HiL and MidE wheat genotypes

According to two MidE and HiL ideotype profile analysis ($ItPrf_{MidE(New90)}$ and $ItPrf_{HiL(New90)}$) derived in this study, the genotypes introduced into cultivation after 1990's have adaptive yield potential for the future growing conditions with elevated temperature and atmospheric CO_2 growing conditions. The modeling results for generic $ItPrf_{MidE(New90)}$ and $ItPrf_{HiL(New90)}$ ideotypes indicated that the non-potential baseline yield (y_b, kg ha^{-1}) comparison without the concurrent CO_2×temperature covariance effect yielded the baseline yield difference (Δy_b) 140 kg ha^{-1} (+102 %) for $ItPrfMidE_{(New90)}$ vs. $ItPrfHiL_{(New90)}$ (y_b 4620 kg ha^{-1}, 100 %).

When taking into account also the projected concurrent CO$_2$×temperature covariance effect $\Delta y_b(\mathrm{CO}_2,_{700ppm},\Delta T,_{+3ºC})$ projected by the year 2100 climate change scenario for southern Finland (Carter 2004), the non-potential average baseline yield change (Δy_b, %) would be 1.035 % (range 1.01-1.06 %) for the generic ItPrf$_{HiL(New90)}$ ideotype. Correspondingly the average Δy_b change for the generic ItPrf$_{MidE(New90)}$ ideotype would be 1.085 % (range 1.04-1.13 %). These results indicate that the ItPrf$_{MidE(New90)}$ non-potential baseline yield (y_b) would be on average 5150 kg ha^{-1} level (Δy_b +108 %) vs. ItPrf$_{HiL(New90)}$ ideotype (y_b 4770 kg ha^{-1}, 100%) and assuming the photoperiodical day length remains constant.

Implications for future adaptation strategies using high yielding spring wheat ideotypes

Previous crop simulation results with the CERES-Wheat crop model (Laurila 2001), Open Top Chamber crop physiological results (Hakala et al. 2005) for cv. ‘Polkka’ (HiL$_{Old80}$) and for cv. ‘Nandu’ (MidE$_{New90}$) indicated, that the concurrent elevated atmospheric CO$_2$ concentration and elevated diurnal temperature will increase the yield potential of the HiL wheat genotypes by 1−6% and by 4−13% with the MidE wheat genotypes in southern Finland. Badger (1992) stated that wheat ideotypes with optimum yielding capacity and with adaptation for elevated atmospheric CO$_2$ concentration should have a fast canopy closure at tillering stage and a long grain filling period with high temperature sum requirements from anthesis to maturity. According to Slafer & Savin (1997) the elevated atmospheric CO$_2$ concentration (720 ppm) did not affect significantly the phyllochron leaf appearance rate (PHINT) or the phenological development in vegetative or generative phases with winter and spring wheat genotypes. The CERES-Wheat crop model takes into account the photoperiodism by using the phenological genetic coefficient P1D, which is linked to PHINT coefficient affecting genotype phyllochron interval and leaf appearance rate (Jones et al. 2003). According to Kontturi (1979) and Saarikko (1999) the Effective Temperature Sum (ETS) requirement of 1050 ± 30° degree-days (dd, Tb +5 °C) from sowing to yellow ripening stage is considered adequate for HiL spring wheat genotypes grown in zones I–IV in Finland. According to Peltonen (2010) new MidE$_{New90}$ genotypes require higher ETS values, exceeding the 1000 dd for full maturity in cultivation zones I–II, e.g. cv. ‘Trappe’ (1052 dd) and cv. ‘Picolo’ (1092 dd). The average ETS requirements with new HiL$_{New90}$ genotypes are for cv. ‘Mahti’ (985 dd), cv. ‘Tjalve’ (996 dd), cv. ‘Anniina’ (962 dd), cv. ‘Aino’ (968 dd).

In this study, the Mixed structural covariance and Cultivation value results indicated a significant increase in baseline yield (y_b, kg ha^{-1}) trends between new and old genotypes (HiL/MidE$_{Old70,\ Old80}$ vs. HiL/MidE$_{New90}$). Results indicated that new HiL and MidE genotypes introduced into cultivation after 1990s (HiL/MidE$_{New90}$) have a significantly higher yielding capacity between 9% and 13% vs. HiL/MidE$_{Old70,\ Old80}$ genotypes. In addition, results indicated a consistently higher yielding capacity (108%) for MidE$_{New90}$ genotypes compared with HiL$_{New90}$ genotypes (100%). Results from the Cultivation value analysis indicated, that especially MidE cultivars belonging to the MidE$_{New90}$ and Elite classes obtained the highest Cultivation value ratings and produced the highest final grain yield levels.

If the concurrent elevated atmospheric CO$_2$ concentration (700 ppm) and elevated diurnal temperature (+3 ºC) increase is also taken into account in the adaptation strategies, the MidE$_{New90}$ non-potential baseline yield levels (y_b) will be permanently surpassing the 5 t ha^{-1} barrier by 2100 in southern Finland. The ideotype profile results obtained in this study also support this increasing yield trend for new HiL and MidE ideotypes. However, these modeled yield levels for generic MidE and Nordic HiL wheat ideotypes comprise only 50% of the theoretical maximum yielding capacity level of 10 t ha^{-1} reported by Austin et al. (1980).

Conclusions

Modeling results obtained in this study with Mixed structural covariance analysis indicated that new high-latitude and mid-European ideotypes, introduced into cultivation after 1990s, have a significantly higher yield capacity compared with genotypes introduced for cultivation earlier. New mid-European genotypes produced a consistently higher yielding capacity (108%) than high-latitude genotypes (100%). These modeling results are supported by both practical field results on farm level in southern Finland (2009−2010) and also by MTT Agrifood Research Finland 1978−2007 official wheat variety trial results indicating a general trend of breaking the 5 t ha^{-1} baseline yield barrier with new high yielding mid-European and high-latitude genotypes.

Path coefficient modeling results for high-latitude genotypes suggested, that especially grains/ear, harvest index (HI) and maximum 1000 kernel weight were significant factors defining the highest yield potential. Cultivation

Value modeling results indicated, that especially genotypes belonging to Elite class inside $\mathrm{MidE}_{\mathrm{New90}}$ and $\mathrm{HiL}_{\mathrm{New90}}$ Mixed contrast categories, obtained the highest Cultivation scoring values.

Spring wheat modeling results obtained in this study can be utilized when designing new wheat genotypes with optimal ideotype profiles for agricultural adaptation strategies. Especially the wheat adaptation plasticity (C_a), cultivation certainty (C_c) and cultivation property (C_p) components are important selection factors when breeding the future wheat ideotypes adapted for elevated temperatures and CO_2 growing conditions in northern latitudes. The modeling results obtained in this study with new high yielding MidE and HiL ideotypes ($\mathrm{MidE}_{\mathrm{New90}}$, $\mathrm{HiL}_{\mathrm{New90}}$) imply that the mid-European non-potential baseline yield (y_b) would be on average 5150 kg ha^{-1} (+ 108 %) vs. high-latitude ideotypes (y_b 4770 kg ha^{-1}, 100%) grown under the elevated $CO_{2(700ppm)}$×$\mathrm{temperature}_{(+3°C)}$ growing conditions projected by the year 2100 climate change scenario in southern Finland.

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Appendix 1

Table 10. Definitions and abbreviations.

Definition, abbreviation	Unit, [range]	Explanation
X		Mean of sample
SD		Standard deviation of sample (n)
SEM	Standard error of mean	Standard error of mean = $\frac{SD}{\sqrt{n}}$
RMSD	d , t ha^{-1}	Root Mean Square Difference algorithm (Laurila, 2001)
C_v	%	Coefficient of variation (%) = SD/X
Ref.		Reference genotype/cultivar/variety in field trials (Table 1)
V_p		Phenotype variation (Eq. 1, Falconer & Mackay, 1996)
V_g		Genotype variation (Eq. 1)
V_e		Environmental variation (Eq. 1)
cov_{ge}		Genotype x environmental covariance variation in broad sense (Eq. 1)
Potential non-limited yield, yield potential	kg ha^{-1}, 15% moisture content	Modeled maximum yield capacity and yield potential (kg ha^{-1}) for a specific genotype without limiting environmental stress factors during growing season (vegetation water stress, nutrient deficiencies, pathogen epidemics etc.)
Non-potential, limited yield	kg ha^{-1}, 15% moisture	Modeled yield level (kg ha-1) for a specific genotype with limiting environmental stress factors during growing season reducing maximum yield capacity, see potential yield.
y_b	kg ha^{-1}, 15% moisture content	Modeled baseline yield estimate for a cereal genotype growing under non-optimal field growing conditions. See potential and non-potential yield. Δyb - Modeled baseline yield difference (%) between genotypes
$\Delta y_{b(CO2,700ppm)}$	%, change range (min. – max.)	Change (%) on y_b (baseline yield, kg ha^{-1}) with doubled atmospheric CO_2 concentration (700 ppm , Carter 2004)
$\Delta y_{b(\Delta T,+3^\circ C)}$	%, change range (min. – max.)	Change (%) on y_b (baseline yield, kg ha^{-1}) with +3°C mean diurnal temperature change (Carter 2004)
$\Delta y_{b(CO2,TempCov)}$	%, change range (min. – max.)	Covariance mean change (%) on y_b (baseline yield, kg ha^{-1}) with concurrent doubled atmospheric CO_2 concentration (700 ppm) and with $_{+3^\circ C}$ mean diurnal temperature change (Carter 2004)
C_{ValTot}		Cultivation total scoring value of a genotype in growing zones I-III
C_a		Adaptation Value in Cultivation Value model
C_q		Cultivation Quality in Cultivation Value model
C_C		Cultivation Certainty in Cultivation Value model
C_b		Baking Quality in Cultivation Value model
HiL		high-latitude genotype/ideotype (growing latitude > 60° N)
MidE		mid-European genotype/ideotype (growing latitude < 60° N)
$ItPrf_{(HiL,MidE)}$		Donald's ideotype profiles for generic HiL and MidE genotypes (Donald, 1968)
Ref.		Reference genotype/cultivar in the corresponding category in the statistical analysis or in the dynamic model. Dependent or response variable is scaled to relative base value in the category (1 or 100).
$r_{a,}\ r_{b,\ ..}\ r_x$	[0.. 1.0]	Correlation coefficients for independent variables, indirect effects in Path-model (Eq. 5, Table 6)
$p_{a,}\ p_{b,\ ..}\ p_x$	[0.. 1.0]	Path-coefficients for independent variables, direct effects in Path-model (Eq. 4)
p_v	[0.. 1.0]	Vegetation Path-coefficient (Table 7)
p_y	[0.. 1.0]	Yield Component Path-coefficient (Table 8)
U		Residual factor, the variance not explained by the Path coefficient model (Eq. 6).
R^2	[0.. 1.0]	Coefficient of determination, R-square, total variance, explained by the Path-model (Eq. 7)
Temperature	degree [C°]	Mean diurnal temperature as calculated from minimum and maximum values
ΔT	degree [C°]	Mean diurnal temperature change
T_b	degree [°]	Threshold temperature
dd	degree days [°]	[°]
ETS(T_b)	dd – degree days	Cumulative temperature sum over threshold temperature (T_b = 5 °)
ppm		Parts per million (CO_2 concentration)
CO_2	ppm	Atmospheric CO_2 concentration [ppm]
PAR	MJ/D m^{-2} [10-20]	Photosynthetically Active Radiation (l=400-700 nm)
RUE	DW g *MJ^{-1} d^{-1} [PAR: 1.0-5.0, Glob. Rad. 0.5-2.5]	Radiation Use Efficiency: Dry matter (DM) increase/ absorbed PAR or global radiation

Table 10. Cont.

CERES-Wheat Submodel Jones et al. (2003)	Genetic coefficients	Description, process or yield component affected	Range	Unit
I Phenological development	PHINT	Phyllochron (plastochron) interval as leaf appearance rate. Measures the age of a plant dependent on morphological traits rather than on chronological age.	<100	dd , °C d leaf^{-1}
	P1V	Vernalization	0-9	-
	P1D	Photoperiodism	1-5	-
	P5	Grain filling duration	1-5	-
II Yield component	G1	Grains/ear (GPP), Grains/m^2 (GPSM)	1-5	-
	G2	1000-seed weight	1-5	-
	G3	Spike number, affects lateral tiller production (TPSM)	1-5	-