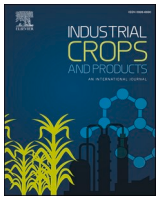
Industrial Crops & Products 208 (2024) 117798

Contents lists available at ScienceDirect

Industrial Crops & Products

journal homepage: www.elsevier.com/locate/indcrop



Genetic variation of annual and biennial caraway (*Carum carvi*) germplasm offers diverse opportunities for breeding

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ARTICLE INFO

Keywords:
Carum carvi
Genetic diversity
Quantitative traits
Umbelliferae
Near infrared spectroscopy (NIRS)

ABSTRACT

Caraway (*Carum carvi*) is an important aromatic plant of the Apiaceae family. Fruits and essential oil are used as spice, pharmaceutical and for various industrial purposes. Cultivation is endangered by on-going climatic changes so that new breeding projects are necessary to secure future cultivation of caraway. However, the initialization of new breeding programs is hampered by poor availability of phenotypic data. To close this gap, 64 annual and 68 biennial caraway accessions were phenotyped under field conditions in two years. We determined the beginning of flowering, the end of flowering, maturity, plant height, thousand-grain weight, stalk attachment rate, shattering rate, limonene, carvone and total essential oil content. Best linear unbiased estimates (BLUEs) and broad sense heritability were computed using linear mixed-effects models. We observed a high variability for all traits with medium to high heritability (h^2 = 0.52 – 0.95). Merely for the carvone to limonene ratio, heritability was lower (0.17–0.25). Thus, the observed phenotypic diversity is applicable to breeding. Insights into correlations between traits may ease selection processes in breeding projects. The distribution of the phenotypic variation of some traits was partially associated with the genetic substructure detected by genotyping by sequencing (GBS) data. This could be explained by selections in former breeding programs.

1. Introduction

Caraway (*Carum carvi* L., 2 n = 2x = 20) belongs to the Apiaceae family (syn. Umbelliferae). Fruits contain essential oil containing R-(+)-limonene and S-(+)-carvone as major components (Ruszkowska, 1998; Pank, 2012). These molecules play a major role for the broad usage of caraway in foods, pharmacy and industry. Complete or ground, fruits are widely used as spice. In pharmacy, fruits or essential oil are used in teas, alcoholic or dried extracts, capsules or liquids. In addition, essential oil is used as supplement in spirits, cosmetics and groceries (Pank, 2012). Additionally, carvone is used for sprout inhibition in potato (Cizkova et al., 2000; Gómez-Castillo et al., 2013).

Due to on-going climatic changes, cultivation of caraway becomes riskier. In particular, the slow growing crop can be severely affected by prolonged drought stress periods in summer. Therefore, new breeding programs are necessary to develop varieties adapted to drought stress. Breeding of early flowering varieties is a major breeding goal to avoid drought stress events during the flowering period. Recent field trials revealed strong associations between early flowering and high yields (von Maydell et al., 2021b),which supports this strategy. Necessarily, new varieties for use in pharmaceuticals must cope with the requirements of the European Pharmacopeia (Ph. Eur.). Caraway fruits must contain a minimum of 3 ml/100 g essential oil measured by distillation (Ph. Eur, 2020a). The essential oil must contain carvone in a range from 50% to 65% and limonene in a range from 35% to 45% (Ph. Eur, 2020b). Breeding of non-shattering varieties can be an additional breeding goal. Cultivation of shattering varieties can cause high yield losses, if not harvested in time. In contrast, non-shattering varieties are unaffected by late harvesting (Toxopeus and Lubberts, 1994). A stronger attachment of pedicles at fruits (high stalk attachment rate) could be an

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https://doi.org/10.1016/j.indcrop.2023.117798
Received 9 May 2023; Received in revised form 21 September 2023; Accepted 9 November 2023
Available online 18 November 2023

Fig. 1. Field trial at the JKI in Quedlinburg in June 2019. Foreground: biennial accessions in leaf rosette stage. Background: annual accessions in flowering stage.

undesirable side effect of reduced shattering (von Maydell et al., 2021b). High stalk attachment rates are detrimental for marketing, but can be reduced by post-harvesting treatments.

Whereas breeding goals are determined, initialization of breeding projects is hampered by poor availability of phenotypic data on available germplasm. Prior evaluations were restricted to 10–43 accessions in individual studies (Toxopeus and Lubberts, 1994; Galambosi and Peura, 1996; Ferrie et al., 2011; Seidler-Lozykowska and Bocianowski, 2012; Raal et al., 2012). Only Seidler-Lozykowska and Bocianowski (2012) distinguished between environmental and genetic effects on phenotypic variation. Yet, an appropriate initial selection of genetic material is the first crucial step for the success of a breeding project. Hence, in this study, we strived to provide a comprising evaluation of caraway germplasm from gene banks, research institutes and companies for the most important quantitative traits. We evaluated 132 accessions from a set which was recently established to analyze the genetic population structure in caraway by genotyping by sequencing (GBS; von Maydell et al., 2021a). This general evaluation of phenotypic and genetic variability in caraway should lay the foundation for new breeding and research projects.

2. Material and methods

2.1. Plant material

The set of accessions used in this study is described in more detail by von Maydell et al. (2021a). The evaluation of quantitative traits was conducted for 132 of 137 accessions. In detail, 64 annual and 68 biennial accessions were evaluated. Annual material mainly consisted of inbred lines from recent breeding programs and a few cultivars. In contrast, biennial material mainly consisted of wild material, cultivars and landraces from gene banks.

2.2. Phenotyping and Chemotyping

The caraway accessions were assigned to two groups according to flowering type. Plants were grown in the greenhouse until the early leaf stage. Subsequently, in 2018 and 2019, annual and biennial plants were planted in adjacent field trials. Annual genotypes were evaluated 2018 and 2019 and biennial genotypes 2019 and 2020. For each subset, a randomized complete block design was used. Seed availability and germination rates of several genotypes were low. Consequently, some modifications of the experimental set-up were necessary in the second year of growing. In 2018, 25 plants per genotype and repetition were planted in a plot with a distance of 10 cm between plants and of 50 cm between plots. Up to three repetitions per genotype were planted. In 2019, the number of plants per genotype and repetition was reduced to six (Fig. 1). The distance between plants was increased to 20 cm. Up to four repetitions per genotype were planted. The increased distance between plants in 2019 allowed single plant analysis for all investigated traits, whereas for genotypes sown in 2018 single plant analysis was limited to the beginning of flowering and height. Other traits were analyzed per plot.

Evaluated traits and methods of measurement are listed in Table 1. Further details on the estimation of essential oils are described below.

2.2.1. NIRS measurements

Intact seeds (portions of 1 – 2 g each per plant) were measured with a Bruker MPA (Bruker Optics, Ettlingen, Germany) FT-NIR spectrometer in quartz cuvettes with 32 scans at 8 cm^{-1} resolution. Portions from 45 and 147 plants (including duplicates) were selected for reference analysis in the growing seasons, respectively.

2.2.2. GC analysis

For the reference, volatiles were extracted from 200 mg dry matter with 4 ml isooctane (Th.Geyer, Hoexter, DE) containing fenchon (Roth, Karlsruhe, DE) at a concentration of 1:2000. One µl was injected into a GC-FID (6890 N, Agilent, Santa Clara, CA) equipped with a HP-5MS column (30 m x 250 µm x 0.5 µm (Agilent) and separated along an 11 min gradient as described by Schulz et al. (2000). Peaks were picked using OpenChrom (https://lablicate.com/platform/openchrom) and peak table compilation was conducted using an R script including an algorithm of the xcms-package (Smith et al., 2006) for the peak alignment.

2.2.3. PLS-Regression

Season-specific PLS models were built in R (R Core Team, 2018) using the packages hyperSpec (Beleites and Sergo 2020) and pls (Mevik and Wehrens, 2007). Spectra were pre-pocessed by cutting the spectral range to 3750 – 6250 cm^{-1} , binning every 4 data points and calculating the 2nd derivative with a Savitzky-Golay (package signal, signal developers, 2014) filter with polynomial order 4 and window size 7 data points. PLS2 models predicting carvone and limonene simultaneously with 5 (1st season) and 4 latent variables (2nd season) were used.

2.3. Genetic analysis

The genotyping and genetic analyses were described in von Maydell et al. (2021a). Briefly, a matrix of 13,155 single nucleotide polymorphisms (SNPs) was generated using genotyping by sequencing (GBS, Elshire et al., 2011). The algorithm BIONJ (Gascuel, 1997) was used to construct a neighbor joining tree.

2.4. Statistics

In general, statistical analyses were carried out using R software (R Core Team, 2018) and annual and biennial accessions were treated separately. Data for shattering rate and stalk attachment rate were transformed by an arcus-sinus-transformation to fulfill the requirements of linear models. Data were visualized using the package ggplot2

Table 1
List of evaluated traits for annual and biennial genotypes. Multiple measurements /Single plant measurements were averaged per plot. Abbr. = abbreviation.

Abbr.	Trait	Unit	Method of measurement
BOF	Beginning of flowering	days	Time after sowing when a single plant had begun flowering, defined as the opening of the first umbel.
EOF	End of flowering	days	Time after sowing when about 90% of plants of a plot (2018/19) or a single plant (2019/20) had finished flowering, defined as the decay of petals in the last flowering umbels.
HGT	Plant height	cm	Height of erected single plants at the end of flowering.
MAT	Maturity	days	Time after sowing when a plot (2018/19) or a single plant (2019/20) reached brown maturity, i.e. was ready for harvesting.
SHT	Shattering rate	%	At brown maturity, ten different umbellets per plot (2018/19) or plant (2019/20) were pulled gently. The proportion of cases in which seeds broke loose from the umbellets was defined as the shattering rate. Three measurements per plot in 2018/19 and one measurement per single plant in 2019/20.
TGW	Thousand grain weight	g	Weight of 100 randomly chosen purified seeds times 10. Complete double achenes were defined as two seeds. Three measurements per plot in 2018/19 and one measurement per single plant in 2019/20.
STA	Stalk attachment rate	%	Proportion of seeds from 100 randomly chosen purified seeds with an attached pedicel (flower stalk) of a minimum length of 1 cm. Double achenes with attached pedicel were defined as two seeds, but one pedicel. Three measurements per plot in 2018/19 and one measurement per single plant in 2019/20.
LIM	Limonene content	g/ 100 g	Predicted limonene content by NIRS. Three replicates per plot in 2018/19 and one replicate per single plant in 2019/20.
CRV	Carvone content	g/ 100 g	Predicted carvone content by NIRS. Three replicates per plot in 2018/19 and one replicate per single plant in 2019/20.
CRV %	*(Approximate) Proportion of carvone in essential oil*	%	*Computed from limonene and carvone content. Minor components of essential oil are neglected (not calibrated by NIRS).*
OIL	(Approximate) Essential oil content	g/ 100 g	Sum of the predicted limonene and carvone content (essential oil not directly calibrated by NIRS method). Minor components of essential oil are neglected.

Table 2
Summary data for all investigated quantitative traits based on BLUEs from 64 annual and 68 biennial accessions, respectively. Mean = arithmetic mean, SD = standard deviation, CV = coefficient of variance, Min = minimum, Max = maximum. See Table 1 for full denomination of traits.

	Annuals					Biennials				
Traits	Mean	SD	CV	Min	Max	Mean	SD	CV	Min	Max
BOF	78.25	6.64	0.08	68.49	96.04	391.96	6.66	0.02	382.08	420.86
EOF	119.56	6.30	0.05	107.58	135.19	436.64	7.05	0.02	415.48	470.39
HGT	53.11	7.71	0.15	35.58	71.28	54.49	7.44	0.14	37.21	69.96
MAT	149.65	6.29	0.04	138.02	165.35	458.85	6.92	0.02	446.02	479.45
SHT	90.19	11.00	0.12	41.45	99.93	87.55	21.61	0.25	23.53	100.00
TGW	2.41	0.40	0.16	1.76	3.52	2.24	0.39	0.18	1.58	3.08
STA	16.78	11.44	0.68	1.95	51.88	8.30	11.48	1.38	0.01	38.80
CRV	2.69	0.53	0.20	1.84	4.35	2.04	0.30	0.15	1.31	2.72
LIM	3.31	0.72	0.22	2.11	5.30	3.08	0.42	0.14	2.32	4.23
OIL	5.99	1.23	0.21	4.01	9.64	5.12	0.68	0.13	3.69	6.96
CRV%	44.49	2.23	0.05	37.98	48.62	39.84	2.39	0.06	31.86	44.47

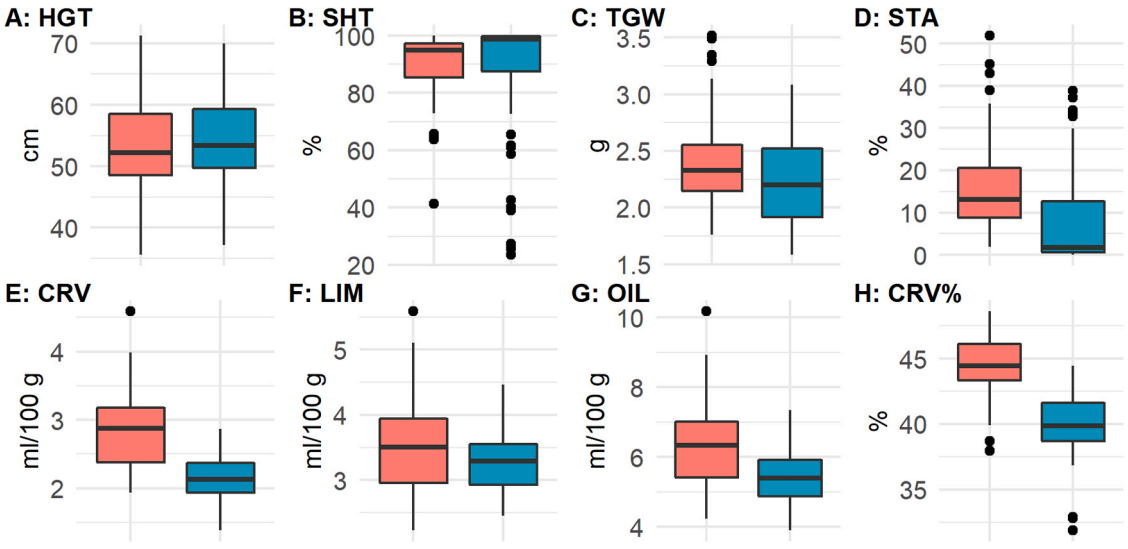

Fig. 2. Boxplots for 8 traits based on BLUEs of 132 accessions investigated in two-year field trials. Red (respective first) plots for annual accessions and turquoise (respective second) plots for biennial accessions. See Table 1 for full denomination of traits.

Table 3
Variance components and heritabilities for all investigated quantitative traits based on 64 annual and 68 biennial caraway accessions, respectively. n = total number of observations, g = number of genotypes, y = average number of years of evaluation per genotype, r = average number of repetitions (plots) per year and genotype, V = variance component [G = genotype, GY = genotype-year interaction, Y = year, R = residual error], h^2 = broad-sense heritability. See Table 1 for full denomination of traits.

Annuals									
Traits	n	g	y	r	V_G	V_Y	V_{GY}	V_R	h^2
BOF	368	64	1.70	3.38	35.54	4.16	13.06	6.23	0.80
EOF	368	64	1.70	3.38	26.91	36.41	21.04	13.65	0.65
HGT	368	64	1.70	3.38	37.49	96.04	32.60	20.59	0.62
MAT	366	64	1.70	3.36	30.38	172.57	10.14	15.05	0.78
SHT	366	64	1.70	3.36	64.97	46.73	71.72	72.46	0.54
TGW	366	64	1.70	3.36	0.14	0.27	0.03	0.04	0.86
STA	366	64	1.70	3.36	107.92	0.00	4.77	70.24	0.88
CRV	366	64	1.70	3.36	0.28	1.38	0.04	0.05	0.91
LIM	366	64	1.70	3.36	0.54	0.69	0.03	0.10	0.94
OIL	366	64	1.70	3.36	1.58	0.12	0.08	0.25	0.95
CRV%	366	64	1.70	3.36	0.84	279.88	6.18	2.09	0.17
Biennials									
Traits	n	g	y	r	V_G	V_Y	V_{GY}	V_R	h^2
BOF	374	68	1.90	2.90	39.20	0.62	6.98	7.83	0.88
EOF	357	68	1.90	2.77	36.13	1.41	17.25	24.07	0.73
HGT	354	68	1.90	2.74	31.15	14.04	0.00	102.35	0.61
MAT	346	68	1.90	2.68	34.16	31.56	9.65	30.67	0.75
SHT	317	68	1.85	2.52	391.80	1.09	68.33	137.74	0.86
TGW	335	68	1.90	2.60	0.13	0.05	0.01	0.08	0.85
STA	335	68	1.90	2.60	118.64	10.27	21.05	47.44	0.85
CRV	335	68	1.90	2.60	0.06	0.01	0.03	0.14	0.59
LIM	335	68	1.90	2.60	0.10	0.08	0.09	0.23	0.52
OIL	335	68	1.90	2.60	0.31	0.02	0.21	0.63	0.56
CRV%	335	68	1.90	2.60	1.40	12.24	4.27	9.44	0.25

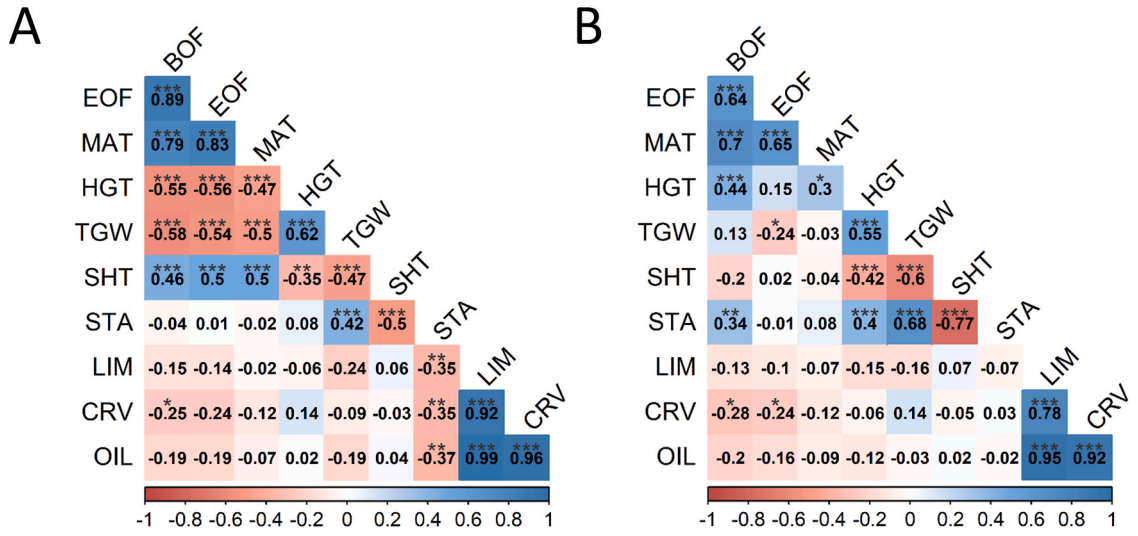

Fig. 3. Spearman correlation coefficients for correlations between traits based on BLUEs from A) 64 annual genotypes and B) 68 biennial genotypes. Negative correlations are highlighted by a red color scale and positive correlations by a blue color scale. In both cases, darker colors indicate stronger correlations. Stars indicate levels of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). See Table 1 for full denomination of traits.

(Wickam, 2016).

Broad-sense heritability (h^2) was computed based on following formula: $h^2 = \frac{V_G}{V_G + \frac{V_{GY}}{y} + \frac{V_R}{yr}}$, where V_G, V_{GY} and V_R stand for the variance components genotype, genotype-year interaction and residual error, respectively, and y and r represent the number of years and repetitions, respectively. To get variance components we used the lme4 package (Bates et al., 2015). All effects were considered as random. To estimate best linear unbiased estimates (BLUEs) per genotype a model was fitted in which the effect of genotype was considered as fixed factor. Year and repetition (nested in year) were added as random effects.

Normal distribution was tested using the Shapiro-Wilk test. Spearman correlation coefficients (r) and associated fdr (false discovery rate) adjusted p-values were computed using the function corr.test from the package psych (Revelle, 2013). The correlation matrix was visualized using the package corrplot (Wei and Simko, 2017). A principal component analysis (PCA) was conducted using the function prcomp.

3. Results and discussion

3.1. Variability of traits

The primary goal of this study was to gather phenotypic data for important quantitative traits on 132 caraway accessions and to provide these data for new breeding projects. Not all accessions could successfully be phenotyped in both years of cultivation due to low seed

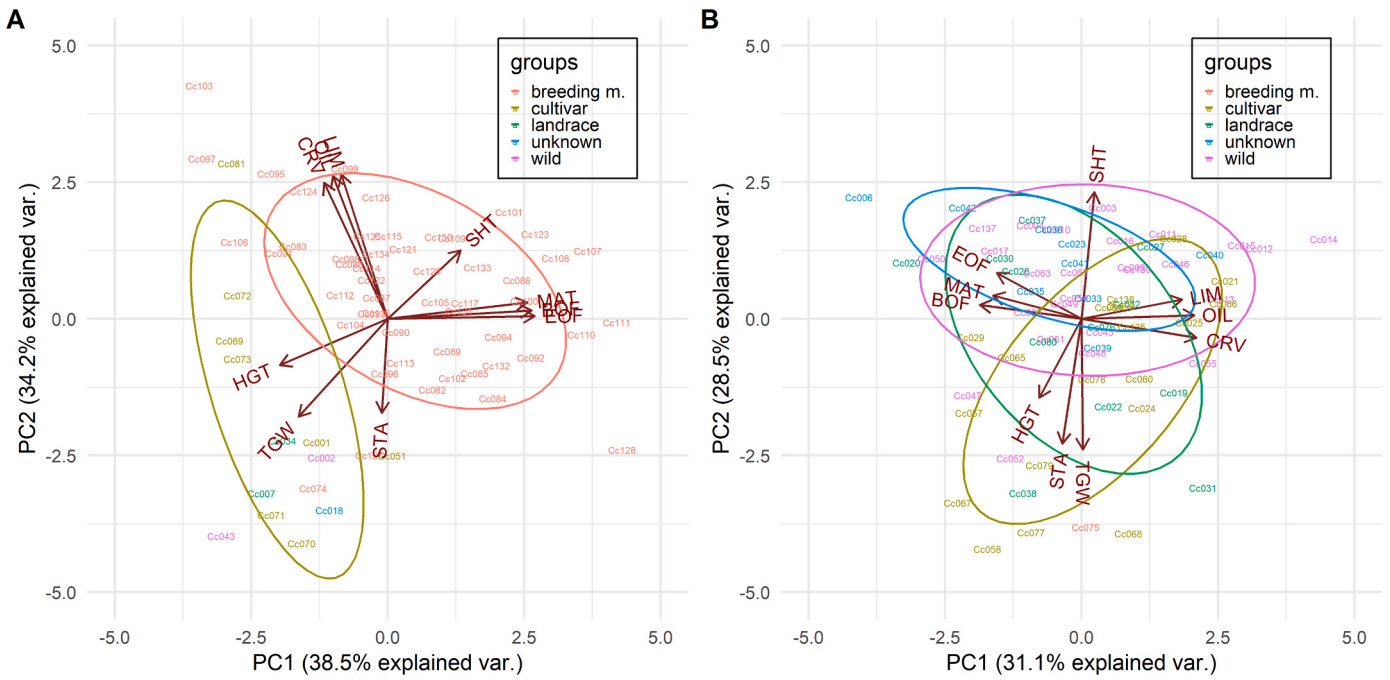

Fig. 4. Principal component analysis (PCA) based on BLUEs from A) 64 annual genotypes and B) 68 biennial genotypes. Colors indicate different classifications. Breeding m. = breeding material. Ellipses = normal data ellipses. See Table 1 for full denomination of traits.

availability or loss of plots. In particular, plots of biennial accessions were negatively affected by mice and frost.

BLUEs for all investigated accessions can be retrieved from Table S1. These data are summarized in Table 2 and the data distribution is shown in Fig. 2. For all investigated traits a high variability was observed, both within the annual and biennial genepool.

The annual genepool seems to have more accessions with a higher carvone, limonene and total essential oil content (Fig. 2). However, values of annual and biennial accessions might differ due to different years of harvesting. For predicting essential oil content, we used NIRS data and GC-FID measurements of extracts as reference. This is a fast and cost efficient alternative to distillations or extractions and GC-FID measurements of all samples. Minor components of the essential oil were neglected. Extraction generally gains a higher total essential oil content but a lower proportion of carvone than distillation, which is the prescribed method of the Ph. Eur. Indeed, the observed proportion of carvone was below 50% for all genotypes after extraction. A validated model to correct this is not available yet. The proportion of carvone of most annuals appears to be higher than the proportion of carvone of most biennials. However, the proportion of carvone was higher in annuals just in the first year. Considering the low heritability, this difference cannot be regarded as reliable.

Conspicuously, most accessions had a high shattering rate (free shattering). The investigated annual genepool seems to lack a variety with very low shattering. Free shattering is necessary for seed dispersal in nature, but can cause severe yield losses in cultivation (Toxopeus and Lubberts, 1994). Future caraway breeding might strive to introduce low shattering from the biennial into the annual genepool. Vice versa, most accessions had a low stalk attachment rate.

3.2. Heritability of traits

It is important to evaluate how far phenotypic variation is attributable to genetic variation utilizable in breeding. For most traits, heritability values ranged from medium to high (0.52 – 0.95, Table 3). Therefore, we can state that a medium to high degree of the observed phenotypic diversity is applicable to breeding. For some traits, we estimated high year effects (Table 3). Partially, this might be explained by the necessary modification of the set-up in the second year of sowing. Year effects were exceptionally high for the proportion of carvone and genetic effects were low resulting in a low heritability compared to all other traits (0.17 for annuals and 0.25 for biennials, Table 3). This might complicate breeding programs, which aim to select genetic material with high carvone to limonene ratios, which would be interesting for industry. Heritability values of biennials were lower for values of essential oil related traits. This might be partially explained by random losses of biennial plants caused by mice, which affected plant densities within plots.

Of course, the procedure of pre-growing and planting in defined distances is not consistent with practical growing conditions with direct sowing and high plant densities. Several annual lines and cultivars were tested in yield tests (12 m^2 plots) as well (von Maydell et al., 2021b). In the yield test, plant development was considerably slower and essential oil content was considerably lower. For selection decisions based on data presented in this study, it is important to consider that the estimated absolute values might not be reached under practical growing conditions. Furthermore, it was not manageable to grow the accessions at several locations to examine genotype-location interaction effects. Hence, breeding projects for other regions have to assess whether differences between genotypes can be reproduced in other environments.

3.2.1. Correlations between traits and PCA of traits

Knowledge of correlations between traits can be useful in selection decisions within the breeding process. Data distribution for several traits deviated from normal distribution. Hence, we computed non-parametric Spearman correlations coefficients. Correlation matrices separately computed for flowering types are provided in Fig. 3. Recently, field tests of annual material revealed a strong association of early flowering with high yield, thousand-grain weight (TGW) and height (von Maydell et al., 2021b). In this study, we found negative correlations between developmental traits and TGW and height in the annual genepool as well. In the biennial genepool, no such clear correlations were found. Hence, selection towards early flowering might be an important breeding goal for breeding annual varieties, but not for breeding biennial varieties. In both genepools, a negative correlation between shattering rate and stalk attachment rate was found that corroborates the findings of von Maydell

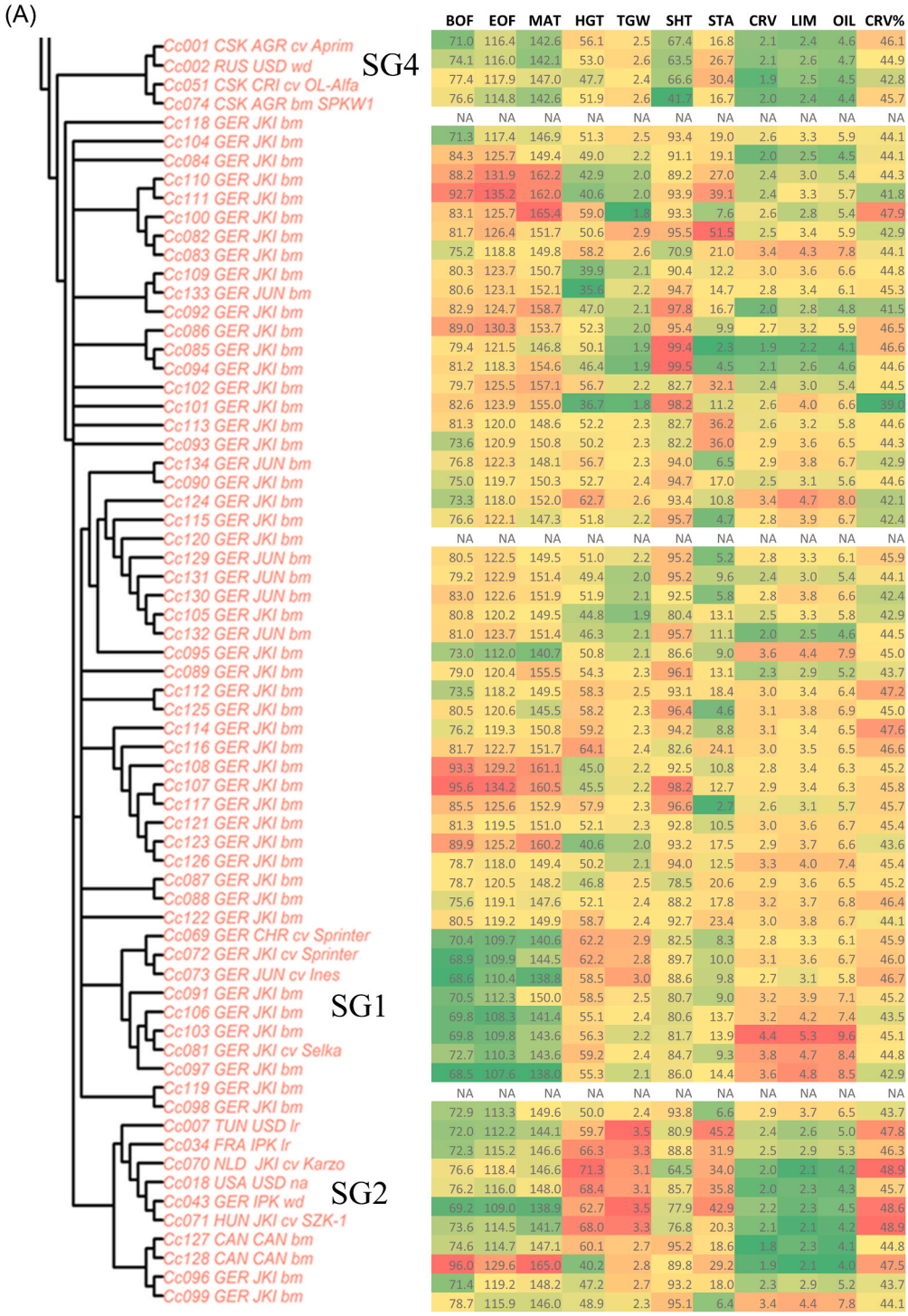

Fig. 5. A BIONJ tree extracted from von Maydell et al. (2021a) for 70 biennial accessions based on 13,155 SNP markers combined with a heatmap of BLUEs of investigated quantitative traits. NA = missing values. Color scale from dark green (= lowest values) to dark red (highest values). See Table 1 for full denomination of traits. Fig. 5 B BIONJ tree extracted from von Maydell et al. (2021a) for 67 annual accessions based on 13,155 SNP markers combined with a heatmap based on BLUEs of investigated quantitative traits. NA = missing values. Color scale from dark green (= lowest values) to dark red (highest values). See Table 1 for full denomination of traits.

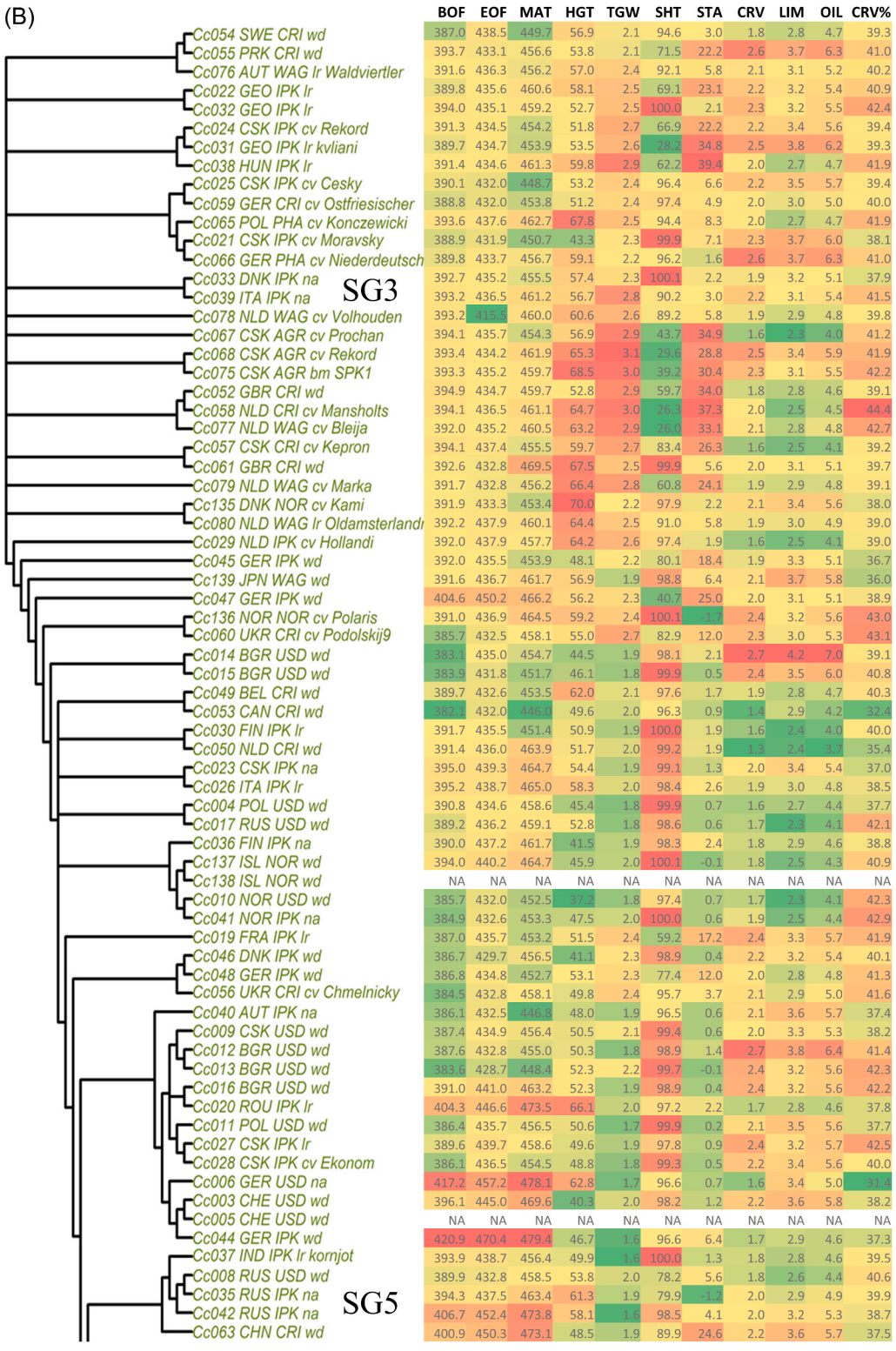

Fig. 5. (*continued*).

et al. (2021b). A genetic background for this correlation could be possible. Correlations between essential oil related traits and other traits were low. This is advantageous for breeding, because essential oil content can be selected independently from other traits.

The principal component analysis (Fig. 4) provides details on the distribution of phenotypic variation across different classifications. Within the annual set (Fig. 4 A), PCA revealed noticeable differences between cultivars and breeding material. Many breeding lines tend to late generative development. This can be explained by inbreeding depression and can be reversed by outcrossing (von Maydell et al., 2021b). Cultivars tend to have a high TGW and height. Within biennial cultivars (Fig. 4 B), a tendency towards higher TGW and height combined with reduced shattering and high stalk attachment rate is visible. As mentioned before, high TGW, high height and reduced shattering are

associated with higher yield or yield stability (Toxopeus and Lubberts, 1994; von Maydell et al., 2021b). Therefore, our observations reflect a usual selection process in breeding.

3.2.2. Associations of traits with the genetic substructure

We further scrutinized whether some phenotypic combinations are associated with the genetic substructure of the annual and biennial genepool as investigated in von Maydell et al. (2021a). To take the kinship between accessions into consideration can provide insights into breeding history and valuable details for breeding decisions. Similar phenotypic characteristics of related accessions likely result from the same genetic background. Therefore, selecting unrelated genotypes with suitable phenotypes results in more beneficial genetic variation than crossing related ones and can substantially increase breeding success.

Within the biennial genepool, one small cluster appears to be conspicuous: The Czech accessions “Rekord”, “Prochan” and “SPK1″, the Dutch accessions “Mansholts” and “Bleija” and a British accession show a low shattering rate, combined with a high stalk attachment rate and TGW (Fig. 5 A). This might be traced back to a Dutch breeding program, which focused on selecting non-shattering biennial genotypes (Toxopeus, 1998). The close relatedness between Dutch and Czech biennial non-shattering varieties indicate an exchange of genetic material.

Within the annual genepool, the accessions of subgroup SG4 show a reduced shattering rate and a low essential oil content. The subgroup SG2 predominately contains accessions with a low essential oil content, but a high TGW and height. The accessions of subgroup SG1 have an early generative development and a high essential oil content (Fig. 5 B), which can be traced back to a German breeding program (Pank et al., 2008).

Of course, the presence of genotypic and phenotypic data calls for the conduction of genome wide association studies (GWAS). However, without any reference genome and genetic map the SNP markers cannot be localized so that results from GWAS cannot be accurately interpreted. If a reference genome is available in future, our data of quantitative traits might be used to find associated marker loci. The possibilities to detect associated loci by GBS data has been shown for the analysis of vernalization in caraway as a “simple” monogenetic trait as well as the limitations due to a missing reference genome (von Maydell et al., 2022). So far, our data can be useful to select accessions with extreme phenotypes to build up biparental or multiparental mapping populations. Genetic mapping of important traits and implementation of marker-assisted selection (MAS) would be a milestone for caraway breeding.

Funding

This project was funded by the "Fachagentur Nachwachsende Rohstoffe" (FNR) on behalf of the Federal Ministry of Food and Agriculture (BMEL) (Funding ID: 22023215, 2220NR103A). The funding was supported by Dr. Junghanns GmbH, Aschersleben OT Groß Schierstedt; BBG Kilian-Horsch GbR, Aschersleben OT Mehringen; Horrmann GbR, Bördeland OT Welbsleben; Landwirtschaftsbetrieb Hans-Eckhard Kittler, Aschersleben, all Germany.

CRediT authorship contribution statement

Daniel von Maydell: Conceptualization, Data analysis, Visualization, Writing - Original Draft. Claudia Beleites: NIRS, Data analysis, Writing - Review & Editing. Anne-Marie Stache: Writing - Review & Editing. David Riewe: Gas-chromatography, Data analysis, Writing - Review & Editing. Andrea Krähmer: NIRS, Data analysis, Writing - Review & Editing. Frank Marthe: Project administration, Funding acquisition, Supervision, Writing - Review & Editing.

Declaration of Competing Interest

The authors declare no competing interests.

Data Availability

Data will be made available on request.

Acknowledgments

We thank Jenny Knibbiche, Sabine Rilk, Mario Harke, Dominic Lamprecht and all helping people who took part in the experiments. We thank all germplasm providers, which enabled the assembly of a diverse caraway collection: The Leibniz Institute of Plant Genetics and Crop Plant Research (IPK, Gatersleben, Germany); the United States Department of Agriculture (USDA, Ames, USA) the Crop Research Institute (CRI, Prague, Czech Republic); the Centre for Genetic Resources, the Netherlands (CGN, Wageningen, Netherlands); the Nordic Genetic Resource Center (NordGen, Alnarp, Sweden); the Julius Kuehn-Institute (JKI, Quedlinburg, Germany); the Dr. Junghanns GmbH (Ascherleben, Germany); the Agritec Ltd. (Šumperk, Czech Republic); the National Research Council Canada (NRC, Ottawa, Canada); the Chrestensen GmbH (Erfurt, Germany); the Pharmasaat GmbH (Artern, Germany).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.indcrop.2023.117798.

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