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MARSCHNER REVIEW

Quantifying country-to-global scale nitrogen fixation for grain legumes: I. Reliance on nitrogen fixation of soybean, groundnut and pulses

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Abstract
Background We collated estimates of the percentage of legume N derived from atmospheric N_2 (%Ndfa) for 14 major grain legumes and then analysed and aggregated the data to derive average values for different crops and regions/countries. The effects of cultivation year and whether data collected from experimental plots were relevant to crops growing in farmers' fields were examined.

Scope A total of 5374 %Ndfa estimates (observations) were sourced, 4205 from field experiments and 1169 on-farm measurements collected from farmer-grown crops. The largest number of reports (82) and %Ndfa estimates (1391) were for soybean.

Conclusions The %Ndfa estimates for each legume species were consistent across years, except for soybean in North America. For some species estimates were also similar across geographic regions. There were no significant differences ($P > 0.05$) between estimates of %Ndfa derived from experimental plots and farmer-grown legume crops for nine of the 10 crops evaluated. Three distinct groups were identified with statistically-similar average %Ndfa values with associated standard deviations, namely: pigeonpea, faba bean and lupin – 74±11.8 %; groundnut, green and black gram, cowpea, chickpea, field pea, lentil, vetches and Bambara groundnut – 62±13.4 %; common bean – 38±11.1 %. There were three distinct different regional groupings for soybean: Brazil – 78±6.3 %; North America, Argentina, Asia, Africa and Oceania – 61±14.0 %; Europe – 44±13.8 %. Our findings provide more certainty and simplify the challenge of using field-scale measures of legume %Ndfa to estimate country-to-global inputs of fixed N from grain legumes.

Keywords Biological nitrogen fixation · Global estimates · Oilseed legumes · Pulses · Soybean · Symbiotic fixation

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Abbreviations

N_2	Dinitrogen
N	Nitrogen
%Ndfa	Percentage of the legume N derived from atmospheric N_2

Introduction

In 2018, annual grain legumes were grown on about 250 Mha globally, producing almost 490 Tg of harvested grain for human consumption and livestock feed (Table 1; FAOSTAT 2021). Area and production were dominated by soybean which was grown on 50% of the land area planted to grain legumes and produced 72% of the total grain. The oilseed groundnut was the second largest legume crop representing 11% of the total area and 9% of production. The remaining 38% of land area and 19% of grain production was associated with a multitude of warm- and cool-season pulses (crops grown predominately for dry grain for food or livestock feed; Table 1). Accurate estimates of biological dinitrogen (N_2) fixation by each of the different grain legume-rhizobia symbioses are crucial for understanding and managing nitrogen (N) flows and nutrient budgets in global agriculture as well as addressing environmental, sustainability and food security challenges at individual country, regional and global scales (Billen et al. 2014; Lassaletta et al. 2016; Zhang et al. 2020). To quantify inputs of fixed N at the field scale or at these broader scales, the total amount of N accumulated by the legume must be partitioned between N derived from atmospheric N_2 and N assimilated from plant-available soil and fertiliser N sources.

Researchers have been measuring the percentage of N derived from atmospheric N_2 (%Ndfa) of nodulated legumes growing in different agricultural

Table 1 Areas of major legume crops and quantities of grain harvested reported by FAO for 2018 (FAOSTAT 2021)

Crop common name(s)	Latin species name	Area harvested (Mha)	Grain harvested (Tg)
Soybean; Soya bean	*Glycine max* (L.) Merrill.	124.9	348.7
Groundnut; Peanut	*Arachis hypogaea* L.	28.5	46.0[c]
Dry Beans[a]			
- Common bean; Navy bean; Kidney bean	*Phaseolus vulgaris* L.	15.5[a]	15.8[a]
- Green gram; Mungbean Black gram; Urad bean	*Vigna radiata* (L.) R. Wilczek. *V. mungo* (L.) Hepper	19.0[a]	14.6[a]
Chickpea; Garbanzo bean	*Cicer arietinum* L.	17.9	17.2
Cowpea; black-eye pea	*Vigna unguiculata* (L.) Walp.	12.5	7.2
Field pea; Pea; Dry pea	*Pisum sativum* L.	7.9	13.5
Pigeonpea	*Cajanus cajan* (L.) Millsp.	7.0	6.0
Lentil	*Lens culinaris* Medik.	6.1	6.4
Faba (Fava) bean; Broad bean	*Vicia faba* L.	2.5	4.9
Lupin; Narrow-leafed lupin White lupin	*Lupinus angustifolius* L. *L. albus* L.	1.0	1.2
Vetches; Common vetch	*Vicia sativa* L. & others[b]	0.5	0.9
Bambara beans; Bambara groundnut	*Vigna subterranea* (L.) Verdc.	0.3	0.2
Other pulses	Not elsewhere specified	5.7	4.4
Total		249.2	487.0

[a]The regional distributions of area harvested and production data from FAOSTAT (2021) for the category "Dry Beans" were assumed to be predominantly common bean in North and South America, Africa and Europe, and green and black gram in Asia and Oceania (see Rawal and Navarro 2019)

[b]In addition to common vetch the category Vetches is assumed to include a range of species such as hairy vetch/woollypod vetch - *V.villosa* Roth, Narbonne vetch - *V.narbonensis* L., and bitter vetch - *V.ervilia* (L.) Willd

[c]Pods rather than grain for groundnut

systems and under a variety of management practices for more than 50 years (e.g. Weber 1966), with the number of estimates reported in the literature increasing rapidly after the mid-1970 s (Chalk 1985). Initially, field experiments utilized ^{15}N-enrichment methodologies to calculate %Ndfa from comparisons of the ^{15}N-composition of the legume with that of neighbouring non-fixing reference plants using only ^{15}N-enriched soil N (Ham and Caldwell 1978; Rennie 1984; Jensen 1986; Giller et al. 1987; Boddey et al. 1990). The non-isotopic N difference method, in which the N uptake by the N_2-fixing legume and a non-fixing reference plant are compared, has also been widely used (Rennie 1984; Guffy et al. 1989; Bell et al. 1994; Lupwayi and Soon 2015). Subsequently, techniques either relying on the small differences in the natural ^{15}N abundance between plant-available soil N and atmospheric N_2 that frequently occur in agricultural soils, or based on the relative abundance of ureides in legume xylem sap and shoot segments, were increasingly deployed (Kohl et al. 1980; Herridge et al. 1990; Espinoza et al. 2012; Peoples et al. 2017; Tamagno et al. 2018). These latter two methods proved particularly valuable in providing, for the first time, the ability to monitor the %Ndfa of farmer-managed, large-scale commercial crops and legumes grown by small landholders (Peoples et al. 1995a; Schwenke et al. 1998; Maskey et al. 2001; Naab et al. 2009; Hauggaard-Nielsen et al. 2010). Each of the four main quantification techniques have their own specific strengths, weaknesses and inherent sources of potential error (Chalk 1985; Unkovich and Pate 2000; Unkovich et al. 2008; Peoples et al. 2009b; Chalk and Craswell 2018), but all are believed to provide sufficiently reliable estimates of %Ndfa to enable legitimate comparisons of the N dynamics of different species at different times in different geographic locations.

Many thousands of %Ndfa estimates have now been published for the major grain legumes to which thousands more unpublished values can be added. Reported estimates vary from as low as zero to close to 100% (Unkovich and Pate 2000; Walley et al. 2007; Peoples et al. 2009a). In many cases, the variations in estimates were the result of experimental treatments (e.g. effects of inoculation in soils otherwise devoid of effective rhizobia, application of increasing rates of fertiliser N, extreme drought or excessive water supply) imposed to elucidate the key factors regulating symbiotic N_2 fixation (Peoples et al. 1995b; Hungria and Vargas 2000; Santachiara et al. 2019). In others, the disparate %Ndfa values reflected the effects of abiotic or biotic variables and agronomic practices (van Kessel and Hartley 2000; Peoples et al. 2009a; Jensen et al. 2010; Schipanski et al. 2010; Collino et al. 2015; Vanlauwe et al. 2019; Zheng et al. 2019).

It is not our intention to revisit the multitude of drivers of %Ndfa. Rather, we consider how the vast body of %Ndfa estimates can be aggregated to provide average values for each legume crop across country or geographic region. While published %Ndfa values have been collated before, such exercises were often restricted in the number of grain legumes examined, to specific crops in particular countries and to data derived from experimental plots (Table 2). Sourcing %Ndfa data from both published and unpublished on-farm studies of farmer's legume crops for this review added to the depth and breadth of the data set and facilitated the testing of the hypothesis that experimental plots estimates of %Ndfa were consistent with those from farmers' crops. A single publication has rarely considered as many different grain legume species as reported here, never collated as many different sources of information, nor provided such detailed analyses across different geographic regions.

The first objective of the current review was to update the existing literature on grain legume %Ndfa by assembling a comprehensive, global dataset of published and unpublished %Ndfa estimates for the legumes listed in Table 1. We examined specifically effects of legume species, country/region, the year in which the grain legumes were grown, and whether data collected from experimental plots were relevant for crops growing in farmers' fields. The second objective was to aggregate the data for each species to determine average %Ndfa values for different regions and crops. These %Ndfa values are used in a companion paper, together with grain legume area and production statistics (FAOSTAT 2021) and other N coefficients (harvest index, N harvest index, %N shoots, %N grain and a factor to account for below-ground N) to estimate inputs of fixed N from grain legumes at country-to-global scales (Herridge et al. 2021).

Table 2 Summary of previous reviews of %Ndfa by grain legumes

Reference	Comments
Van Kessel and Hartley 2000	Global estimates for soybean, common bean, pea and lentil
Unkovich and Pate 2000	Global estimates for soybean, groundnut and 6 pulses
Evans et al. 2001	Lupin, pea and chickpea in Australia
Alves et al. 2003	Soybean in Brazil
Walley et al. 2007	Pea, lentil, chickpea, common bean, and faba bean in Canada
Herridge et al. 2008	Global estimates for soybean, groundnut and 6 pulses
Salvagiotti et al. 2008	Global estimates for soybean
Peoples et al. 2009	Global estimates for soybean, groundnut and 7 pulses
Jensen et al. 2010	Global estimates for faba bean
Unkovich et al. 2010	Soybean, groundnut and 11 pulses in Australia
Anglade et al. 2015	Global estimates for pea, faba bean and lentil
Cernay et al. 2016	Global estimates for soybean, groundnut and 12 pulses
Ciampitti and Salvagiotti 2018	Global estimates for soybean
Karima et al. 2020	Soybean and 5 pulses in Canada

Sourcing %Ndfa estimates and determining the appropriate level of aggregation

Data were sourced from peer-reviewed publications based on a search using Clarivate Analytics Web of Science. Search terms included each of the legume common names listed in Table 1 – soybean (soyabean), groundnut (peanut), common bean, green gram, black gram, chickpea, cowpea, dry pea (field pea), pigeonpea, lentil, broad (faba or fava) bean, lupin, vetches and Bambara groundnut – with either 'biological N_2 fixation', 'BNF', 'nitrogen fixation', 'N fixation', or 'symbiotic fixation'. Additional %Ndfa data were sourced from the reference lists of publications accessed through the Web of Science search and from project reports containing %Ndfa data not published in the peer-reviewed literature. There were six such reports containing 82 unpublished estimates of %Ndfa.

Only publications where field-based estimates of %Ndfa were either stated, or could be calculated, were included. Estimates of %Ndfa obtained from ^{15}N enrichment, ^{15}N natural abundance and N-difference techniques were determined from total aboveground biomass data apart from a few publications where estimates were determined from ^{15}N analyses of grain. The %Ndfa measures using the ureide technique, which provides an instantaneous measurement at one point in time, were either integrated values calculated from multiple samples throughout the growing season (e.g. Herridge et al. 1990; Unkovich et al. 2008), or estimates based on sampling during early pod-fill which had been shown to be representative of %Ndfa over the growing season (Herridge and Peoples 2002). Values obtained using more than one method within a single study were generally combined and the average calculated. The mean %Ndfa for each species from each study was recorded together with the number of site-treatment-years of data, i.e. observations, determining that value. Also noted were the year and location of the study, various environmental, biophysical and soil data (were available), and treatment details.

Most %Ndfa estimates were derived from experimental plots, apart from Bambara groundnut where all data were collected from crops growing in farmers' fields. The experimental treatments were often designed to vary %Ndfa and amounts of N_2 fixed to gain a mechanistic understanding of the N_2 fixation process (Peoples et al. 1995b; Santachiara et al. 2019; Vanlauwe et al. 2019). Frequently grain legumes were supplied with different rates of fertiliser N to assess the inhibitory effects of elevated soil mineral N on nodulation and N_2 fixation (e.g. Herridge et al. 1995; Voisin et al. 2002; Hungria et al. 2006; Salvagiotti et al. 2008; Guinet et al. 2018). The largest rates of N fertiliser applied in such studies were usually much greater than those typically used by farmers and, as a consequence, we excluded values from atypical high fertiliser-N treatments from the final %Ndfa database. Defining a fertiliser-N rate that represented the upper limit of farmer practice was problematic. Such information is not available for many regions and, where reported, there is often wide variation in both the frequency of N fertiliser application and the rate of N applied to different crops, within and among countries (Ruiz Sainz et al. 2005; Beshir et al. 2015; Akter et al. 2018; Cao et al. 2018; FAOSTAT 2021; Johnbright et al. 2021).

Specific focus on updating %Ndfa values for soybean at country, regional and global scales was deemed to be of the highest priority because of its dominant role in total legume grain production (Table 1) and therefore the amount of N fixed. Based on information gleaned from the global literature, commercial soybean is generally grown without fertiliser N, or with very low rates of N, in many parts of the world. In the USA, however, 6–65% (29% average) of the total soybean area within different States in 2018 was fertilized with N at rates of 10–35 kg N ha^{-1} (17 kg N ha^{-1} average) (USDA 2020). In China, on-farm surveys indicated rates of 60–75 kg fertiliser N ha^{-1} as a common farmer practice (Gan et al. 2002; Zou 2020).

Although legumes differ in their sensitivity to the suppressive effects of fertiliser and soil mineral N on N_2 fixation (Guinet et al. 2018), we imposed a standard rule to all crops except common bean whereby only %Ndfa data for legumes supplied with < 85 kg fertiliser N ha^{-1} would be included in the database. This upper threshold was chosen based on the meta-analysis of Salvagiotti et al. (2008) that suggested %Ndfa by soybean was not significantly suppressed by fertiliser N rates < 85 kg ha^{-1}. In the case of common bean, a higher upper limit was set at 120 kg fertiliser N ha^{-1}, based on the observations reported in Beshir et al. (2015) and Akter et al. (2018) that 100 kg fertiliser N ha^{-1} reflected local farmer practice for common bean grown under irrigation in Ethiopia and Canada, respectively. This effectively only excluded a small amount of data from two publications on common bean (George and Singleton 1992; Guinet et al. 2018). The only other %Ndfa values excluded from the dataset came from uninoculated treatments at sites where populations of effective rhizobia were known to be absent, and under conditions of extreme drought and crop failure.

Applying these decision rules, the final database contained 329 reports and 5374 %Ndfa observations (Table 3). The 329 reports came from 193 publications, of which 139 considered only one species, with the remaining 54 providing estimates for between two and eight different crops. The estimates of %Ndfa were derived from crops across different levels of productivity with grain yield data (where available) ranging from 0.9 to 5.8 t ha^{-1} for soybean, 0.7–4.2 t ha^{-1} for groundnut and 0.3–4.9 t ha^{-1} for the pulses except field pea (0.6–8.6 t ha^{-1}) and faba bean (0.5–11.8 t ha^{-1}). These values were generally in line with the grain legumes statistics

Table 3 Summary of the numbers of reports and individual estimates of %Ndfa contained within them, and the range of years during which the observations were undertaken[a]

Crop	Number of reports	Number of estimates of %Ndfa	Years when %Ndfa determined
Soybean	82	1391	1973–2018
Groundnut	27	267	1984–2014
Common bean	30	1233	1980–2015
Green gram/black gram	11	168	1987–2005
Chickpea	22	352	1985–2016
Cowpea	18	556	1984–2013
Field pea	42	504	1981–2016
Pigeonpea	12	123	1977–2008
Lentil	21	336	1981–2016
Faba bean	34	211	1981–2017
Lupin	15	131	1981–2017
Vetch	11	52	1982–2014
Bambara groundnut	4	50	1999–2014
Grand total	329	5374	1973–2018

[a]Details provided in Supplementary Tables S1-S4

published by the FAO (FAOSTAT 2021). Supplementary Tables S1, S2, S3 and S4 provide the details for each report of the number of %Ndfa observations, the average %Ndfa for those observations, the country and the year in which the information was collected and whether the data were from experimental plots or farmer-grown crops. As previously stated, only six of the 329 reports from which data was extracted were not peer-reviewed publications. Crops from which the %Ndfa data were derived were grown over a 45-year period, between 1973 and 2018.

The largest number of reports and %Ndfa observations contained in those reports were for soybean ($n=82$ and 1389, respectively) and common bean ($n=30$ and 1233, respectively), while the least number were for vetches ($n=11$ and 52, respectively) and Bambara groundnut ($n=4$ and 50, respectively). Data for green gram and black gram were combined (total $n=11$ reports and 168 observations). The number of reports and observations for the remaining grain legumes varied from 12 to 42 to 123 and 556, respectively (Table 3).

Once the database for the different grain legumes had been assembled, our objective was to derive and compare average values for %Ndfa. To determine the most appropriate level to process the data, mean %Ndfa values for the combined North America + South America soybean subset were calculated and compared at each of three levels (±SD) – individual observations, treatment/site/year averages, or report average. The resulting mean %Ndfa and the variance around those values were found to be similar across the three levels (Fig. 1). The mean %Ndfa of 59 ± 15.6% for the soybean subset, calculated from the 32 report %Ndfa averages, was not significantly different ($P > 0.10$) from the average subset value of 62 ± 18.9%, calculated from 410 individual observations contained in those 32 reports. However, there was a significant difference ($P < 0.01$) between the subset mean %Ndfa of 56 ± 17.7% based on the 94 report/treatment/year values and the subset %Ndfa of 62% from the individual observations.

As a result, the single (average) report %Ndfa values, for which there were 329 across the soybean, groundnut and the other warm- and cool-season grain legume datasets (Table 3), were aggregated to estimate species and regional means and associated standard deviations (SDs). Relationships among %Ndfa and other factors, e.g. year of study, were assessed using regression analysis. The Student's t-test was used to compare %Ndfa values from the two populations, e.g. data collected from research trials and farmer-managed crops. Analysis of variance was used to compare %Ndfa values from more than two populations.

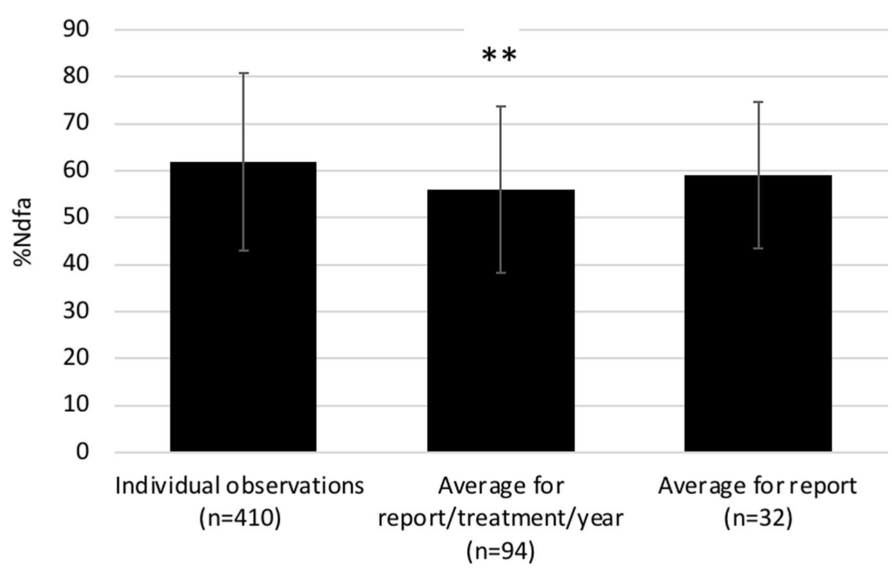

Fig. 1 Average %Ndfa values (±SD) for North and South/Central American soybean, calculated as averages for individual observations ($n=410$), report/site/years ($n=94$) and reports (publications) ($n=32$). A significant difference ($P < 0.01$) between the average %Ndfa for report/treatment/year and individual observations indicated by **

Comparing %Ndfa estimates from experimental plots and farmer-grown crops

The area and grain production data from FAOSTAT describe farmers' crops. To be able to calculate country-to-global estimates of N_2 fixation by grain legumes based on these statistics in the companion paper (Herridge et al. 2021), it was important to test whether the %Ndfa estimates sourced from experimental plots were consistent with data from farmer-managed crops. The average %Ndfa from experimental plots and farmers' crops for each grain legume species for which data were available are presented in Fig. 2. Only experimental data obtained from the same geographic regions as the on-farm estimates were compared. Common bean, vetches and Bambara groundnut were not included because of insufficient experimental (Bambara groundnut) or farmer crop data (common bean, vetch; Tables S3 and S4) to allow meaningful comparisons.

There was no consistent pattern of the relative %Ndfa estimates between experimental plots and farmers' crops with all showing large variation around the mean. A significant difference ($P<0.05$) in average %Ndfa between experimental and farmer-grown legumes was found for only one of the 10 species examined – lentil. There was no obvious explanation for this. Overall (including data for common bean, vetches and Bambara groundnut), the 265 reports containing 4196 experimental plot observations from research trials had an average %Ndfa of 61 ± 16.3%, which was identical to the average %Ndfa of 61 ± 16.0% from the farmer crops in 63 reports containing 1169 observations.

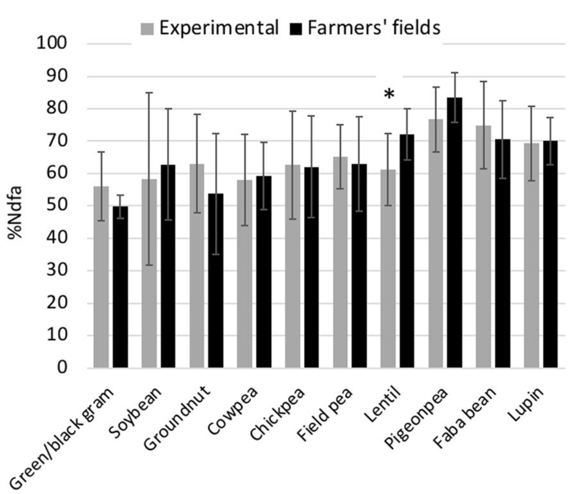

Fig. 2 Average %Ndfa values (± SD) for farmer-grown grain legumes and legumes sampled from experimental plots. Significant difference ($P<0.05$) for lentil indicated by *

Trends in %Ndfa in soybean grown in North America from 1973 to 2017

The review by van Kessel and Hartley (2000) examined the trends in %Ndfa for various grain legumes during the period 1970–2000. They reported a significant decline in soybean %Ndfa between pre-1984 and post-1984 but increases in %Ndfa values for common bean and field pea. No trend was observed for lentil. They noted that the timeframe over which the pulses were studied was short, i.e. <10 years and that the observed trends should be treated with caution. Examination of our current multispecies dataset indicated no significant differences ($P>0.05$) in average %Ndfa values pre-2000 and post-2000 for either soybean, groundnut, the pulses, or all grain legumes combined (Table 4).

Table 4 Average %Ndfa values (± SD) for soybean, groundnut, the pulses and all grain legumes combined, from field experiments and on-farm surveys conducted before and after the year 2000, and t-test significance when compared[a]

Crop & period when BNF measured	Number of reports	Number of observations	%Ndfa	±SD	t-test
Soybean					
Pre 2000	45	616	58	17.7	n.s.
Post 2000	39	773	61	12.8	
Groundnut					
Pre 2000	20	138	62	13.3	n.s.
Post 2000	7	129	55	14.5	
Pulses					
Pre 2000	95	1221	62	17.5	n.s.
Post 2000	120	2252	62	16.3	
All legumes[b]					
Pre 2000	160	1975	60	17.1	n.s.
Post 2000	166	3154	61	15.5	

[a]Details provided in Supplementary Tables S1-S4

[b]Analyses do not include data from studies where the year of experimentation was not specified

Because there was a more comprehensive dataset for soybean, van Kessel and Hartley (2000) also examined the trend of %Ndfa during the 20-year period (1975–1995), including data only from North America and Australia. They concluded that %Ndfa declined at a rate of 0.7 % per year. Examination of our current North American dataset of experiments conducted during 1973–2017 also revealed a significant, but positive, trend ($P < 0.01$) particularly for studies conducted after 1990 (Fig. 3). For that cohort of values, the average %Ndfa pre-2000 was 43 ± 16.3 %, and for post-2000 was 62 ± 13.6 %. Analyses indicated a weak but non-significant relationship between soybean productivity and %Ndfa, so improvements in yield potential over time cannot explain the observed trend. There was also little evidence of any significant genetic change in either the inherent capacity for N_2 fixation or its sensitivity to soil mineral N in North American soybean varieties released between 1930 and 2005 (Donahue et al. 2020). Improved agronomy combined with increased adoption of conservation tillage practices that reduce soil nitrate concentrations (Egli 2008; Torabian et al. 2019) were factors more likely to have contributed to the increased reliance of soybean on N_2 fixation post-2000.

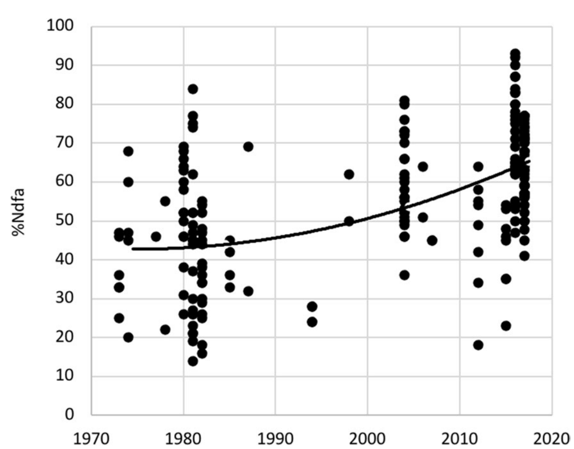

Fig. 3 Long-term trends in %Ndfa values for North American soybean. Each point represents a single %Ndfa observation for the year (x-axis) in which the experiment was conducted. There were 209 individual observations during 1973–2017 contained in the 20 published studies. The line of best fit is described by: $y = 0.0123x^2 - 48.58x + 48,003$ ($r^2 = 0.30$)

Soybean %Ndfa values for different countries and regions

There was substantial variation in soybean %Ndfa among regions (Fig. 4). Because of the significant trend of increasing %Ndfa with year of study for North American soybean, we only used post-2000 data in the analysis. For soybean estimates collated across all other countries and regions, small differences in pre-2000 and post-2000 %Ndfa were not significant ($P > 0.05$). Average values for North America, Argentina, Asia, Africa and Oceania were not significantly different ($P > 0.05$) from each other and were combined into one group with an average %Ndfa of 61±14.0 %. The average %Ndfa values of 78±6.3 % for Brazil and 44±13.8 % in Europe were significantly different from each other and from the aggregated group ($P < 0.001$).

The global %Ndfa average for soybean was calculated as a weighted mean, based on each country's/region's production for 2018 as reported by FAOSTAT (2021). Global grain production was dominated by North America (37 % of total) and Brazil (34 %) followed by Argentina (11 %) and Asia (9 %). Central America and other soybean-producing countries of South America, for which no %Ndfa data were available, but which produced 15.8 Mt grain (5 % of total) in 2018, were assumed to have the same

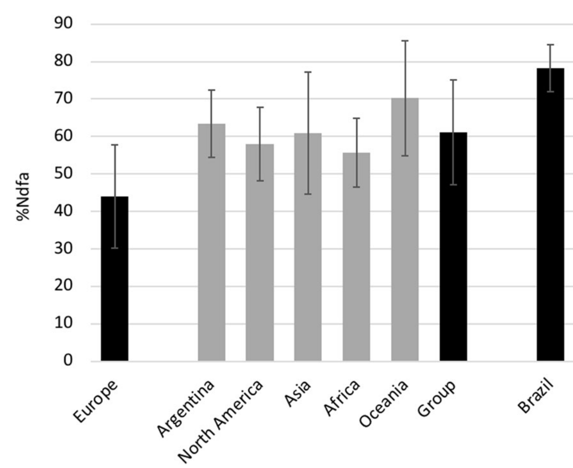

Fig. 4 Country/regional groupings for %Ndfa for soybean. Data for Argentina, North America, Asia, Africa and Oceania (grey histograms) were aggregated to generate the Group (black histogram). Differences in average %Ndfa between Brazil, Europe and the aggregated group were highly significant (P < 0.001)

%Ndfa value as for Argentina (i.e. 61 %) in the calculations. On this basis the analysis resulted in an overall global average %Ndfa for soybean of 66 %.

%Ndfa values for other grain legumes in different regions

Average values for groundnut, green and black gram, cowpea, chickpea, field pea, lentil, vetches and Bambara groundnut were not significantly different ($P > 0.05$) from each other and were combined into one group with an average %Ndfa of 62±13.4 % (Fig. 5). Similarly, average values for pigeonpea, faba bean and lupin were not significantly different ($P > 0.05$) and these were combined into one group with an average %Ndfa of 74±11.8 %. With an average %Ndfa of only 38±11.1 %, common bean remained in a group of its own. Each of the three groups were significantly different from each other ($P < 0.001$).

The regional %Ndfa averages for the warm- and cool-season pulse crops were also calculated as weighted means, based on each region's production of the different grain legumes for 2018 (FAOSTAT 2021). They were 42 % for South/Central America/Caribbean, 55 % for Africa, 58 % for North America, 63 % for Europe and 64 % for Asia and Oceania (Fig. 6). The variation in the regional %Ndfa values reflected the production of pulses in each region, particularly common bean on one hand (low %Ndfa) and pigeonpea, faba bean and lupin on the other (high %Ndfa). The global average %Ndfa for all pulses was estimated to be 60 %.

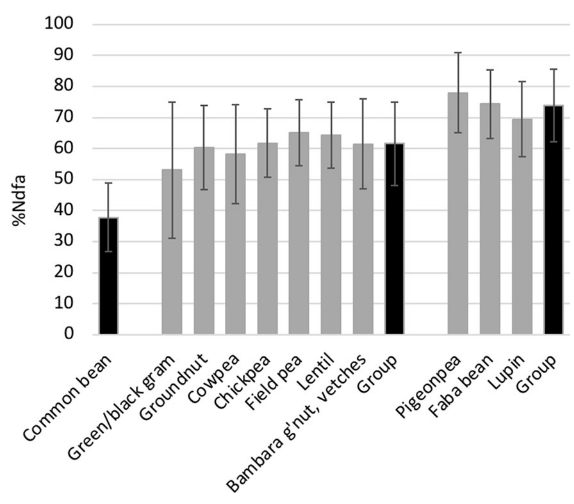

Fig. 5 Specific pulse and groundnut %Ndfa values (±SD) (grey histograms) and suggested groupings (black histograms). Differences in average %Ndfa between common bean, the aggregated group comprising green/black gram, groundnut, cowpea, chickpea, field pea, lentil, Bambara groundnut and vetches and the aggregated group comprising pigeonpea, faba bean and lupin were highly significant ($P < 0.001$)

Comparing updated %Ndfa values with those from previous reviews

A number of reviews of %Ndfa for grain legumes have been published during the last two decades (Table 2). Some have considered a wide range of species from a global perspective, while others have been more restricted in the number of crops or geographic area considered. A comparison of the global %Ndfa values for different crop species in the present study with average values from previous reviews showed very similar estimates for common bean, field pea, lentil, faba bean, lupin, and other legumes. Our estimates for soybean, groundnut, cowpea and chickpea, however, were 13–15 % higher than reported in earlier reviews, and about 60 % higher for green and black gram and pigeonpea (Fig. 7). The inclusion of more soybean data from Brazil with a high average %Ndfa (78 %) and the utilization of only post-2000 soybean data from North America are likely to be responsible

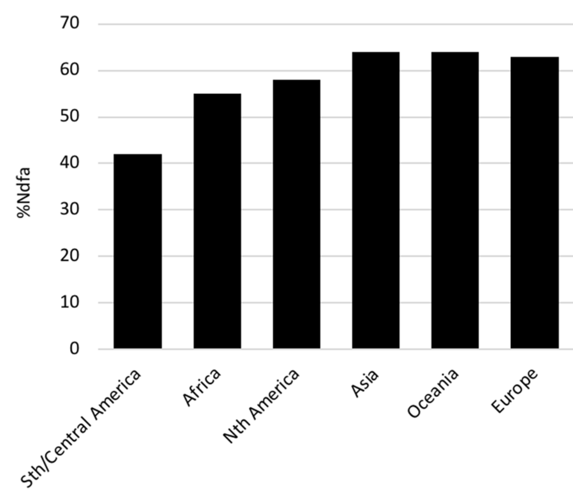

Fig. 6 Average %Ndfa values for warm- and cool-season pulses for the different regions

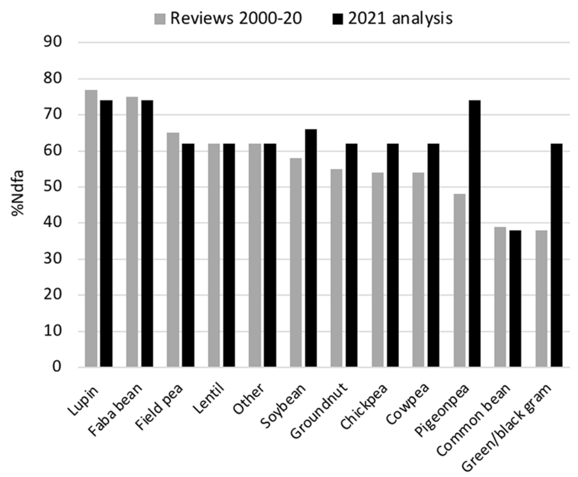

Fig. 7 Comparison of %Ndfa values for the individual grain legumes, determined as simple arithmetic averages across previous reviews published between 2000 and 2020 (referenced in Table 2) and the current review

for our higher estimate of %Ndfa in soybean. Reasons why our values for other legumes were higher than previously published would also be due to the inclusion of more data from Asia for green and black gram where %Ndfa values were somewhat greater (~60% average) than measured elsewhere (e.g. 41% in Oceania), and the collection of more cowpea and pigeonpea %Ndfa data from Africa (on average 62% and 87%, respectively) to complement the earlier smaller values from Asia for cowpea (50%) and pigeonpea (67%; Table S3).

The uniquely poor %Ndfa in common bean

Our analysis (Fig. 2) confirms the well-known observation that field-grown common bean has a much weaker ability to fix N than other grain legumes (Graham 1981; Redden and Herridge 1999; Giller 2001; Peoples et al. 2009a). For example, the mean %Ndfa of all common bean crops collated in the current dataset grown without the application of additional fertiliser N or manure was 41 ± 14.4% compared to 56 ± 16.4% for the combined zero N-fertiliser soybean treatment data collected from the same geographic regions (i.e. North and South America, Europe and Africa). The underlying reasons behind this difference in %Ndfa between common bean and other grain legume species remain something of an enigma because common bean can nodulate profusely and fix abundant N in glasshouse experiments and occasionally in the field when conditions are favourable (Giller 1990; Beshir et al. 2015; Habinshuti et al. 2021).

The most likely reasons for the continuing poor N_2 fixation performance in the field are two-fold. First, common bean is very sensitive to both biotic and abiotic stresses. Biotic stresses such as root rot and insect pests often affect the establishment of a strong root system preventing effective nodulation. Abiotic stresses include sensitivity to lack of water, nutrient limitations (particularly phosphorus) as well as soil N supply (Giller 1990). Common bean is frequently considered by agronomists and farmers to need some 'starter N' to ensure good establishment of the crop yet, at the same time, nodulation and N_2 fixation is very sensitive to soil mineral N (George and Singleton 1992; Guinet et al. 2018; Reinprecht et al. 2020). If there is an abundant supply of available soil N, a very effective auto-regulation response prevents common bean from forming nodules. This leads to farmers applying N fertilizer to common bean to overcome the risk of crop failure and ensure crop uniformity and good yields (Beshir et al. 2015; Akter et al. 2018; Habinshuti et al. 2021). Second, the crop is a relatively promiscuous legume that nodulates with a wide range of fast-growing rhizobial species, and not all combinations are equally effective in N_2 fixation. This results in common bean nodulating with poorly-effective native rhizobial strains in the field. It also probably explains why common bean responds erratically to inoculation with rhizobia (Graham 1981; Giller 2001; Reinprecht et al. 2020).

There is significant genetic variation in beans in relation to the ability to fix N. This is most apparent in the difference between climbing varieties of common bean which form many more nodules than bush bean varieties (Graham 1981). The potential for breeding for N_2 fixation in common bean has been explored though programmes in Latin America (Kipe-Nolt and Giller 1993), North America (Reinprecht et al. 2020; Wilker et al. 2020), Africa (Wortmann et al. 1995) and Australia (Redden and Herridge 1999). Although variation in the ability to fix N among varieties has been demonstrated, there is little evidence these differences have been successfully exploited to result in increased N_2 fixation in farmers' fields. The challenges for breeders to combine multiple traits to endow both effective nodulation (N_2 fixation) ability and to overcome the biotic and abiotic constraints, whilst maintaining the specific seed-types of common bean demanded by different markets, can be substantial.

The need for more %Ndfa estimates from farmers' crops

There were > 1000 estimates of %Ndfa from 63 studies of farmers' grain legume crops across all regions, representing about 20% of our database of reports. The farmer crop surveys were far more numerous in Africa ($n = 15$; 272 observations), Asia ($n = 18$; 507 observations) and Oceania (Australia; $n = 22$; 288 observations). There was just a single report from North America, two from South America and three from Europe (Tables S1-4). Clearly, more reports of %Ndfa values for farmer crops are needed, particularly for crops from the most important regions for grain legume production – North and South America. Nonetheless, the results from farmers' commercial crops provide some degree of ground-truthing of the findings from the far more numerous experimental studies. The lack of significant differences between the farmer-grown and experimental crops substantiates the relevance of research plots to what is occurring on-farm. This generates confidence in the legitimacy of applying the calculated regional %Ndfa values for the various legume groupings to the reported FAOSTAT (2021) commercial crop production data when calculating global inputs of fixed N (Herridge et al. 2021).

Conclusions

Analyses of the 5374 estimates of %Ndfa collated from the 329 reports compiled for this review indicated that the %Ndfa estimates for each grain legume species except North American soybean were relatively consistent across years. For many of the grain legumes, average %Ndfa determinations were also often similar across geographic regions (Tables S1-4). For the pulses and groundnut, three distinct groups were identified with statistically similar average %Ndfa, namely: pigeonpea, faba bean and lupin – 74%; groundnut, green and black gram, cowpea, chickpea, field pea, lentil, vetches and Bambara groundnut – 62%; common bean – 38%. Analyses also revealed three distinct different regional grouping for soybean: Brazil – 78%; North America, Argentina, Asia, Africa and Oceania – 61%; Europe – 44%. Collectively these findings will provide more certainty and simplify the challenge of calculating country-to-global inputs of fixed N by grain legumes as described in Herridge et al. (2021).

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Author contributions The large dataset was generated and analysed by MBP and DFH. The manuscript was drafted by MBP. During a 2-year period leading to submission, all authors contributed to regular, extensive discussions about the review and provided critical insights into various aspects of biological N_2 fixation. All authors read and approved the final manuscript.

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Declarations

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Conflict of interest/competing interests None to declare.

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