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Agronomic performance of normal-leafed and semi-leafless pea (*Pisum sativum* L.) genotypes

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Abstract

Pea (*Pisum sativum* L.) is a major pulse crop important as feed and food. Due to the symbiosis with N-fixing bacteria, it is a valuable component of low-input cropping systems. The traditional cultivation of peas was limited by their high susceptibility to lodging. This problem was reduced, though not completely solved, by a semi-leafless mutant. Almost all modern cultivars carry this mutant. It is still an open question as to whether the lack of leaflets may have impaired the productivity. In organic farming, there is still interest in normal-leafed peas as they can better compete with weeds. To compare the two leaf types, 24 normal-leafed and 30 semi-leafless genotypes were evaluated in three environments. Semi-leafless genotypes had a higher seed (51%) and straw (40%) yield, but most normal-leafed genotypes were older or less adapted than the semi-leafless ones. Some newer normal-leafed cultivars achieved the same yield level, but their cultivation is only possible in mixtures with a supporting crop. Nitrogen content in seed (10%) and in straw (30%) was lower in semi-leafless genotypes. A negative correlation of yield and N content was observed in both leaf types. However, semi-leafless peas had a higher N yield in seed and in straw. No correlation between N yield in seed and straw was found, so it is possible to combine a high seed yield with a high N yield in the straw. This is particularly important in organic production systems, where peas are also grown to provide N to the following crop.

1 | INTRODUCTION

Pea (*Pisum sativum* L.) is grown worldwide on about 10 million ha. About 2.8 million ha are used as green vegetables and more than 7 million ha as dry peas for animal feed and human nutrition. Peas are mainly cultivated in Europe, North America, China, and India. Globally, pea is the fourth most important legume crop after soybean, groundnut, and common bean. In Europe, it is the most important cool season grain legume (FAOSTAT, 2019).

Pea seeds are rich in protein (Atta et al., 2004). Because of the symbiosis with atmospheric-N fixing rhizobacteria, peas do not require N fertilizer and sometimes they contribute N to the following crop (Burstin et al., 2018). Therefore, peas are of particular interest in organic crop rotations (Gollner et al., 2019), but they can also contribute to crop diversity and energy efficiency in conventional production (Nemecek et al., 2008).

Advances in breeding for increased yield led to higher harvest indices that are usually accompanied by high N harvest indices. Thus, the cultivation of these genotypes may be associated with a negative N balance (Gollner et al., 2019; Reiter

Abbreviations: PC, principal component; PL, plant length.

et al., 2002). In order to achieve a positive N balance, it would be important to select for a high N yield of the straw that stays in the field.

For a long time, the main limitation for pea production in areas with precipitation close to the harvest season was the high susceptibility to lodging of the normal-leaf wild type and, consequently, severe problems with harvesting. Reductions in yield and seed quality have also been attributed to lodging. When peas are grown in a pure stand, they often exhibit severe lodging after flowering (Stelling, 1997), and large yield reductions of normal-leafed cultivars have been recorded in conventional management (Stelling, 1994). Contributing to this reduction is the large amount of foliage in leafed cultivars that shades lower plant parts and results in decreased light penetration and photosynthetic activity of the lower leaves and the potential build-up of pathogens in the moist lower-canopy environment (Meadley & Milbourne, 1971). Among the many leaf mutants in pea, two are of practical importance: *afila* (*af*) that replaces the leaflets with tendrils, and *stipules reduced* (*st*) that drastically reduces the size of the stipules (Mikic et al., 2011). Combining these two mutants (*afaf stst*) results in nearly leafless peas, and it was soon observed that their yield is greatly reduced due to their small photosynthetic area (Hedley & Ambrose, 1981; Stelling, 1994). This was also observed in 'Filby', the first fully leafless (*afaf stst*) U.K. pea cultivar, released in 1978 by Snoad (Mikic et al., 2011). Also, the mutant *stst* alone resulted in significantly reduced yield. Therefore, semi-leafless genotypes are preferred, in which only the leaflets, but not the stipules, are modified (*afaf StSt*). Today semi-leafless pea cultivars account for more than 95% of the total dry pea production in western Canada, more than 80% in the European Union, and more than 30% in Russia (Mikic et al., 2011). All 23 spring pea cultivars on the recommended list in Germany are semi-leafless (Federal Plant Variety Office, 2020). They have also become dominant in Australia over the past decade because of their better resistance to lodging and hence easier harvesting (French, 2016). They allow more light and more air movement through the crop and consequently create less favorable conditions for fungal disease (Grevsen, 2003).

Normal-leafed cultivars are still of interest in organic agriculture due to their better competition against weeds (Gronle et al., 2014; Spies et al., 2011). They are also of interest as a genetic resource to increase protein content and to broaden the genetic diversity of the present breeding material. In addition, pea and cereal mixtures have been traditionally used in different parts of the world. Dry matter yields of the mixtures were generally higher than monoculture stands (Bedoussac et al., 2015; Rauber et al., 2001). In recent years, semi-leafless peas have become preferred in mixtures over the normal-leafed cultivars (Rauber et al., 2000, 2001). However, semi-leafless peas were reported to be less competitive than normal-leafed peas with greater leaf area, plant height, and shoot dry matter attributes (Semere & Froud-Williams, 2001). In addition, mixtures of normal-leafed and semi-leafless peas were reported to be successful (Syrovy et al., 2015).

Comparisons of the performance of normal-leafed and semi-leafless pea genotypes can be found in the literature, but in most cases only a very limited number of genotypes have been included. The results are contradictory: when studying six field pea genotypes (two semi-leafless and four normal-leafed) in eight environments for dry matter and seed yield, Acikgoz et al. (2009) concluded that the semi-leafless cultivars newly registered at that time in Turkey had a significant 6% seed yield advantage over the normal-leafed genotypes. Studies by Cupic et al. (2013) illustrated that normal-leafed pea cultivars had a lower forage and dry matter yield but higher protein content, though these results were not consistent over different seasons. Narits (2008) reported that semi-leafless cultivars had a higher seed yield (cited in Olle, 2017a), but this was not evident in the investigation of Olle (2017b). Kalev and Narits (2004, cited in Olle, 2017a) showed that in years when the weather conditions favored vegetative growth, normal-leafed types gave a higher yield and better quality than semi-leafless cultivars and vice versa. Normal-leafed cultivars also had a higher protein content than semi-leafless genotypes (Olle, 2017a). In another study of 13 pea cultivars, Olle et al. (2019) recorded that normal-leafed cultivars had the highest and most stable average yield. Only one out of four semi-leafless cultivars yielded a higher and more stable protein content. In Germany, a higher protein content in normal-leafed genotypes was observed both in winter pea (Quendt et al., 2014) and in spring pea (Lietzow et al., 2013). These studies with a limited number of genotypes did not cover the diversity present within the two leaf types.

Therefore, we analyzed a diverse set of 24 normal-leafed and 30 semi-leafless cultivars from different breeding eras and backgrounds, including exotic genotypes. One problem with this material, however, is that the leaf types differ in their genetic background, because many normal-leafed genotypes

Core Ideas

- A high protein yield of pea seeds can be combined with a high pre-crop value of the whole plant.
- A positive correlation of seed and straw yield was observed in field pea.
- A negative correlation of yield and N content was observed in field pea.
- Normal-leafed peas were lower in seed and straw yield than semi-leafless peas, but most of the tested normal-leafed genotypes were older and/or less adapted.

are older and less adapted than the more modern semi-leafless cultivars. This will be discussed.

The objectives of this study were to compare the two leaf types for general differences in yield and N content as well as the relationships between seed yield and straw yield and N content in seed and straw. Of special interest was the possibility to identify genotypes as a resource for combining a high protein content in the seed with a high N yield in the straw to increase the pre-crop value.

2 | MATERIALS AND METHODS

2.1 | Genotypes

The research material was collected from gene banks, seed companies, and breeders. Included were cultivars of different ages (recently released to very old), recent breeding lines, and some genetic resources. The characteristics of 24 normal-leafed and 30 semi-leafless genotypes are described in Table 1.

2.2 | Field experiments

Seed lots of similar age were used to provide homogenous seed quality. To achieve this, most genotypes were multiplied in homogenous conditions before starting the field experiments. Generally, stand establishment was good for all genotypes. The field experiments were performed in a randomized complete block design with three environments in Goettingen, Germany (Reinshof in 2017 and 2018 and Niedernjesa in 2018) and two replicates for each environment (Table 2). The plots were sown with a Hege-95 with 5 m^2 plot size, 100 seeds per m^2, and six rows per plot. The sowing times were on 21 Apr. 2017 as well as 6 Apr. 2018 (Niedernjesa) and 18 Apr. 2018 (Reinshof). Plots were harvested from the end of July until early August. The field trial was harvested by hand in 2017 and by HG-160 plot combine harvester in 2018.

2.3 | Data collection

Morphological and agronomic traits were assessed as follows: light interception is the ratio of photosynthetically active radiation measured above and below the canopy. Measurements were taken 20 cm above the canopy and 10–20 cm above the ground. Each plot was measured in three positions around noon (10:00–14:30) with an AccuPAR ceptometer LB80. Lodging was scored about 1 wk after flowering (2017) or 3 wk after flowering (2018) on a scale of 1–9 (1 = no lodging with plants upright, 9 = plants flat on the ground). The plant length (PL) of each genotype was scored after flowering by measuring the length of five plants in different positions of the inner rows. Plot height was measured about 2 wk before harvest from the ground level to the average height of each plot. Seed dry yield was calculated from the amount of seed per plot multiplied by seed dry matter (%). To measure seed dry matter (%), a sample of about 150 g was dried at 60 ˚C for 4 d. To determine N content in seed, these samples were milled to powder < 0.2 mm by the RETSCH Ultra Centrifugal Mill ZM 200. Then, 15−16 mg of the milled sample was packed with aluminum paper as a small pill for C/N analysis by Vario EL cube with Advanced Purge and Trap Technology from Elementar. Nitrogen yield in seed was computed by multiplying N content in the seed with seed dry yield. Straw dry yield was calculated from the amount of straw multiplied by straw dry matter (%). To measure straw dry matter (%) a sample of 100 g of shredded straw was dried at 60 ˚C for 48 h. To determine N content in straw, these samples were cut into smaller pieces by a RETSCH Cutting Mill SM300 and subsequently milled to powder < 0.2 mm by a RETSCH Ultra Centrifugal Mill ZM 200. Then, 16−18 mg of the milled sample was packed with aluminum paper as a small pill for C/N analysis by the Vario EL cube with Advanced Purge and Trap Technology from Elementar. Nitrogen yield in straw was computed by multiplying N content in straw and straw dry yield. Biomass yield is the sum of seed dry yield and straw dry yield. Total N yield is the sum of N in seed and straw. The harvest index was estimated by dividing seed dry yield by biomass yield. The N harvest index was calculated by dividing the N yield of seed by total N yield.

2.4 | Statistical analysis

The ANOVA correlation coefficients and estimates of heritability (h^2) were calculated using PLABSTAT software version 3A (Utz, 2011). The following ANOVA models were used:

Single environments: $Y_{ij} = \mu + g_i + r_j + gr_{ij}$

Multi-environments: $Y_{ijk} = \mu + g_j + e_k + r_{jk} + ge_{jk} + ger_{ijk}$

Including leaf type as a factor: $Y_{ijkl} = \mu + t_l + g_{il} + e_k + te_{lk} + ge_{ilk} + tegr_{ijkl}$

where Y_{ij}, Y_{ijk}, Y_{ijkl} are the observations of a plot, and μ is the general mean, with the effects g_i for genotype i (g_{il} within leaf type), r_j for replicate j (r_{jk} within environment k), e_k for environment k, t_l for leaf Type l, and with the respective interactions and the error terms gr_{ij}, ger_{ijk}, and $tegr_{ijkl}$.

The ANOVA for scored traits was first performed for all 54 genotypes; then, we applied the same model for (a) 24 normal-leafed genotypes and (b) 30 semi-leafless genotypes. To test the difference between the leaf types, a sum of squares for leaf types was calculated by subtracting the sum of squares

TABLE 1 Characteristics of 54 pea genotypes

Genotype	Form	Leaf type	Year of release	Use	Country of origin	Breeder/source	Reference[a]
Alvesta	s	semi-leafless	2008	grain	Germany	KWS Lochow	1, 2
Astronaute	s	semi-leafless	2013	grain	Germany	Norddeutsche Pflanzenzucht	1, 2
Baccara	s	semi-leafless	1992	grain	France	S. A. Florimond Desprez	2
Camilla	s	semi-leafless	2006	grain	Austria	KWS Lochow	3
Casablanca	s	semi-leafless	2007	grain	Germany	KWS Lochow	1
Cheyenne	w	semi-leafless	1998	grain	France	GAE Recherche	3
Eiffel	s	semi-leafless	1996	grain	Denmark	Danisco Seed	2
Gambit	s	semi-leafless	2011	grain	Czechia	Selgen	2
James	w	semi-leafless	2009	grain	France	RAGT	2
KA 258[b]	s	semi-leafless	2016	grain	Italy	CREA-FLC	
KA-L11[b]	s	semi-leafless	2016	grain	Italy	CREA-FLC	
Kleopatra	s	semi-leafless	2005	grain	Germany	Südwestdeutsche Saatzucht	3
KWS La Mancha	s	semi-leafless	2009	grain	Germany	KWS Lochow	1, 2
Madonna	s	semi-leafless	1999	grain	Germany	Norddeutsche Pflanzenzucht	1, 2
Myster	w	semi-leafless	2016	grain	France	RAGT	1, 2
Navarro	s	semi-leafless	2010	grain	Germany	Norddeutsche Pflanzenzucht	1
Poseidon	s	semi-leafless	2016	grain	Czechia	Selgen	2
Radley	s	semi-leafless	1989	grain	UK	Booker Seeds	3
Respect	s	semi-leafless	2006	grain	Austria	Maribo Seed International	3
Rocket	s	semi-leafless	2004	grain	Germany	Erbengemeinschaft Dr. Hans Rolf Späth	1
Salamanca	s	semi-leafless	2009	grain	Germany	Norddeutsche Pflanzenzucht	1, 2
Santana	s	semi-leafless	2000	grain	Germany	KWS Lochow	1, 2
Solara	s	semi-leafless	1984	grain	Belgium	INNOSEEDS	3
Specter	w	semi-leafless	2007	grain	Austria	Werner Vogt-Kaute	2
Tip	s	semi-leafless	2013	grain	Czechia	Selgen	1, 2
15834[b]	s	semi-leafless	2016	grain	Switzerland	Getreidezüchtung Peter Kunz	
15850[b]	s	semi-leafless	2016	grain	Switzerland	Getreidezüchtung Peter Kunz	
15852[b]	s	semi-leafless	2016	grain	Switzerland	Getreidezüchtung Peter Kunz	
15853[b]	s	semi-leafless	2016	grain	Switzerland	Getreidezüchtung Peter Kunz	
15859[b]	s	Semi-leafless	2016	grain	Switzerland	Getreidezüchtung Peter Kunz	
AF 447	s	normal-leafed	<1935	grain	Afghanistan	IPK Gatersleben	4
AF 448	s	normal-leafed	<1935	grain	Afghanistan	IPK Gatersleben	4
AF 467	s	normal-leafed	<1935	grain	Afghanistan	IPK Gatersleben	4
Akoja	s	normal-leafed	2009	grain	Germany	Norddeutsche Pflanzenzucht	2
Bohatyr	s	normal-leafed	1980	grain	Czechia	Selgen	2
Breslau	s	normal-leafed	<1945	grain	Germany	IPK Gatersleben	4
Cerosa	s	normal-leafed	<1945	grain	Germany	IPK Gatersleben	4
Dolores	s	normal-leafed	2009	green fodder	Germany	Norddeutsche Pflanzenzucht	1, 2
ET 118	s	normal-leafed	<1948	grain	Ethiopia	IPK Gatersleben	4
ET 336	s	normal-leafed	<1949	grain	Ethiopia	IPK Gatersleben	4
Florida	s	normal-leafed	1993	green fodder	Germany	Norddeutsche Pflanzenzucht	1, 2
GR 293 EW	w	normal-leafed	1942	grain	Greece	IPK Gatersleben	4
GR 409	w	normal-leafed	1941	grain	Greece	IPK Gatersleben	4

(Continues)

TABLE 1 (Continued)

Genotype	Form	Leaf type	Year of release	Use	Country of origin	Breeder/source	Reference[a]
GR 440	s	normal-leafed	1942	grain	Greece	IPK Gatersleben	4
GR 5	s	normal-leafed	1943	grain	Greece	IPK Gatersleben	4
Grana	s	normal-leafed	1997	grain	Czechia	NORDSAAT	2
Grapis	s	normal-leafed	1991	grain	Poland	NORDSAAT	2
Klif	s	normal-leafed	2008	grain	Poland	Poznanska Hodowla Roslin	2
Natura	s	normal-leafed	2007	grain	Czechia	Selgen	2
Pandora	w	normal-leafed	2014	grain	Austria	Werner Vogt-Kaute	2
Pisum Vilmorin III	s	normal-leafed	<1948	grain	France	IPK Gatersleben	4
Protecta	s	normal-leafed	2009	grain	Czechia	Selgen	2
Rosakrone	s	normal-leafed	1970	green fodder	Germany	Kruse	5
RU 165	s	normal-leafed	1945	grain	Russia	IPK Gatersleben	4

Note. s, spring; w, winter.
[a]1, Federal Plant Variety Office (2017); 2, European Commission (2017); 3, CPVO (2021); 4, Genbankinformationssystem IPK Gatersleben (2017); 5, Federal Plant Variety Office (1997).
[b]Breeding line.

TABLE 2 Experimental environments

Variable	Reinshof 2017	Reinshof 2018	Niedernjesa 2018
Location	51°30′01.6″ N, 9°55′50.4″ E	51°30′01.6″ N, 9°55′50.4″ E	51°28′14.8″ N, 9°55′34.1″ E
Mean temperature Apr.–July (°C)[a]	14.5	16.9	16.9
Precipitation Apr.–July (mm)[a]	268	172	172
Pre-crop	winter wheat	winter wheat	maize
Soil	alluvial loess, silty loam	alluvial loess, silty loam	alluvial loess, silty loam
Altitude (m asl)	140	140	160

[a]Wetterstation Göttingen, Germany, www.wetterstation-goettingen.de.

of the normal-leafed group and the semi-leafless group from the sum of squares for all genotypes (Supplemental Table S1). Principal component analysis and the figures were created by R using the packets *ggplot2*, *ggbiplot*, and *factoextra*. For the principal component analysis, the data of the traits with different units were standardized by rescaling and centering the units.

3 RESULTS

The ANOVA for normal-leaf and semi-leafless peas (Table 3) shows significant differences for all traits between the two leaf types. The heritability was very high for all traits (>80%). The normal-leafed group intercepted 2.4 percentage points more light, whereas much more lodging was observed (scores of 7.9 and 2.4, respectively). The plants of the normal-leafed cultivars were about 19 cm longer than those of semi-leafless cultivars. Probably, most of the more recently released semi-dwarf cultivars also carry a mutation for short internode length (no information available). However, plant length is not significantly correlated with seed yield ($r = -.27$ for semi-leafless and $r = -.16$ for normal-leafed, see Supplemental Tables S4 and S5). Nitrogen content in seed and straw was higher for normal-leafed genotypes in the range of approximately 10 and 30%, respectively). However, seed dry yield and straw dry yield of this group were lower than for the semi-leafless genotypes by 34 and 29%, respectively. (The seed dry yield of all genotypes in three environments is given in Supplemental Table S2). In general, N yield in seeds is around twice as high as the N yield in straw for both leaf types (ratio 1.9 and 2.5, respectively). For both traits, a better performance was recorded for the group of semi-leafless cultivars, but the difference between the two groups is larger for N yield in the seeds, with 26.53 kg ha^{-1} in comparison with just 1.87 kg ha^{-1} in N yield in the straw. Consequently, harvest and N harvest indices were higher for semi-leafless genotypes.

The results of the ANOVA for seven important traits (seed and straw dry yield, N content in seed and straw, N yield in seed and straw, and total N yield) are shown in Table 4. The differences between normal-leafed and semi-leafless genotypes were highly significant for all traits, except N yield in

TABLE 3 Heritability of morphological and agronomic traits and mean values of normal-leafed ($n = 24$) and semi-leafless pea genotypes ($n = 30$)

Number	Traits	Abbreviation	Mean of all genotypes (n = 54)	Mean of normal-leafed (n = 24)	Mean of semi-leafless (n = 30)	F_{test} normal vs. semi-leafless	Heritability (n = 54)
1	Light interception (%)	LI	82.14	83.50	81.11	25.92**	.85
2	Lodging	Lg	4.83	7.86	2.41	1,890.16**	.98
3	Plant length (cm)	PL	80.66	91.27	72.15	671.17**	.98
4	Plot height (cm)	PlotH	61.74	55.58	66.80	221.24**	.96
5	Seed dry yield (t ha^{-1})	SDY	2.10	1.64	2.48	508.10**	.96
6	N content in seed (%)	Nseed	3.73	3.91	3.60	462.69**	.96
7	N yield in seed (kg ha^{-1})	NYS	77.70	63.10	89.63	359.84**	.95
8	Straw dry yield (t ha^{-1})	StrDY	2.93	2.55	3.57	375.81**	.95
9	N content in straw (%)	Nstraw	1.15	1.30	1.03	309.06**	.95
10	N yield in straw (kg ha^{-1})	NYStr	34.49	33.51	35.38	3.77 +	.88
11	Biomass yield	BY	5.04	4.20	5.72	653.28**	.97
12	Total N yield	TNY	112.27	96.72	125.02	336.92**	.94
13	Harvest index	HI	0.41	0.38	0.43	126.64**	.94
14	N harvest index	NHI	0.68	0.63	0.72	179.68**	.94

+Significant at the .1 probability level.
**Significant at the .01 probability level.

straw, which was only significant at $p = .10$. The interactions with environments were highly significant for all traits, both for leaf types and for the variance within leaf types. Within each leaf type, there was a highly significant variation for all traits, it was always larger within the normal-leafed peas.

The differences between the two leaf types were generally consistent over the three environments though considerable interactions were observed (Table 5). Seed dry yield of all genotypes in all environments is given in Supplemental Table S2. The semi-leafless group showed a better performance in all environments in the traits seed dry yield, straw dry yield, N yield in seed, and total N yield, On the other hand, normal-leafed genotypes had higher N contents in seed and straw in each of the environments. When comparing the three environments, there was a much larger difference between the two leaf types in Reinshof 2017 compared with the two other environments for seed dry yield, straw dry yield, N yield in seed, and total N yield. The most obvious interaction can be observed for seed dry yield and N yield in seed. At Reinshof 2017, semi-leafless peas had more than twice the yields of normal-leafed peas, whereas at the other two locations this difference was much smaller though in the same direction. For N yield in straw, even a crossover interaction occurs with higher values for semi-leafless peas at Reinshof 2017 and Reinshof 2018, but lower values at Niedernjesa 2018.

The relationship between yield and N content is of great interest. For all 54 genotypes, a highly significant negative correlation was observed between seed yield and N content in seed and between straw yield and N content in straw (r = −.69 and r = −.58, respectively) (Figures 1 and 2). Within the normal-leafed group, a significant negative relationship between yield and N content was recorded. For the semi-leafless group, the correlation between yield and N content was also negative but not statistically significant. Despite this negative correlation, the semi-leafless types incorporated more N than normal-leafed cultivars due to their higher seed yield (see total N yield in Table 3).

Nitrogen yield in seed and N yield in straw were not correlated, neither for all genotypes nor within the two groups (Figure 3). Semi-leafless peas show a much higher N yield in seed, whereas the N yield in straw is similar for both leaf types. However, a few more recent normal-leafed cultivars have similar high N yield in seed as most of the semi-leafless cultivars.

The correlations between the seven most important traits for semi-leafless and normal-leafed genotypes are presented in Table 6. The correlations between all traits for all 54 genotypes and within both leaf types are given in Supplemental Tables S3–S5. Generally, the correlations within the two leaf types are rather similar. Only the negative correlation of N content in seed with seed dry yield, N yield in seed, and total N yield is only significant for normal-leafed genotypes. Within the semi-leafless group, the N content in seed was not significantly correlated with other traits except with N content in straw (r = .43). Within the normal-leafed genotypes, N content in seed was positively correlated with N content in straw (r = .67), and negatively with seed dry yield, N yield

TABLE 4 Analysis of variance of seed and straw yield and N yield of 24 normal-leafed and 30 semi-leafless pea genotypes in three environments

Source of variation	*df*	Mean square	Variance components	*F* test
Seed dry yield				
Leaf type	1	55.0275	0.1700	508.10**
Normal-leafed	23	1.9811	0.3118	17.95**
Semi-leafless	29	1.3231	0.2039	13.28**
Leaf type × environments	2	9.0527	0.0828	83.59**
Normal-leafed × environments	44	0.2491	0.0694	2.26**
Semi-leafless × environments	55	0.3361	0.1182	3.37**
N content in seed				
Leaf type	1	8.3747	0.0258	462.69**
Normal-leafed	23	0.4860	0.0777	24.57**
Semi-leafless	29	0.1358	0.0200	8.56**
Leaf type × environments	2	1.0018	0.0091	55.35**
Normal-leafed × environments	44	0.0736	0.0269	3.72**
Semi-leafless × environments	55	0.0498	0.0170	3.14**
N yield in seed				
Leaf type	1	56,050.0243	172.5131	359.84**
Normal-leafed	23	2,292.0063	356.5511	15.01**
Semi-leafless	29	1,607.0525	243.4120	10.96**
Leaf type × environments	2	19,055.1602	174.9944	122.33**
Normal-leafed × environments	44	359.8682	103.5842	2.36**
Semi-leafless × environments	55	411.6104	132.5149	2.81**
Straw dry yield				
Leaf type	1	38.0696	0.1171	375.81**
Normal-leafed	23	1.6925	0.2645	16.08**
Semi-leafless	29	1.4092	0.2185	14.38**
Leaf type × environments	2	8.3693	0.0765	82.62**
Normal-leafed × environments	45	0.3235	0.1091	3.07**
Semi-leafless × environments	55	0.3627	0.1324	3.70**
N content in straw				
Leaf type	1	6.0266	0.0185	309.06**
Normal-leafed	23	0.4094	0.0635	14.48**
Semi-leafless	29	0.1706	0.0265	14.54**
Leaf type × environments	2	0.3177	0.0027	16.29**
Normal-leafed × environments	45	0.0634	0.0175	2.24**
Semi-leafless × environments	55	0.0195	0.0049	1.84**
N yield in straw				
Leaf type	1	121.3196	0.2750	3.77+
Normal-leafed	23	312.8551	45.4710	7.82**
Semi-leafless	29	232.5595	34.7232	9.60**
Leaf type × environments	2	1,560.9964	14.1555	48.48**
Normal-leafed × environments	45	117.1140	38.5424	2.93**
Semi-leafless × environments	55	129.4798	52.6298	5.35**
Total N yield				
Leaf type	1	63,689.5076	63,689.5076	336.92**
Normal-leafed	23	56,890.6624	2,473.5071	16.08**

(Continues)

TABLE 4 (Continued)

Source of variation	*df*	Mean square	Variance components	*F* test
Semi-leafless	29	48,181.1387	1,661.4186	8.47**
Leaf type × environments	2	53,500.8190	26,750.4095	141.51**
Normal-leafed × environments	44	21,630.8018	491.6091	3.20**
Semi-leafless × environments	55	31,028.2119	564.1493	2.88**

+Significant at the .1 probability level.
**Significant at the .01 probability level.

TABLE 5 Mean values for selected traits of normal-leafed ($n = 24$) and semi-leafless ($n = 30$) pea genotypes in three environments

	Reinshof 2017			Niedernjesa 2018			Reinshof 2018		
Traits	Normal-leafed	Semi-leafless	F_{test}	Normal-leafed	Semi-leafless	F_{test}	Normal-leafed	Semi-leafless	F_{test}
Seed dry yield (t ha^{-1})	1.06	2.56	458.77**	2.19	2.93	105.26**	1.60	1.88	14.49**
N content in seed (%)	3.94	3.88	0.00	4.10	3.66	305.18**	3.68	3.26	295.13**
N yield in seed (kg ha^{-1})	41.37	99.74	412.96**	88.10	106.67	49.21**	57.90	60.72	0.00
Straw dry yield (t ha^{-1})	3.00	4.23	174.64**	2.36	2.48	6.98*	2.32	2.97	160.04**
N content in straw (%)	1.80	1.47	122.38**	1.15	0.81	170.23**	0.96	0.81	26.18**
N yield in straw (kg ha^{-1})	52.52	61.32	22.59**	26.67	20.24	59.04**	21.57	23.74	5.08*
Total N yield (kg ha^{-1})	94.37	160.78	355.51**	114.77	126.94	16.88**	79.47	84.54	5.96*

**Significant at the .01 probability level.

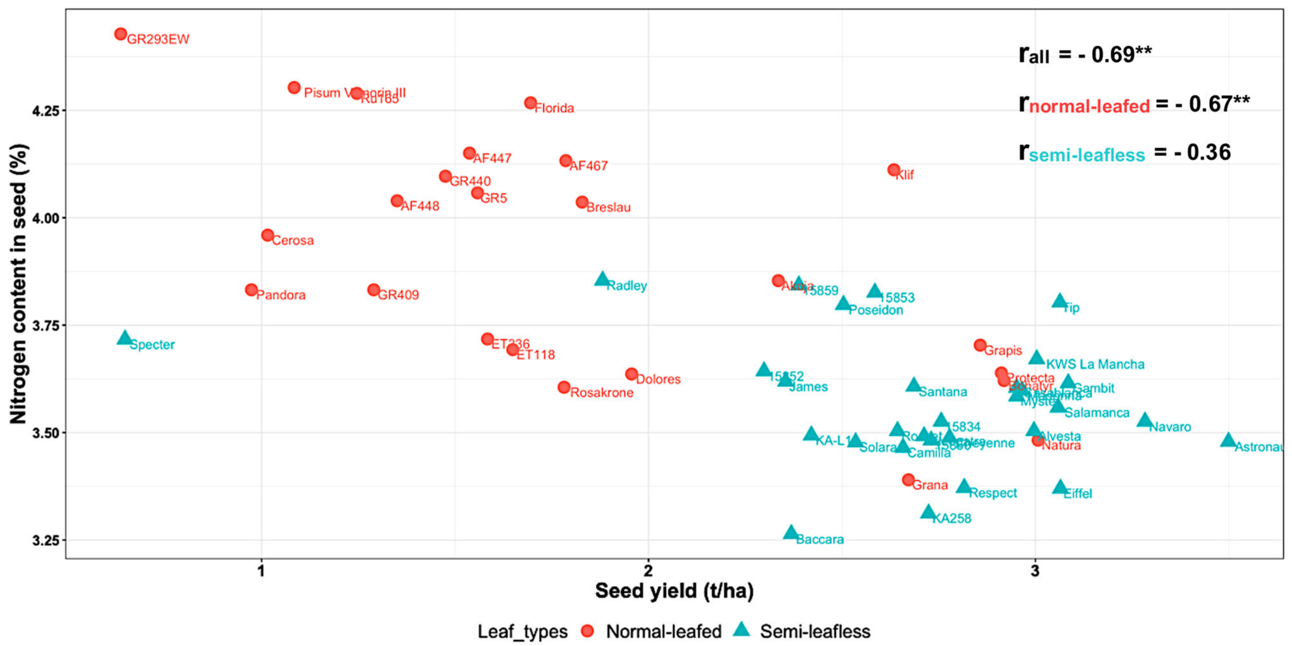

FIGURE 1 Nitrogen content in seed and seed yield of 54 pea genotypes, mean of three environments

in seed, and total N yield. A significant correlation of N yield in the seed with N content in straw was recorded for both leaf types.

Principal component (PC) analysis was applied to show the pattern of variation of all 54 genotypes and 14 traits. The first three PCs (PC1, PC2, PC3) explained almost 90% of the total variation, with the first component explaining 55.4%, the second component explaining 27.2%, and the third component explaining only 7.0% of the total variance (Supplemental Table S7). Thus, a biplot of PC1 and PC2 explained almost 83% of the total observed variance and is shown in Figure 4. The PC1 separated the two leaf types with some outlier

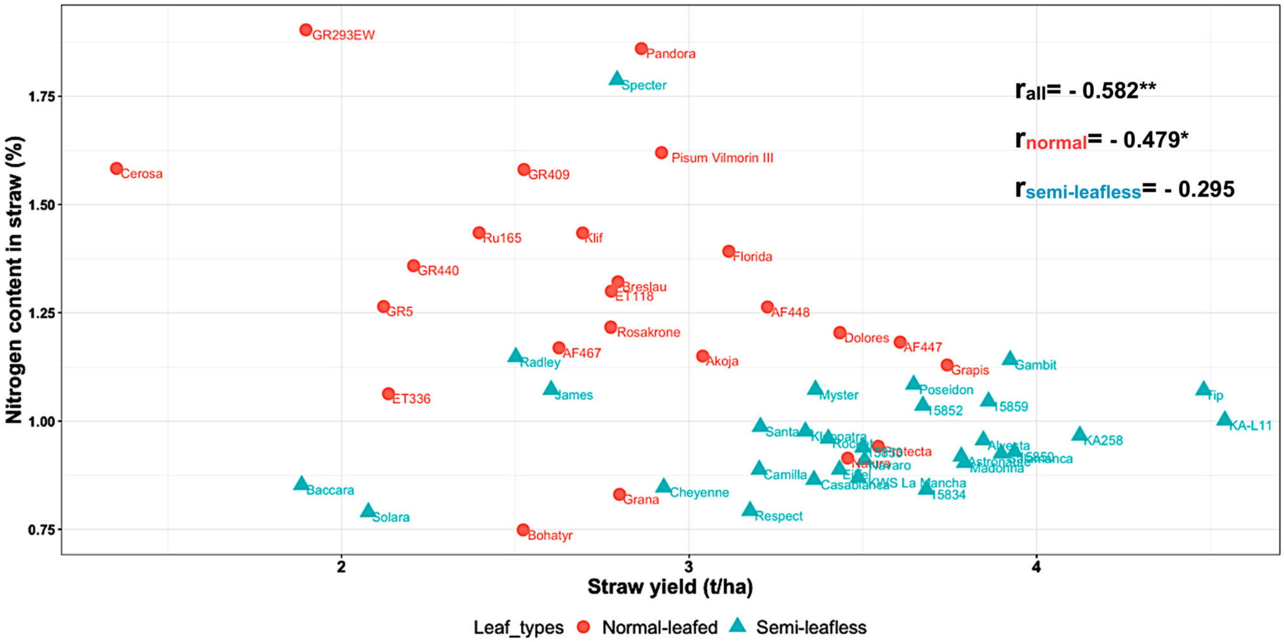

FIGURE 2 Nitrogen content in straw and straw yield of 54 pea genotypes, mean of three environments

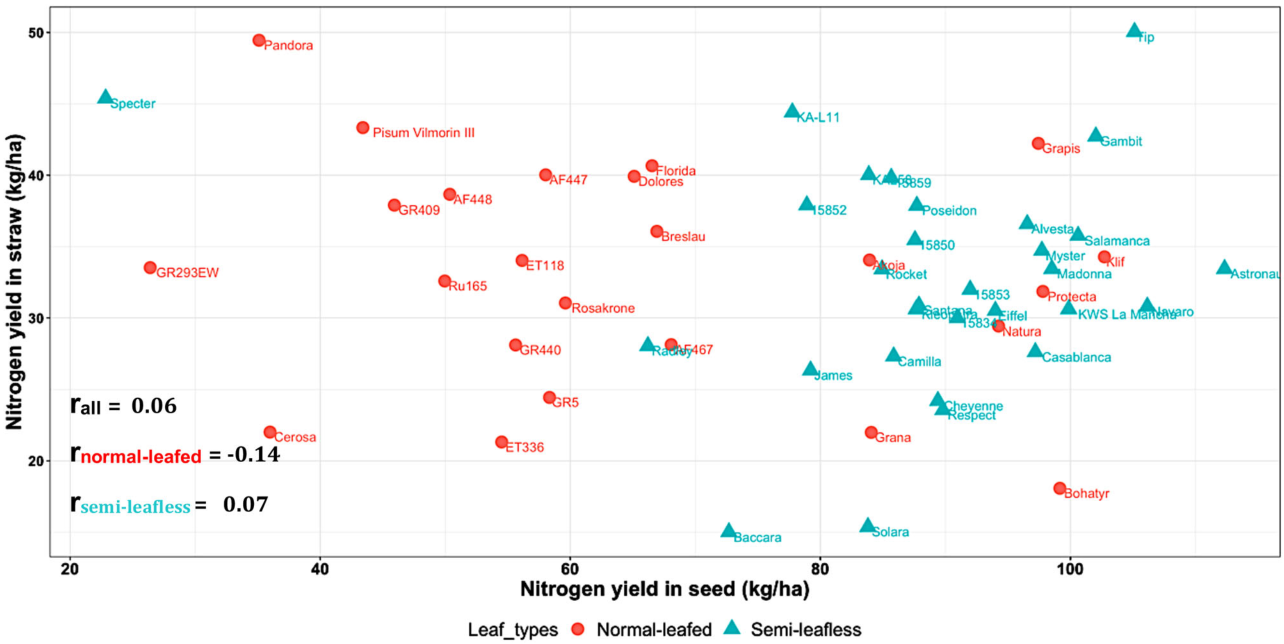

FIGURE 3 Nitrogen yield in seed and straw of 54 pea genotypes, mean of three environments

genotypes like ‘Specter’ and ‘Radley’ of the semi-leafless group and ‘Bohatyr’, ‘Natura’, ‘Protecta’, ‘GR293EW’, and ‘Grapis’ of the normal-leafed group. The first component, PC1, was positively influenced by the traits seed dry yield, N yield in seed, total N yield, biomass yield, straw dry yield, plot height, N harvest index, harvest index, and PL, with higher values for the semi-leafless group. The traits N content in seed, N content in straw, and lodging had negative values of PC1 and were related to the normal-leafed group. On the other hand, the two groups of leaf types were not different in PC2. Some outlier genotypes were observed, in particular, ‘Cerosa’, ‘Bohatyr’ (normal-leafed), ‘Baccara’, and ‘Solara’ (semi-leafless). Light interception, N yield in straw, and PL were traits with a positive influence on PC2. The eigenvalues for all PCs are given in Supplemental Table S7 and the principal components in Supplemental Table S6.

TABLE 6 Correlation coefficients among selected traits of normal-leafed ($n = 24$) and semi-leafless ($n = 30$) pea genotypes

Seed dry yield	(SDY)	Left value: normal-leafed; Right value: semi-leafless					
N content in seed	(Nseed)	−0.67**,−0.36					
N yield in seed	(NYS)	0.98**, 0.98**	−0.52**, −0.17				
Straw dry yield	(StrDY)	0.60**, 0.41*	−0.31, −0.06	0.61**, 0.43*			
N content in straw	(Nstraw)	−0.82**, −0.87**	0.67**, 0.43*	−0.76**, −0.83**	−0.49*, −0.28		
N yield in straw	(NYStr)	−0.16, −0.20	0.28, 0.30	−0.10, −0.14	0.57**, 0.71**	0.42*, 0.44*	
Total N yield	(TNY)	0.89**, 0.90**	−0.41*, −0.05	0.94**, 0.93**	0.79**, 0.69**	−0.59**, −0.65**	0.26, 0.23
		SDY	Nseed	NYS	StrDY	Nstraw	NYStr

*Significant at the .05 probability level.
**Significant at the .01 probability level.

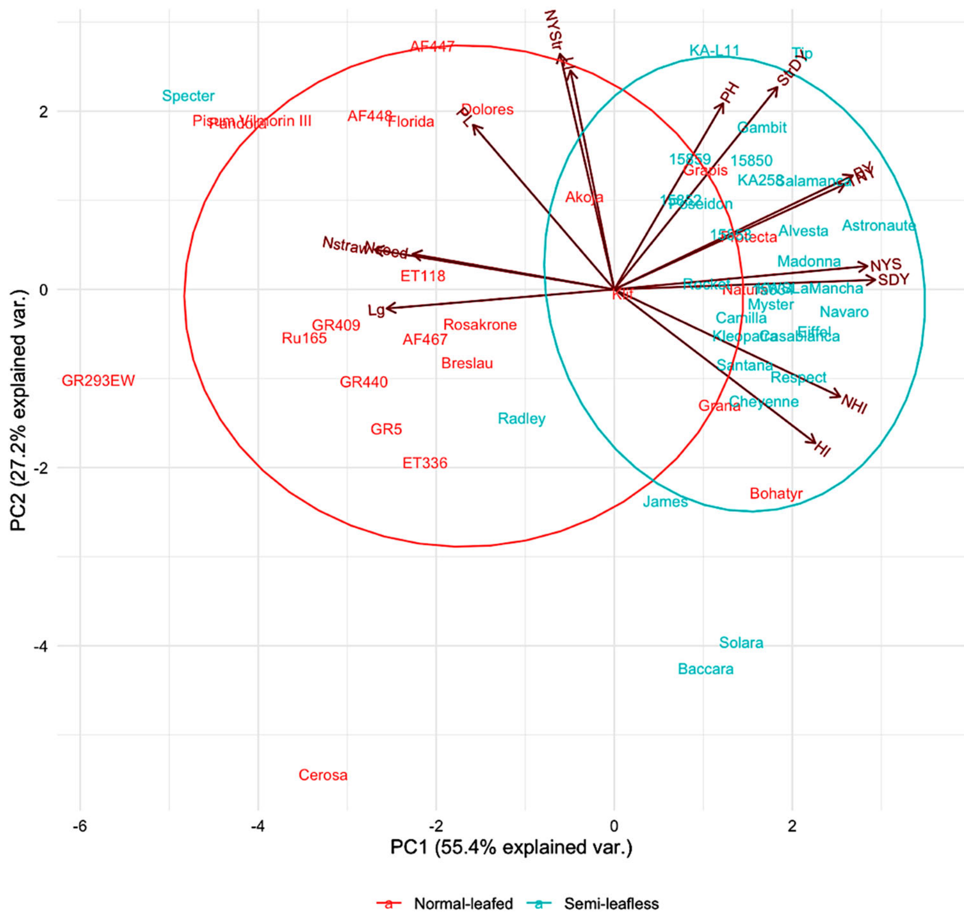

FIGURE 4 The first two principal components of a principal component analysis of 54 pea genotypes and 14 traits. BY, biomass yield; HI, harvest index; Lg, lodging; LI, light interception; Nseed, N content in seed; PL, plant length; PlotH, plot height; NHI, N harvest index; Nstraw, N content in straw; NYS, N yield in seed; NYStr, N yield in straw; SDY, seed dry yield; StrDY, straw dry yield

4 | DISCUSSION

Normal-leafed genotypes might be expected to produce higher seed and straw yields due to the larger area of photosynthesis. Stelling (1994) illustrated that normal-leafed peas had a higher yield potential than semi-leafless types in growing systems with or without supporting wire. Our results, however, do not indicate that semi-leafless types are generally associated with a loss in yield. Their average yield was significantly higher than the yield of normal-leafed genotypes. Additionally, the seed yield of normal-leafed genotypes is probably overestimated compared with practical cropping, where the yield of normal-leafed cultivars would be lower due to harvesting problems caused by lodging (Ambrose, 2008). In our experiment, yield data were recorded from experimental plots, which were harvested very carefully.

The difference between normal-leaf and semi-leafless peas was examined through the evaluation of a diverse set of genotypes (30 semi-leafless and 24 normal-leafed) grown in different environments. Our results give insights into the capability of the two main plant architectures in pea. However, the genotypes of the two leaf types are genetically diverse and not directly comparable. This is also the case in the other published experiments and may explain the partially contradicting results in the literature. Most of the normal-leafed genotypes in our experiment were older and/or less adapted to the trial environments. Thus, experiments with genotypes segregating for leaf type within the same genetic background are required. The publication of results from such an experiment is in preparation.

The research material was clearly separated into two groups according to the leaf type (Figure 4), with a considerable overlap. Generally, the semi-leafless genotypes had a higher seed yield and straw yield (Table 3), but a lower N content. However, some normal-leafed cultivars, for example, 'Grapis', 'Protecta', 'Natura', 'Grana', 'Klif', and 'Dolores' had the same yield level as semi-leafless cultivars (Figure 1). These cultivars were all released after the year 2000 (Table 1), supporting the assumption that the low average yield level of the normal-leafed genotypes is partly due to the fact that many of these cultivars are relatively old.

The semi-leafless cultivar 'Specter' had the lowest seed yield, and other genotypes, such as 'Pandora', 'GR 409', and 'GR 293' were also low-yielding (Figure 1). All of these are winter types. In the literature, winter peas have been reported to be more productive than spring peas (e.g., Chen et al., 2006; Urbatzka et al., 2011). In such experiments, winter peas are sown in fall and spring peas in spring, resulting in a longer vegetation period for winter peas. When winter peas are sown in spring, as in our experiment, they often start flowering late (data not shown).

The largest difference between the two leaf types is in lodging (Table 3); the normal-leafed group was seriously lodging right after flowering and during pod filling. Normal-leafed peas had, on average, a higher plant length than semi-leafless cultivars, because many of the more recent semi-leafless cultivars carry the semi-dwarf mutant (Burstin et al., 2018). However, due to lodging, normal-leafed peas had a lower plot height. Although lodging is not a very serious problem for semi-leafless cultivars, a negative relationship between lodging and seed and straw yield was also observed in this group (Supplemental Tables S3–S5). Semi-leafless genotypes have also been reported lodging before harvest in other experiments (Schouls & Langelaan, 1994; Stelling, 1989; Uzun et al., 2005; Zajac et al., 2012). Tar'an et al. (2003) identified two major **quantitative trait loci** for lodging resistance within semi-leafless material. Normal-leafed peas showed a more serious yield reduction due to lodging. This circumstance was also recorded by Singh and Srivastava (2015); serious lodging after flowering reduced irradiation to the leaflets on lower internodes of normal-leafed genotypes. Semi-leafless peas that stand more upright create better conditions for sunlight to penetrate to the lower part of the plants.

Some results were rather different between the three environments, in particular, the seed yield and N yield of normal-leaf genotypes was very low in 2017 at Reinshof (Table 5) compared with 2018. In 2017, there was an unusually high rainfall in July before and during harvest (142 mm compared with 41 mm in 2018). This resulted in heavy lodging of the normal-leafed genotypes, but seed losses were low because the harvest was carried out by hand. Uzun et al. (2005) also observed that the differences between normal-leafed and semi-leafless peas were not consistent in different experimental years.

Within both kinds of leaf types, seed yield correlated positively with straw yield, and a similar relationship was observed for N content in seed and straw. A negative correlation between yield and N content was significant for seed and straw for all genotypes and within the normal-leafed group, but not within the semi-leafless group (Figures 1 and 2). A negative correlation between yield and protein content has frequently been observed in cereals (Simmonds, 1995). For pea, the situation is less obvious. In a meta-analysis of nine populations, Klein et al. (2020) observed only a slightly negative overall correlation (−0.11), which was inconsistent over populations. Despite the negative correlation between yield and N content in our experiment, yield was positively correlated with N yield. Therefore, genotypes with higher yields yielded more N per area. The negative correlation between yield and N content arises from the fact that with increasing yield, other components (mainly carbohydrates and fiber) increase more than N.

No correlation between N yield in seed and N yield in straw was observed within both leaf types as well as for all genotypes (Figure 3). This indicates that a high protein yield in the seed can be combined with a high amount of N in the straw, which is important for the pre-crop value of pea. The value of pea in crop rotations can be increased by choosing and breeding cultivars with high N yield in the seed plus high N yield in the straw.

Even some normal-leafed cultivars like 'Klif' fulfill these requirements. Due to the better competition against weeds, they are of special interest in organic production and other systems where the use of herbicides is not desirable or is banned. However, due to their high susceptibility to lodging, normal-leafed peas will require mixed cropping with a supporting crop.

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AUTHOR CONTRIBUTIONS

Chi Thanh Tran: Formal analysis; Investigation; Writing – original draft; Writing – review & editing. Heiko C. Becker: Funding acquisition; Methodology; Resources; Supervision; Writing – review & editing. Bernd Horneburg: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing – review & editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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