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Effects of soil compaction on grain yield of wheat depend on weather conditions

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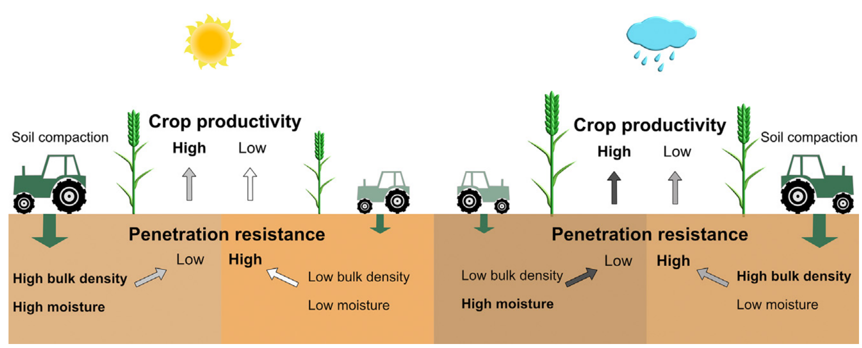
HIGHLIGHTS

- Soil compaction effects on wheat growth strongly depended on the weather conditions.
- High soil penetration resistance, but not high bulk density decreased wheat growth.
- High early vigor reduced grain yield under drying and hardening soil conditions.

GRAPHICAL ABSTRACT



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ABSTRACT

The use of heavy farm machinery has resulted in widespread soil compaction in many regions of the world. Compacted soil limits the access of crops to soil water and nutrients and is expected to reduce crop productivity, but the influence of weather conditions on the interactions between compacted soil and crop productivity is unclear. Furthermore, early vigor has been regarded as a promising trait for improving the yield of crops grown under edaphic stress such as soil compaction. We aimed to assess the combined effects of soil compaction and contrasting weather conditions on growth and grain yield of spring wheat, and to evaluate the association between early vigor and grain yield under temporal variations of the soil physical conditions. Nine spring wheat genotypes were grown on compacted and non-compacted soils during two cropping seasons with contrasting weather conditions in Central Sweden. Compared to the non-compacted treatment, soil compaction increased the relative growth rate of shoot biomass from sowing to stem elongation, and from stem elongation to flowering in the drier year (2018), but decreased the same traits in the wetter year (2019). The contrasting effects of soil compaction on shoot growth in the two years could be explained by soil moisture and penetration resistance associated with the interactive effects of soil compaction and weather condition. Higher early vigor, here indicated by higher relative growth rate from sowing to stem elongation, was associated with reduced grain yield under the progressively drying and hardening soil conditions during the entire cropping season of both years. We conclude that the interactive effects of soil physical and weather conditions need to be considered when evaluating the impact of soil compaction on crop growth and productivity. The potential of early vigor to increase grain yield is strongly influenced by the temporal dynamics of soil physical conditions.

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1. Introduction

The use of heavy farm machinery in intensive agriculture has resulted in widespread soil compaction in many regions of the world, and it is estimated that an area of 68 million hectares of arable land has been degraded by soil compaction (Batey, 2009; Hamza and Anderson, 2005). Compacted soil typically shows a degraded structure with low porosity, and low pore continuity and connectivity (Horn et al., 1995). Compaction increases soil penetration resistance through lowering soil porosity (Batey, 2009; Hamza and Anderson, 2005). Moreover, compaction decreases air and water transport capability of soil due to its negative effects on soil pore continuity and connectivity, which in turn may lead to soil hypoxia (Horn and Smucker, 2005; Kuncoro et al., 2014). Both high soil penetration resistance and poor soil aeration can reduce root elongation rate, delay the initiation of lateral roots, and result in shallow root systems (Barraclough and Weir, 1988; Blackwell and Wells, 1983; Colombi et al., 2018; Dresbøll et al., 2013). Thus, root growth into deeper soil layers is reduced under compaction and soil exploration by plant roots is often limited to the topsoil. These effects of soil compaction on root system development can limit the access of plants to soil water and nutrients and ultimately reduce shoot growth and crop productivity (Colombi et al., 2018; Grzesiak et al., 2013; Tubeileh et al., 2003).

Soil penetration resistance and aeration are strongly affected by soil moisture. Soil penetration resistance increases upon soil drying, whilst soil aeration decreases when soil moisture increases (Bengough et al., 2011; Tracy et al., 2011). Hence, high soil penetration resistance is likely to be the dominant physical stress for root growth under dry conditions (Whalley et al., 2008), and poor soil aeration is likely to limit root growth in compacted soil under wet conditions. Therefore, weather conditions in a given year might have a strong influence on the interactions between soil compaction, root growth, and ultimately shoot growth and grain yield. Since soil moisture fluctuates during a cropping season, crops growing on compacted soil can experience high soil penetration resistance and low soil aeration multiple times during a single cropping season. Due to the projected increase in extreme weather events with climate change (Pachauri et al., 2014), the risks of periodically high soil penetration resistance and poor soil aeration will likely increase in the future. Therefore the risk for reduced crop productivity caused by soil compaction is likely to increase in the course of climate change.

Whilst the impacts of high soil penetration resistance and poor soil aeration on crop growth and productivity have been investigated in previous studies, the temporal variations in soil penetration resistance and aeration are rarely taken into account (Colombi et al., 2018; Souza et al., 2021). Since penetration resistance is a function of dry bulk density and soil moisture (Jakobsen and Dexter, 1987), temporal dynamics of penetration resistance can be quantified with the measurement of dry bulk density and the in-situ continuous recording of moisture throughout the cropping season. Air-filled porosity is strongly linked to gas diffusivity and often used to evaluate soil aeration, and a threshold value of <10% is regarded as critical for plant growth (Lipiec and Hatano, 2003). Temporal dynamics of air-filled porosity can be quantified with soil total porosity and the dynamics of soil moisture. To better understand the interactive effects of soil compaction and future climate scenarios on soil resource accessibility and crop productivity, consideration of the temporal patterns of soil moisture, penetration resistance and aeration is needed.

Adapting plants through breeding to the soil physical conditions that typically occur in compacted soil is a promising yet underexploited approach to alleviate the adverse impacts of soil compaction on crop productivity (Bishopp and Lynch, 2015; Colombi and Keller, 2019; Palta and Watt, 2009). Information on the genotypic variation of plant traits is highly desired for breeding purposes. During crop establishment, plant growth is near to exponential so that a small increase in growth at the early crop phases will often result in a considerable increase in biomass production during later phases. Previous studies have reported the potential to increase wheat yield by selecting for genotypes with higher early vigor (Botwright et al., 2002; Regan et al., 1992; Turner and Nicolas, 1998), which usually refers to rapid shoot and root growth early in the growing season. Compared to wheat genotypes with lower early vigor, genotypes with higher early vigor have greater leaf transpiration and increased water and nutrient uptake from soil early in the growing season (Fischer and RA, 1979). In addition, genotypes with higher early vigor have larger leaf canopies and enhanced light interception to maximize plant growth rate early in the growing season (Liu et al., 2021). Furthermore, genotypes with high early vigor have early and fast root extension and proliferation (Palta and Watt, 2009), which improve the access to water and nutrients in subsoil layers. Early vigor is therefore expected to be a promising characteristic in order to favorably predispose plants to the adverse conditions occurring in compacted soil; and thereby positively affect wheat productivity on compacted soil. However, improving early vigor may also promote more rapid depletion of soil water and leave less soil water available for later growth if there is a terminal drought (Richards et al., 2002). Hence, the potential of early vigor to increase crop productivity on compacted soil should be evaluated along with the temporal variation of the soil physical conditions that the plants are exposed to during the cropping season.

We aimed to assess the combined effects of soil compaction and contrasting weather conditions on growth and grain yield of spring wheat, and to evaluate the association between early vigor and grain yield under temporal variations of soil physical conditions. We hypothesized that (H1) shoot growth and grain yield is reduced by soil compaction; and (H2) high early vigor promotes grain yield. Nine spring wheat genotypes were grown on compacted and non-compacted soils during two cropping seasons with contrasting weather conditions in Central Sweden. Seasonal dynamics of soil physical conditions, shoot growth rate during different phenological periods and grain yield were quantified.

2. Materials and methods

2.1. Site description and experimental design

Field experiments were carried out during the 2018 and 2019 cropping seasons in Uppsala, Sweden (59° 45′ N, 17° 42′ E), a region that is characterized by a boreal-temperate climate. May, June and July (i.e., from the emergency to the grain-filling of spring wheat) in 2018 were warmer and drier than the long-term mean (Supplementary Fig. S1); whilst May, June and July in 2019 were cooler and wetter than in 2018 (Fig. 1). Temperatures in May, June and July of 2019 were similar with the long-term means; precipitation in May 2019 was higher than the long-term mean whilst the precipitation values in June and July 2019 were lower than the corresponding long-term means (Supplementary Fig. S1). Due to an extended dry period without any precipitation that occurred in 2018, artificial irrigation of ca. 10 mm of water was applied 28 and 34 days after sowing (i.e., during stem elongation). The soil is classified as Cambisol (WRB, 2014) with a silt loam texture (16% clay, 70% silt, 14% sand) and an organic matter of 4% in the uppermost 0.3 m. At the same depth, the pH (H_2O) was 5.8 and the particle density was 2.61 Mg m^{-3}.

The field experiment had a split-plot design with four blocks, where each block contained soil compaction and non-compaction treatments. Nine spring wheat genotypes were grown in individual plots (2 m × 12 m) under each treatment. Mouldboard ploughing to approximately 0.2 m depth was performed in October 2017. Soil compaction treatment was carried out in April 2018 by double track-by-track passing using a front loader with four wheels and an average wheel load of 42 kN. To ensure crop establishment, the soil surface was loosened to a depth of approximately 50 mm with a tine harrow before sowing. After harvesting all the plants in August, mouldboard ploughing was

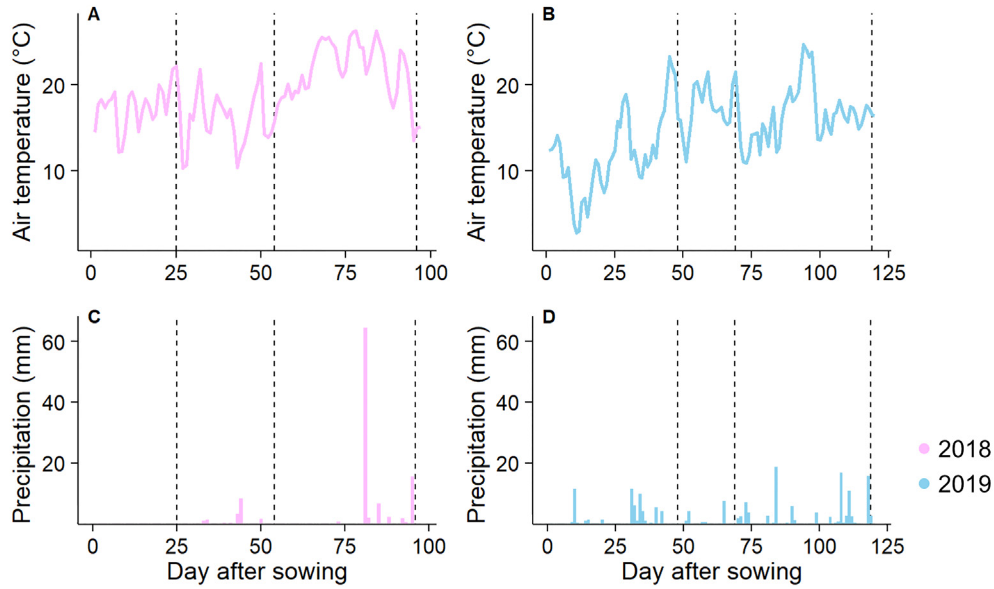

Fig. 1. Weather conditions near the field trial in Central Sweden during the cropping seasons in the years 2018 and 2019. All data were collected at the Ultuna climate station situated 3 km south-west from the experimental site. Dash lines indicate the beginning of stem elongation, flowering and maturity of spring wheat.

performed in October 2018. In 2019, the same experimental field was used, the soil was re-compacted using the same method, and the positions of the genotypes were re-randomized. The following spring wheat genotypes (Supplementary Table S1) were grown during both years: 'Bjarne', 'Boett', 'Dacke', 'Diskett', 'Happy', 'KWS Alderon' (Alderon), 'Quarna', 'Rohan' and a landrace originated from in Dalecarlia (Dala). These genotypes represent commonly grown spring wheat cultivars in northern Europe, and have been shown previously to vary considerably in shoot and root growth at an early growth stage (Liu et al., 2021). In addition, the chosen genotypes vary considerably in, e.g., leaf size, canopy height, disease resistance, grain yield and protein content (information from the Swedish wheat breeder Lantmännen). Wheat seeds were sown on 10th May 2018 and 23rd April 2019. Seed rates were 550 seeds m^{-2} as common in the region. At sowing, 140 kg ha^{-1} of N, 24 kg ha^{-1} of P and 46 kg ha^{-1} of K were applied.

2.2. Measurement of soil moisture

Soil volumetric water content was continuously recorded using time-domain reflectometry (TDR) sensors (5TM, Decagon Devices, Pullman, USA) from crop emergence until maturity. Two probes per depth were installed at 0.1 and 0.3 m depth in the plot of 'Diskett' under compacted and non-compacted treatments in two out of four blocks. Data were recorded in 30-min intervals using data loggers (Em50, Decagon Devices, Pullman, USA). To account for the influence of soil texture and clay mineralogy on TDR readings (Roth et al., 1992), the probes were calibrated using soil sieved to <2 mm taken from the top 30 cm from the same field site. The soil was air-dried and brought to a volumetric water contents of 0.06, 0.12, 0.18, 0.24, 0.30, 0.36 and 0.42 m^3 m^{-3} at a dry bulk density of 1.3 Mg m^{-3} in plastic containers (diameter: 0.1 m; height: 0.17 m). The measured output (i.e., dielectric constant) from the probes was then regressed against volumetric water content. This yielded a logarithmic regression equation ($R^2 = 0.99$; Supplementary Fig. S2), which was applied to calculate the in situ volumetric water content with the measured output from the probes.

2.3. Measurement of soil bulk density, porosity and penetration resistance

At crop flowering in 2018 and 2019, soil cylinders of 72 mm diameter and 50 mm height were sampled at 0.1 and 0.3 m depths from four randomly-selected plots in each treatment (i.e. compacted and non-compacted) of all blocks. The soil cylinder samples taken from 2018 were oven dried at 105 °C for 72 h to determine soil bulk density. Soil total porosity was then calculated from bulk density and particle density.

The soil cylinder samples taken from 2019 were used to quantify soil penetration resistance. We divided the soil cylinders taken from the same treatment and depth into two groups. Hence, both groups consisted of two samples from each treatment and soil depth. All soil samples were slowly saturated from below. The soil samples from the first group were equilibrated on a ceramic suction plate to soil matric potentials of −300 hPa, and the samples from the second group were equilibrated to −750 hPa matric potential. To represent average penetration resistance for each sample, four cones (base diameter: 2.6 mm, opening angle: 30°) with a recessed shaft were inserted simultaneously into the sample. The cones were inserted into the sample at a penetration speed of 4 mm min^{-1}. Penetration force was recorded by two 50 N load cells (S2M/50 N, HBM GmbH, Darmstadt, Germany) that were connected via an aluminum plate to the cone shafts. Mean penetration force was calculated from the point at which the cone was fully inserted into the soil until a penetration depth of 25 mm. Penetration resistance was determined by dividing mean penetration force by the cone base area. The soil samples from the first group were then equilibrated to −1500 hPa on ceramic pressure plates, whilst the samples assigned to the second group were equilibrated to −3000 hPa, and soil penetration resistance was measured again as described above. Hence, one half of the soil samples was used for penetration resistance measurements at −300 and −1500 hPa, whilst the other half of the samples was used for penetration resistance measurements at −750 and −3000 hPa. Weighing the samples at the different matric potentials yielded gravimetric water content. Soil bulk density was determined from oven-dried samples (105 °C, 72 h). Volumetric water content was determined for the different matric potentials using bulk density and gravimetric water content.

We used the model proposed by Jakobsen and Dexter (1987) to explain soil penetration resistance (Q [MPa]) as a function of volumetric soil water content (θ_v [m^3 m^{-3}]) and soil bulk density (ρ_b [Mg m^{-3}]) based on treatment mean values:

$$Q = e^{a\theta_v + b\rho_b + c} \qquad (1)$$

Temporal dynamics of soil penetration resistance at 0.1 and 0.3 m depths of compacted and non-compacted soil were quantified as follows. In-situ soil volumetric water content data, which was obtained from the recordings of time-domain reflectometry sensors, and soil bulk density were averaged for compacted and non-compacted soil for each depth (at 0.1 and 0.3 m) separately. This data was then combined with the regression equation (Eq. (1)) to quantify the temporal dynamics of soil penetration resistance in 2018 and 2019.

Temporal dynamics of soil air-filled porosity (ε_a) were quantified using total porosity (ε [$m^3\ m^{-3}$]) and soil volumetric water content (θ [$m^3\ m^{-3}$]):

$$\varepsilon_a = \varepsilon - \theta \tag{2}$$

2.4. Plant sampling

To assess the aboveground plant biomass at different developmental phases, shoots within 0.5 m × 0.5 m areas in each plot were sampled at the beginning of stem elongation (BBCH 30), flowering (BBCH 65) and maturity (BBCH 89). The shoots were harvested with scissors at approximately 15 mm above the soil surface, oven-dried at 65 °C for 72 h and weighted. The relative growth rate of shoot biomass (RGR) from sowing to the beginning of stem elongation, from the beginning of stem elongation to flowering, and from flowering to maturity were calculated according to the following:

$$RGR = \frac{\ln w2 - \ln w1}{t2 - t1} \tag{3}$$

where w1 and w2 are the shoot biomass values at times (t) 1 and 2, respectively. The RGR from sowing to the beginning of stem elongation was here used as an indicator of early vigor. To assess grain yield, the central plot area (2 m × 6 m) was harvested with a combine harvester on 17th August 2018 (i.e., 99 days after sowing) and 23rd August 2019 (i.e., 122 days after sowing), respectively.

2.5. Statistical analyses

All statistical analyses were performed using R version 4.0.0 (R Core Team, 2020). Two-way analysis of variance (ANOVA) was performed to test the effects of soil compaction treatment, year and their interaction on soil bulk density. Treatment means were compared using Tukey's honesty significant difference test at $p < 0.05$. Linear mixed-effects models were used to test the effects of year, soil compaction treatment, genotype and their interactions on RGR and grain yield with the 'lme4' package (Bates et al., 2015). Year, soil compaction treatment, genotype and their interactions were set as fixed effects, and block, main-plot and plot as random effects. Linear regression analyses were used to assess the relationships between RGR and grain yield based on genotype mean values. Non-linear least square methods provided by the 'stats' package was used to evaluate the regression model predicting soil penetration resistance as a function of soil volumetric water content and soil bulk density.

3. Results

3.1. Effects of compaction treatment on soil bulk density

The effects of soil compaction on soil bulk density were similar in the two years (Fig. 2). Compaction increased the soil bulk density at 0.1 m by 10.1% in 2018 and 17.1% in 2019. The effects of compaction on soil bulk density were less pronounced at 0.3 m depth than at 0.1 m depth. Compaction increased the soil bulk density at 0.3 m by 4.9% in 2018 and 7.9% in 2019.

3.2. Temporal dynamics of soil physical conditions

Soil penetration resistance was estimated from bulk density and volumetric water content using Eq. (1). The fitted soil penetration resistance was highly correlated with the measured penetration resistance ($R^2 = 0.81$; Supplementary Fig. S3), indicating that soil penetration resistance could be explained by bulk density and volumetric water content in this study.

The contrasting weather conditions in the two years affected the soil water contents at 0.1 m depth differently under the compacted and non-compacted treatments. Compared to the non-compacted treatment, the compacted treatment had higher soil water content at 0.1 m

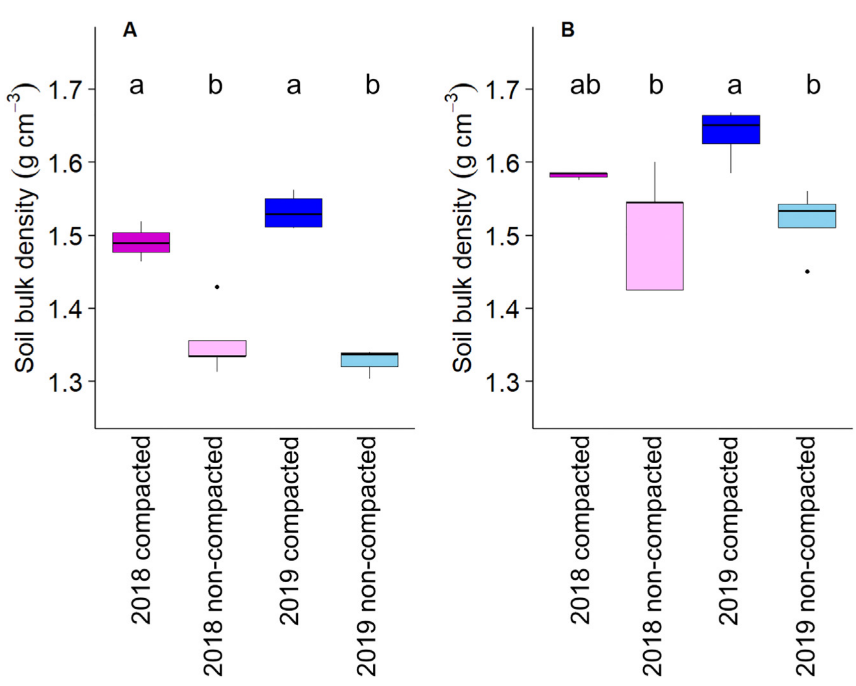

Fig. 2. Soil bulk density at (A) 0.1 m and (B) 0.3 m depth in the field trial under the compacted and non-compacted treatments in the years 2018 and 2019. Different letters indicate significant difference between the treatment means using Tukey's honesty significant difference test at $p < 0.05$.

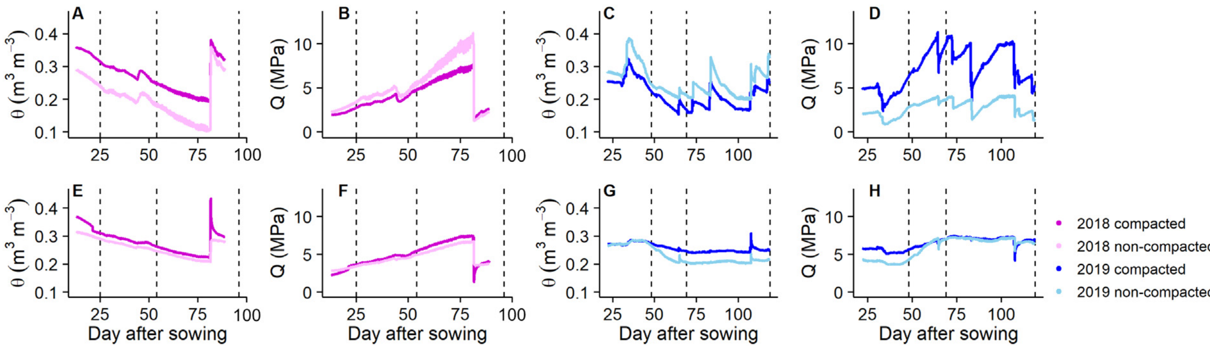

Fig. 3. Dynamics of soil volumetric water content (Θ) and penetration resistance (Q) at 0.1 m (A–D) and 0.3 m (E–H) depth in the field trial under two soil compaction treatments in the years 2018 and 2019. Dash lines indicate the beginning of stem elongation, flowering and maturity of spring wheat.

depth in the dry year 2018, whilst it resulted in lower soil water content at 0.1 m depth in the relatively wetter year 2019 (Fig. 3). In contrast, the compacted treatment resulted in slightly higher soil water contents at 0.3 m depth compared to the non-compacted treatment in both years (Fig. 3E and G). Although the compacted treatment significantly increased soil bulk density, it did not always result in higher soil penetration resistance due to the interplay between soil water content and penetration resistance. Soil penetration resistance at 0.1 m depth under the compacted treatment was lower than the non-compacted treatment in 2018, whilst the pattern was reversed in 2019 (Fig. 3B and D). In contrast, penetration resistances at 0.3 m depth under the compacted treatment were slightly higher than the non-compacted treatment in both years (Fig. 3F and H). Compared to the non-compacted treatment, soil compaction decreased soil air-filled porosity at both depths in both years. Except for the first 33 days and the last eight days under the compacted treatment in 2018, air-filled porosity was above 10% (Supplementary Fig. S4).

In 2018, soil water content was high in the beginning of the cropping season due to a wet winter season. However, soil water contents were rapidly decreasing and consequently, penetration resistances were increasing from crop emergence to the end of the season (Fig. 3), indicating that the plants were exposed to progressively deteriorating soil physical conditions throughout the cropping season in 2018. In 2019, soil water content and penetration resistance at 0.1 m depth were fluctuating throughout the cropping season. In spite of the fluctuations, the mean water content was higher and the mean penetration resistance was lower from crop emergence to stem elongation compared to those from stem elongation to maturity (Table 1). A similar trend was also observed at 0.3 m depth (Table 1). These results indicate that the soil physical conditions were better at the early plant growth phase than at the major plant growth phase and post-anthesis in 2019.

3.3. Effects of year, compaction treatment and genotype on plant growth and grain yield

The RGR from sowing to the beginning of stem elongation, RGR from the beginning of stem elongation to flowering, RGR from flowering to maturity, and grain yield were all significantly different among the nine investigated genotypes. Effects of soil compaction treatment on plant growth and grain yield were different between the two years (Y × T in Table 2). In 2018, the compacted treatment, exposing plants to decreased soil penetration resistance at 0.1 m depth, significantly increased the RGR from sowing to the beginning of stem elongation and the RGR from the beginning of stem elongation to flowering compared to the non-compacted treatment (Table 2). No significant effect of soil compaction on grain yield was found in 2018, but grain yield tended to be higher under the compacted treatment than the non-compacted treatment in 2018 (Fig. 4). In 2018, neither the RGR during three periods nor grain yield were affected by the interaction of soil compaction and genotype.

In 2019, RGR from sowing to the beginning of stem elongation and RGR from the beginning of stem elongation to flowering were significantly reduced by soil compaction. In spite of these differences in RGR between the compacted and non-compacted treatments, peak flowering and thus the transition from vegetative to generative

Table 1
Mean values of soil volumetric water content and penetration resistance during different periods in a field experiment exposing nine spring wheat genotypes to two soil compaction treatments during two years (2018 and 2019).

Soil parameter	Depth	Year	Soil treatment	Mean value from crop emergence to the beginning of stem elongation	Mean value from the beginning of crop stem elongation to flowering	Mean value from crop flowering to maturity
Volumetric water content ($m^3\ m^{-3}$)	10 cm	2018	Compacted	0.33	0.25	0.22
Volumetric water content ($m^3\ m^{-3}$)	10 cm	2018	Non-compacted	0.24	0.19	0.17
Volumetric water content ($m^3\ m^{-3}$)	10 cm	2019	Compacted	0.23	0.17	0.18
Volumetric water content ($m^3\ m^{-3}$)	10 cm	2019	Non-compacted	0.29	0.20	0.22
Volumetric water content ($m^3\ m^{-3}$)	30 cm	2018	Compacted	0.34	0.26	0.23
Volumetric water content ($m^3\ m^{-3}$)	30 cm	2018	Non-compacted	0.28	0.24	0.21
Volumetric water content ($m^3\ m^{-3}$)	30 cm	2019	Compacted	0.25	0.23	0.22
Volumetric water content ($m^3\ m^{-3}$)	30 cm	2019	Non-compacted	0.25	0.20	0.18
Penetration resistance (MPa)	10 cm	2018	Compacted	2.30	3.76	5.40
Penetration resistance (MPa)	10 cm	2018	Non-compacted	2.84	4.50	6.81
Penetration resistance (MPa)	10 cm	2019	Compacted	4.63	8.65	8.05
Penetration resistance (MPa)	10 cm	2019	Non-compacted	1.82	3.42	3.01
Penetration resistance (MPa)	30 cm	2018	Compacted	2.97	4.59	6.02
Penetration resistance (MPa)	30 cm	2018	Non-compacted	3.12	4.25	5.47
Penetration resistance (MPa)	30 cm	2019	Compacted	5.49	6.45	7.03
Penetration resistance (MPa)	30 cm	2019	Non-compacted	3.96	6.11	6.92

Volumetric water content were recorded every 30 min. Penetration resistance was estimated with soil bulk density and volumetric water content.

Table 2
Effects of year (df = 1), soil compaction treatment (df = 1), genotype (df = 8) and their interactions on relative growth rate of shoot biomass (RGR) and grain yield analyzed with analysis of variance (ANOVA); mean values of nine wheat genotypes grown under each treatment (compacted and non-compacted) and years (2018 and 2019).

	ANOVA							Treatment mean			
Trait (unit)	Year (Y)	Treatment (T)	Genotype (G)	Y × T	T × G	Y × G	Y × T × G	2018 compacted	2018 non-compacted	2019 compacted	2019 non-compacted
RGR from sowing to stem elongation (d^{-1})	***	n.s.	***	***	n.s.	**	n.s.	0.015	0.011	0.035	0.038
RGR from stem elongation to flowering (d^{-1})	***	n.s.	***	***	n.s.	n.s.	n.s.	0.078	0.073	0.052	0.056
RGR from flowering to maturity (d^{-1})	n.s.	n.s.	***	***	n.s.	n.s.	n.s.	0.006	0.008	0.009	0.007
Grain yield (Mg ha^{-1})	*	n.s.	***	***	n.s.	***	n.s.	2.17	1.91	2.52	2.57

***, ** and * denote significant effects at $p < 0.001$, $p < 0.01$ and $p < 0.05$, respectively, n.s. denotes non-significant effects (n = 4).

development were reached ca. 69 days after sowing under both treatments. No significant effect of soil compaction on grain yield was found in 2019, but grain yield was significantly affected by the interaction of soil compaction and genotype in 2019. Thus, the grain yield of one genotype ('Alderon'), but not the other genotypes was significantly reduced by soil compaction (Fig. 4). Similar to 2018, the RGR during three periods were not affected by the interaction of soil compaction and genotype in 2019.

3.4. Relationships between early vigor and grain yield

Grain yield consistently decreased with higher RGR from sowing to the beginning of stem elongation (early vigor) in both years; whilst it significantly increased with higher RGR from the beginning of stem elongation to flowering under both treatments in 2018 and the compacted treatment in 2019 ($0.47 < R^2 < 0.70$, $p < 0.05$; Fig. 5). Grain yield significantly increased with higher RGR from flowering to maturity under both treatments in 2018 ($0.61 < R^2 < 0.66$, $p < 0.05$; Fig. 5). The above results indicate that higher early vigor consistently reduced grain yield in our study, whilst faster shoot growth during the major growth phase and post-anthesis promoted grain yield.

4. Discussion

By investigating the effects of soil compaction on plant growth and grain yield under contrasting weather conditions in two years, we found that soil compaction increased shoot growth in the drier year, but decreased shoot growth in the wetter year. By exploring the seasonal dynamics of soil physical conditions and plant growth, we found that higher early vigor reduced grain yield, and this relationship was associated with the progressively deteriorating soil physical conditions during the entire cropping season. The strengths of this study include the combination of soil compaction, contrasting weather conditions and contrasting plant genotypes, facilitating the investigation of links between important soil physical properties, weather condition and plant characteristics affecting biomass growth and grain yield; and the consideration of the temporal dynamics of soil physical conditions when evaluating the effects of soil compaction on plant growth and yield. A limitation of this study is that soil moisture dynamics were only measured in the plots of one genotype (i.e., 'Diskett'); assuming similar effects of all genotypes on soil moisture dynamics, although it has been shown that different wheat genotypes can have differential effects on soil moisture (Hodgkinson et al., 2017). The main focus of this study was on the combined effects of soil compaction and contrasting weather conditions on wheat growth and grain yield (using a set of genotypes representative for the cultivation region), and the above limitation implies that conclusions on the genotype-specific effects on soil moisture cannot be made in this study.

4.1. The necessity to assess dynamics of soil physical conditions and plant growth

Bulk density is a relatively simple measurement and commonly used to quantify soil compaction (Lipiec and Hatano, 2003). However, we found that higher penetration resistance rather than higher bulk density was associated with the reduced shoot growth and grain yield in 2018, suggesting that penetration resistance is more suitable than bulk density to link the soil mechanical conditions to crop growth and yield. Although the impacts of high soil penetration resistance on plant growth have been studied before (Barraclough and Weir, 1988; Bengough et al., 2011; Colombi et al., 2018; Whalley et al., 2008), the temporal variation in penetration resistance is rarely reported (Souza et al., 2021), and it is not linked with plant growth in the above study (Souza et al., 2021). In our study, we quantified the temporal dynamics of penetration resistance by considering both soil bulk density and the variation in soil moisture following the compaction, which improves our understanding of the effects of soil compaction on plant growth during different periods of the cropping season. Since tillage modifies soil bulk density

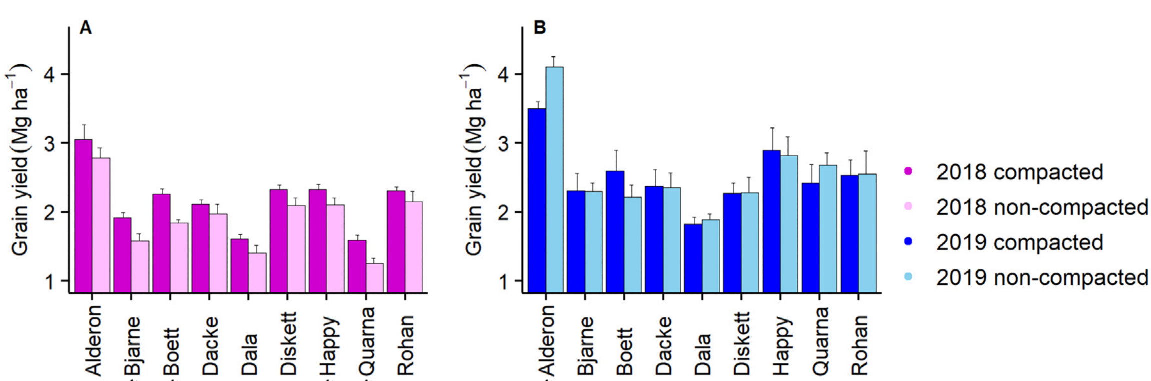

Fig. 4. Grain yield of nine spring wheat genotypes grown under different soil compaction treatments in the years 2018 and 2019. The genotypes that significantly responded to soil compaction are marked with asterisks. Bars represent standard errors (n = 4).

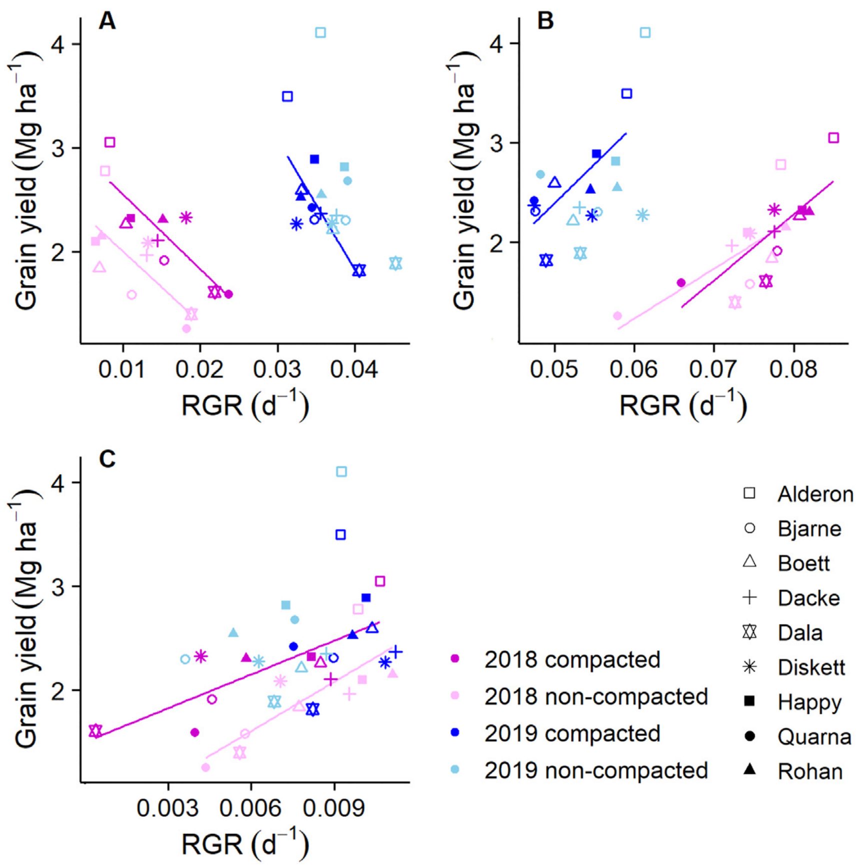

Fig. 5. Relationships between grain yield and (A) relative growth rate of shoot biomass (RGR) from sowing to the beginning of stem elongation, (B) RGR from the beginning of stem elongation to flowering, and (C) RGR from flowering to maturity of nine spring wheat genotypes grown under different soil compaction treatments in the years 2018 and 2019. Statistics: (A) 2018 compacted: $r^2 = 0.70$, $p = 0.005$; 2018 non-compacted: $r^2 = 0.52$, $p = 0.029$; 2019 compacted: $r^2 = 0.51$, $p = 0.030$; (B) 2018 compacted: $r^2 = 0.65$, $p = 0.009$; 2018 non-compacted: $r^2 = 0.47$, $p = 0.041$; 2019 compacted: $r^2 = 0.52$, $p = 0.028$; (C) 2018 compacted: $r^2 = 0.61$, $p = 0.013$; 2018 non-compacted: $r^2 = 0.66$, $p = 0.008$.

and soil hydraulic properties (Strudley et al., 2008) and thus soil penetration resistance, our findings may also be relevant when evaluating impacts of different tillage systems on crop growth and productivity.

4.2. Soil compaction increased plant growth in the drier year but decreased plant growth in the wetter year

In the drier year 2018, the non-compacted treatment significantly decreased shoot growth rate (Table 2) when compared to the compacted treatment, which has rarely been reported by others (Arvidsson and Håkansson, 2014; Moraes et al., 2018). Also, the non-compacted treatment was associated with slightly (but not significantly) lower grain yield in 2018, which is contrary to our first hypothesis (H1). The air-filled porosity at 0.1 and 0.3 m depths under the non-compacted treatment was higher than 10% during most time of the cropping season (Supplementary Fig. S4), indicating a sufficient oxygen status for plant growth (Lipiec and Hatano, 2003). Plants might have suffered from low soil water availability and restricted accessibility to soil water. Soil penetration resistance is the main soil property that determines water accessibility, because high soil penetration resistance can result in reduced root elongation rate, delayed initiation of lateral roots and shallower root growth (Bengough et al., 2011; Colombi et al., 2018). Therefore, the reduced shoot growth and grain yield under the non-compacted treatment were presumably caused by the decreased soil water content (as an indication of reduced soil water availability) at both 0.1 and 0.3 m depths and the decreased water accessibility due to high soil penetration resistance at 0.1 m depth. The interpretation of plant responses is complicated by the fact that low soil water content and high soil penetration resistance are often highly related (Bengough et al., 2011), making it difficult to identify whether the plant is responding to low water availability or low water accessibility caused by high soil penetration resistance. When soil dries, penetration resistance increases nonlinearly with decreasing water content, which may result in penetration resistance limiting root growth to a relatively greater extent than water availability (Bengough et al., 2011). The critical value of penetration resistance for being a major limitation to root growth may vary depending on the tillage system but is assumed to be between 2 and 3.5 MPa (Bengough et al., 2011; Moraes et al., 2014). In our study, penetration resistance under the non-compacted treatment was above these values for most of the cropping season 2018 (Fig. 3B). Therefore, high soil penetration resistance might have been a greater limitation to plant growth than low water availability. Although root growth was likely limited by the high soil penetration resistance in our site, roots could have used biopores and cracks to pass hard soil layers in order to access water and nutrients in the subsoil (Athmann et al., 2013; Kautz et al., 2013; White and Kirkegaard, 2010).

In the relatively wetter year 2019, the compacted treatment significantly decreased shoot growth (Table 2) compared to the non-compacted treatment, which is consistent with previous studies (Andersen et al., 2013; Colombi and Walter, 2017; Whalley et al., 2008). The reduced shoot growth under the compacted treatment was probably caused by the decreased soil water content at 0.1 m depth and the decreased water accessibility due to high soil penetration resistance at both 0.1 and 0.3 m depths. The compacted treatment significantly reduced grain yield of only one genotype but not the others, thus not generally supporting our first hypothesis (H1). High soil penetration resistance was associated with low grain yield in the dry year

2018 but not in the relatively wetter year 2019 for most of the genotypes investigated here, suggesting that soil penetration resistance is not a limiting factor to grain yield under favorable water conditions. Soil compaction had contrasting effects on shoot growth and grain yield in the two years due to the reverse patterns of soil water content, as well as penetration resistance, under the two soil compaction treatments observed in the two years. Thus, the interactive effects of soil compaction and weather condition on soil physical conditions should be considered when evaluating the impacts of soil compaction on plant growth and crop productivity.

4.3. High early vigor does not always predispose high yield

It has been frequently reported that higher early vigor was associated with higher grain yield of wheat (Botwright et al., 2002; Regan et al., 1992; Turner and Nicolas, 1998; Whan et al., 1991), because early vigor improved water use efficiency by shading the soil surface to reduce water loss from evaporation (López-Castañeda and Richards, 1994) and by increasing the ability of the crop to compete with weeds (Coleman et al., 2001; Dingkuhn et al., 1999; Mwendwa et al., 2020). In contrast to these studies, we observed that higher early vigor (here assessed as RGR from sowing to the beginning of stem elongation) consistently reduced grain yield, which is contrary to our second hypothesis (H2). The maintenance of early vigorous root systems may demand additional carbon investment in roots (Atwell, 1990; Xiong et al., 2006), but we did not monitor root growth in our field study. In addition, higher early vigor is associated with larger leaf area (Liu et al., 2021; Pang et al., 2014), which could increase plant water loss by transpiration. Compared to the genotypes with lower early vigor, the genotypes with higher early vigor (e.g., 'Dala', 'Quarna' and 'Bjarne') presumably lost more plant water through transpiration due to the high air temperatures (Fig. 1) especially during the later growth phases. Furthermore, the decreasing soil water content and increasing soil penetration resistance (Fig. 3) indicate that the availability and accessibility of soil water was limited to replenish the plant water loss during the later growth phases. Therefore, in our study, the genotypes with higher early vigor suffered relatively more from the progressively deteriorating soil physical conditions than the ones with lower early vigor; a pattern that was reflected by negative correlations between the relative growth rate (RGR) from sowing to the beginning of stem elongation (early vigor) and the RGR during the later growth phases (Supplementary Fig. S5). Early vigor has been regarded as a promising trait in wheat breeding towards improved water and nutrient use efficiencies and grain yield (Botwright et al., 2002; Liao et al., 2006; Pang et al., 2014; Richards et al., 2002). However, our study suggests that the potential of early vigor to increase grain yield needs to be further investigated, especially along with the prevailing weather conditions and associated temporal dynamics of soil physical conditions, before being generally applied in crop breeding.

5. Conclusion

Soil compaction had contrasting effects on shoot growth and grain yield under contrasting weather conditions in this study, suggesting that the impacts of soil compaction on crop productivity should be evaluated in the context of the interactive effects of soil physical and weather conditions. Higher early vigor reduced grain yield under progressively drying and hardening soil conditions during entire cropping seasons, emphasizing that the potential of early vigor to increase grain yield is strongly influenced by the temporal dynamics of the soil physical conditions.

Data availability statement

The data supporting the finding of this manuscript are available on reasonable request to the corresponding author.

CRediT authorship contribution statement

Hui Liu: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing (original draft preparation). **Tino Colombi:** conceptualization, formal analysis, investigation, methodology, supervision, writing (original draft preparation). **Ortrud Jäck:** conceptualization, investigation, methodology, supervision, writing (review and editing). **Thomas Keller:** conceptualization, funding acquisition, methodology, supervision, writing (review and editing). **Martin Weih:** conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing (review and editing). All authors have read and agreed to the published version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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