RESEARCH ARTICLE

Biomass partitioning in response to intraspecific competition depends on nutrients and species characteristics: A study of 43 plant species

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Abstract

1. Competition simultaneously limits the availability of above- and below-ground resources for plants. How plants respond to density with changes in patterns of biomass allocation is poorly understood. Previous studies had inconsistent results, but emphasised increased biomass allocation to stems in response to density. However, the response of plants to density may depend on environmental conditions and on characteristics of the species.

2. We grew 43 herbaceous plant species at three densities (1, 8 and 64 individuals per pot) and two nutrient levels in a common garden and measured biomass allocation to roots (RMF), leaves (LMF) and stems (SMF), and specific root (SRL) and stem length (SSL). The species differed in functional group (grasses, forbs and legumes), life span and realised niche with respect to nutrients (Ellenberg's nutrient indicator value).

3. Intraspecific competition and self-thinning increased with nutrient supply. Overall, plants increased their RMF with density independent of nutrient level, indicating that competition was mainly for below-ground resources. However, characteristics of the species influenced their responses to density and nutrients in terms of biomass allocation, SRL and SSL. At high densities, legumes were more productive than the other functional groups and hardly changed their allocation patterns, suggesting that they were less nutrient limited due to their mutualism with nitrogen-fixing rhizobia. The SRL of perennials was lower, and their RMF was higher and increased more strongly in response to density than that of annuals, which could be interpreted as mechanisms to increase survival. The realised niche of species with respect to nutrients influenced the response to density and nutrients in terms of SMF, LMF, SRL and SSL in line with adaptations to both nutrient availability and competition for light in the typical habitats.

4. *Synthesis*. We found that intraspecific competition was mainly for below-ground resources, which may be typical for many species growing in moderately nutrient-rich but high-light habitats. Our results show that growth conditions, species

characteristics and their interactions influence patterns of biomass allocation and plant morphology.

1 | INTRODUCTION

As sessile organisms, plants rely strongly on phenotypic plasticity to deal with variation in environmental conditions (Nicotra et al., 2010; Sandner & Matthies, 2018; Sultan, 2000; Valladares et al., 2006, 2014; van Kleunen & Fischer, 2005). One of the most fundamental responses of plants to different environments is a change in the allocation of biomass to different organs (Kleyer et al., 2019; Poorter et al., 2012; Weiner, 2004). Among the plant organs, roots are mainly responsible for the uptake of nutrients and water, while stems provide mechanical support and position the leaves which in turn are most important for photosynthesis. It has long been noted that plants increase the allocation of biomass to those organs that increase the uptake of the most limiting resource (termed 'optimal partitioning' or 'balanced growth', Bloom et al., 1985; Brouwer, 1963; Poorter et al., 2012; Shipley & Meziane, 2002). As a consequence, the relative allocation of vegetative biomass to roots (root mass fraction, hereafter 'RMF'), stems (stem mass fraction, 'SMF') and leaves (leaf mass fraction 'LMF') shows predictable responses to most abiotic stresses (reviewed by Poorter et al., 2012).

A stress that poses challenges to the theory of optimal partitioning is intraspecific competition. Increasing density of conspecifics leads to a reduction of individual biomass and saturating total biomass production per area ('constant final yield', Farazdaghi & Harris, 1968; Li et al., 2016; Shinozaki & Kira, 1956, reviewed by Weiner & Freckleton, 2010) accompanied by density-dependent mortality at high densities ('self-thinning', Westoby, 1984; Yoda et al., 1963). However, in spite of the large number of studies on plant competition, little is known about the functional responses of plants to intraspecific competition, including changes of biomass allocation (Poorter et al., 2016). Increasing density results in the shortage of both above-ground (light) and below-ground resources (nutrients, water). The relative importance of competition for above- and below-ground resources depends on the availability of water (Totsuka & Monsi, 1964), nutrients (Berendse & Möller, 2009; Lentz, 1999; Tezuka, 1960) and light (Forster et al., 2011; Hautier et al., 2009; Meekins & McCarthy, 2000). Studies examining the effects of intraspecific competition on biomass allocation have given inconsistent results: with increasing density plants either increased their RMF (Berendse & Möller, 2009; Lentz, 1999), their LMF or SMF (Forster et al., 2011; Hecht et al., 2016; Meekins & McCarthy, 2000; Puri et al., 1994), or did not change their biomass allocation at all (Flint & Patterson, 1983; Kamel, 1959). In a review of the results of the available studies, Postma et al. (2020) found that there was large variation among studies and species in the response to density, and concluded that the most consistent response was an increased biomass allocation to stems, interpreted as shade avoidance.

When above- and below-ground resources are both limiting at the same time, the benefits of changes in biomass allocation are limited by trade-offs. However, plants can also respond to different environments by changing morphological or physiological traits (Freschet et al., 2015; Kramer-Walter & Laughlin, 2017; Poorter et al., 2012, 2019; Sandner & Matthies, 2018). For example, in response to shade by competitors, plants may increase their specific stem length (Poorter et al., 2019; Postma et al., 2020) and in response to nutrient shortage due to competition may increase their specific root length (Schippers & Olff, 2000, Trubat et al., 2006, Dybzinski et al., 2019, but see Freschet et al., 2015; Kramer-Walter & Laughlin, 2017).

The inconsistent results of previous studies about the effects of density on patterns of biomass allocation may have also been due to differences in characteristics of the species studied: First, plant functional groups are known to differ in their general patterns of biomass allocation (Niu et al., 2008). For example, grasses have a special root morphology (Craine et al., 2001; Roumet et al., 2016) and generally allocate more biomass to roots than eudicotyl forbs (Freschet et al., 2015; Poorter et al., 2015). In contrast, legumes can form mutualistic interactions with nitrogen-fixing soil microbiota (e.g. Gibert et al., 2019). This rhizobia–legume interaction strongly depends on the environment (Araújo et al., 2015; Batstone et al., 2020; Heath et al., 2010; Rehling et al., 2019; Zahran, 1999), but is particularly beneficial at high light, but low nutrient conditions (Friel & Friesen, 2019; Lau et al., 2012; Taylor & Menge, 2018). Second, the life span of a plant represents a trade-off between survival and reproduction (Friedman, 2020) that affects its biomass allocation and response to different environments (Eziz et al., 2017; Husáková et al., 2018; Poorter et al., 2015). Perennial plants are expected to invest more into structures that increase their chance to survive periods during which conditions are unfavourable (Garnier & Laurent, 1994; Roumet et al., 2006). Third, species differ in their realised niche along a productivity gradient (Hellegers et al., 2020; Schaffers & Sýkora, 2000). As competition between plants in nutrient-poor habitats is particularly strong for below-ground resources and in nutrient-rich habitats for light (DeMalach et al., 2016; Grime, 1977; Tilman, 1982), species from highly productive habitats usually have larger LMFs (Poorter & Remkes, 1990), higher relative growth rates (Poorter & Remkes, 1990), and are more competitive in nutrient-rich soils than species from nutrient-poor habitats (Klinerová & Dostál, 2020).

Here, we investigated the effect of density and two nutrient levels on the production and allocation of biomass and on the shoot and root morphology of 43 herbaceous species. The species were chosen to differ in three characteristics potentially relevant for their response to density: functional group (grass, legume, non-leguminous forb), life span (annual vs. non-annual) and realised niche with respect to nutrients (N-indicator value, Ellenberg et al., 1992). We studied the effects of density in combination with that of nutrients, because we expected that nutrients strongly influence the relative importance of above- and below-ground competition and thus patterns of biomass allocation. We addressed the following questions: (a) How do species allocate their biomass in response to density and nutrient levels? (b) Do species' functional group, life span and realised niche with respect to nutrients influence their responses?

2 | MATERIALS AND METHODS

2.1 | Study species

In this experiment we used 43 herbaceous plant species commonly occurring in European open habitats and crop plants. The species were chosen to represent a large range of angiosperms (14 families) and to differ in important characteristics (Table 1): We chose species from three functional groups (12 grasses, 12 legumes and 19 non-leguminous forbs) with different life histories (17 annuals, 26 non-annual species) and with different realised niches with respect to nutrients as characterised by their indicator values for nutrients (Ellenberg et al., 1992). This indicator value ranges from 1 (plant restricted to nutrient-poor habitats) to 9 (plant typical for highly productive habitats) and is available for the species of Central Europe. The N-indicator value of a species is closely correlated with its relative growth rate (Poorter & Remkes, 1990).

We selected species to represent all combinations of these three characteristics as balanced as possible (Table 1). Based on the BIOLFLOR database (Klotz et al., 2002), we grouped summer- and winter-annual species as annuals, and biennial and perennial as non-annual species. Species that can be both annual and perennial were classified as non-annuals. Nutrient indicator values were not available for the four crop plants (*Glycine max*, *Linum usitatissimum*, *Pisum sativum* and *Zea mays*). We assigned these species the highest N-indicator value of 9, because they have been bred to achieve maximum yield in fertilised fields. A further species without an indicator value was *Vicia cracca* which has no clear preference for a certain nutrient level and was assigned the intermediate value of 5. Seeds of the species were obtained from various regional seed producers. Species names are based on http://www.plantlist.org.

2.2 | The experiment

In May 2016, we filled pots (11.3 cm × 11.3 cm × 21.5 cm) with 2 L of sand and added 10 g of top soil from a meadow to ensure soil inoculation with microbiota and placed them in a glasshouse. In each pot we sowed as many seeds of one plant species as necessary to establish the target densities of 1, 8 or 64 individuals per pot. To ensure that a similar number of seedlings was available at the same time, the number of seeds and the date of sowing were adjusted based on the findings of a pilot germination study. To increase their germination, we treated seeds of *Lamium purpureum*, *Legousia speculum-veneris*, *Melilotus albus* and *Setaria viridis* with gibberellic acid (500 ppm) for 24 hr, and scarified the seed coat of *Lathyrus pratensis*, *Melilotus albus*, *Securigera varia*, *Vicia cracca* and *Vicia sepium* with abrasive paper. After 14 days of growth, we established three replicates of all combinations of two levels of nutrient availability and the three levels of seedling density. To each pot we added weekly throughout the experiment 40 ml of a nutrient solution containing 6.25 g/L fertiliser in the high nutrient treatment ('Hakaphos Gartenprofi', Compo, Wien; N:P:K 14:7:14 wt per cent) and 0.78 g/L in the low nutrient treatment. In the three density levels, the number of seedlings was reduced to one, 8 or, if possible, 64 individuals per pot. However, a few days of extreme heat in the glasshouse during establishment reduced the number of seedlings of some species resulting in a range of 20–64 individuals per pot at the highest density treatment (mean number of seedlings: 57.4). For six species (Table 1), the number of seedlings was too low to establish the highest density treatment. After 17 days of growth, we transferred the plants from the glasshouse to flowerbeds in the Botanic Garden of the University of Marburg, Germany. We watered and weeded the pots when necessary and randomised their position every 2 weeks. We restricted the lateral spread of plants by wrapping strings around poles placed at the four corners of the pots and fastened the climbing lianas on lattice frames.

After a mean period of growth of 77 days (range: 55–95 days), we harvested 727 pots with 12,430 individuals in total. We harvested species in a random order, but harvested species before they could flower, because flowering affects biomass allocation in plants. All individuals of a species were harvested at the same time. We counted the number of individuals per pot, measured the height of an individual of average height with a folding rule, cut the plants at ground level and separated leaves and stems, as well as live and dead above-ground parts. We then carefully washed the roots free of soil. No rhizomes were produced by the plants. We extracted a representative sample of roots (5 cm of primary root + lateral roots) from the upper soil layer (<10 cm beneath soil surface). We placed the root sample in a glass tray filled with water and scanned it at a resolution of 600 dpi using a flatbed scanner with transparency unit (Epson Perfection 4490, Suwa, Japan). The length of primary and lateral roots of the samples were determined using the image analysis software RootGraph (Cai et al., 2015). We dried all plant material for 48 hr at 80°C and weighed it. We calculated total biomass per pot as the total amount of live and dead plant tissue per pot and mean biomass per individual as living biomass per pot divided by the number of individuals alive at harvest. We calculated biomass allocation to leaves, stems and roots by dividing the mass of the respective live plant parts by the total live plant mass per pot. We calculated

TABLE 1 Study species and their characteristics

Species	Family	Functional group	N-indicator value	Life span
Vulpia myuros	Poaceae	Grass	1	Annual
Bromus erectus	Poaceae	Grass	3	Non-annual
Bromus tectorum	Poaceae	Grass	4	Annual
Digitaria sanguinalis	Poaceae	Grass	5	Annual
Trisetum flavescens	Poaceae	Grass	5	Non-annual
Poa pratensis	Poaceae	Grass	6	Non-annual
Arrhenatherum elatius	Poaceae	Grass	7	Non-annual
Lolium perenne	Poaceae	Grass	7	Non-annual
Setaria viridis	Poaceae	Grass	7	Annual
Echinochloa crus-galli	Poaceae	Grass	8	Annual
Alopecurus aequalis	Poaceae	Grass	9	Non-annual
*Zea mays**	Poaceae	Grass	9*	Annual
*Alyssum alyssoides**	Brassicaceae	Forb	1	Annual
Pilosella officinarum	Asteraceae	Forb	2	Non-annual
Sanguisorba minor	Rosaceae	Forb	2	Non-annual
*Silene vulgaris**	Caryophyllaceae	Forb	2	Non-annual
*Galium verum**	Caryophyllaceae	Forb	3	Non-annual
*Legousia speculum-veneris**	Campanulaceae	Forb	3	Annual
Leucanthemum vulgare	Asteraceae	Forb	3	Non-annual
Berteroa incana	Brassicaceae	Forb	4	Annual*
Crepis capillaris	Asteraceae	Forb	4	Annual
Achillea millefolium	Brassicaceae	Forb	5	Non-annual
Matricaria chamomilla	Asteraceae	Forb	5	Annual
Digitalis purpurea	Plantaginaceae	Forb	6	Non-annual
Papaver rhoeas	Papaveraceae	Forb	6	Annual
Salvia pratensis	Lamiaceae	Forb	6	Non-annual
Geranium pusillum	Geraniaceae	Forb	7	Annual*
*Lamium purpureum**	Lamiaceae	Forb	7	Annual
*Urtica dioica**	Urticaceae	Forb	8	Non-annual
*Linum usitatissimum**	Linaceae	Forb	9*	Annual*
*Malva neglecta**	Malvaceae	Forb	9	Annual*
Anthyllis vulneraria	Fabaceae	Legume	2	Non-annual
Trifolium aureum	Fabaceae	Legume	2	Annual
*Lotus corniculatus**	Fabaceae	Legume	3	Non-annual
*Melilotus albus**	Fabaceae	Legume	3	Non-annual*
Securigera varia	Fabaceae	Legume	3	Non-annual
Trifolium dubium	Fabaceae	Legume	5	Annual
*Vicia cracca**	Fabaceae	Legume	5*	Non-annual
*Vicia sepium**	Fabaceae	Legume	5	Non-annual
*Lathyrus pratensis**	Fabaceae	Legume	6	Non-annual
Trifolium repens	Fabaceae	Legume	6	Non-annual
*Glycine max**	Fabaceae	Legume	9*	Annual
*Pisum sativum**	Fabaceae	Legume	9*	Annual

Notes: N-indicator values of Ellenberg et al. (1992), ranging from 1 indicating species from nutrient-poor habitats to 9 indicating those from nutrient-rich habitats. Information about the life span of the species is based on BIOLFLOR (Klotz et al., 2002, see Section 2).

*Species without a rosette for which we calculated specific stem length.

[†]No N-indicator value available, values were assigned (see Section 2).

[‡]Life span of some species was adjusted according to their behaviour in the experiment (see Section 2).

specific root length of plants as the length of primary and lateral roots divided by the mass of the scanned root sample and specific stem length as the average height of individuals per pot divided by the mean mass of the stem of an individual.

2.3 | Statistical analyses

We analysed the effects of nutrients, density (number of individuals at harvest) and their interactions on (log) biomass per pot, (log) individual biomass, and biomass allocation to roots, stems and leaves with linear mixed models (type III sums of squares). We used species as a random factor using the R-package LME4 version 1.1-23 (Bates et al., 2015) and the R program version 4.0.2 (R Core Team, 2020). We included a maximal random effects structure by including random intercepts for the species and random slopes for species responses to nutrients, density and their interaction as suggested by Barr et al. (2013). Significance values were obtained with Satterthwaite's correction using the R-package LMERTEST version 3.1-2 (Kuznetsova et al., 2017). We tested the effect of species identity (random) on the response variables with a likelihood ratio test using LMERTEST. In additional analyses, we investigated if plant responses to nutrients and density depended on their life span, functional group or N-indicator value by including these characteristics as fixed factors in the analyses. The duration of growth influenced both biomass production and allocation of the species. However, including the duration of growth in the models did not change the results qualitatively and we therefore present models without duration of growth.

The analysis of changes in allocation pattern by analysing biomass fractions has been criticised, because the effects may be size dependent (Poorter & Sack, 2012; Weiner, 2004). As an alternative method to analyse the effect of nutrients and density on biomass allocation, we used linear models with log root mass as response variable and log above-ground biomass, density and nutrient level as explanatory variables. We calculated for each species the mean biomass values per combination of density and nutrient level to study the effect of nutrients and density on allometric relationships among species separately (McCarthy & Enquist, 2007). The results of these analyses were qualitatively the same as those based on the analyses of biomass (Supporting Information Notes S1, Table S1, Figure S1).

To study the effects of density, nutrient levels and species characteristics on specific stem length (SSL) and specific root length (SRL) we applied the same linear mixed models that we used for analysing the effects on biomass production and allocation. We restricted the analysis of SSL to species that did not produce a (semi-)rosette ('erosulate' species sensu Klotz et al., 2002) and excluded the single remaining grass species *Zea mays* to avoid including the functional group of grasses without replicate species. In the analysis of SRL and SSL, we faced singularity problems caused by the maximal structure of the random effects. To allow a non-singular fit (Barr et al., 2013), we excluded the most complex part of the maximal structure of the random effect which were the random slopes of the interaction between nutrients and density with species.

To analyse the mortality of the individuals, we used generalised linear mixed models (binomial error distribution and a logit link) with the number of individuals that had died before harvest and the number of survivors in the same pot as the response. We only analysed the data for the highest density, because mortality in pots with one or eight plants was negligible. In a few species, the number of plants at harvest exceeded the number of 8 or 64 plants per pot, because apparently some seeds germinated after the initial thinning. In these cases, mortality was assumed to be zero. Because the delayed germination obscured differences between species, we only tested the effect of nutrients on the mortality of individuals. We used a likelihood ratio test to compare a model with only the random effect (species intercept) with one that included the effect of nutrient availability (fixed factor) and its interaction with species identity (random slopes). In these models, we used a logit link and a beta-binomial error distribution to correct for overdispersion and included a parameter for zero inflation using the R-package GLMMTMB version 1.0.2.1 (Brooks et al., 2017).

3 | RESULTS

3.1 | The effect of density and nutrients on plant performance

Plants produced more total biomass per pot at high than at low nutrient levels and at high than at low densities. However, these two factors interacted and biomass per pot increased more strongly with density at low than at high nutrient levels (Table 2, Figure 1a). The studied species differed strongly in the biomass produced per pot ($df = 1$, chi-square = 107.3, $p < 0.001$) and responded differently to nutrients and density ($df = 4$, chi-square = 74.17, $p < 0.001$). These differences among species were not related to their life span or N-indicator value, but to their functional group (Table 3). The functional group of a species also influenced its response to density. Forbs produced the least biomass at all densities. Although biomass of legumes was lower than that of grasses at low densities, they produced more biomass per pot at high densities (Figure 1b). Functional groups did not differ in their response in total biomass to nutrients.

Mean biomass per individual was higher at high nutrient levels and decreased with density, but this decrease was stronger at high nutrient levels (Table 2, Figure 1c). The life span or N-indicator value of a species did not explain differences among species in individual biomass or in the response to nutrients and density, but functional groups varied in their growth and their response to density (Table 3). The individual biomass of forbs was lowest at all densities, while that of legumes decreased less with density than that of grasses (Figure 1d). Mortality of the individuals in a pot was influenced by an interaction between density and nutrients. While almost all individuals survived at low and intermediate plant densities, many plants died at high density, more at high than at low nutrient levels (21% versus. 16%; chi-square = 11.01, $p = 0.001$).

TABLE 2 Mixed model analyses of variance of the effects of nutrients and density on biomass production per pot and per individual, biomass allocation to roots (root mass fraction, RMF), stems (stem mass fraction, SMF) and leaves (leaf mass fraction, LMF), and on the morphology of stems (specific stem length, SSL) and roots (specific root length, SRL)

| | | Productivity | | | | Biomass allocation | | | | | | Morphology | | | |
| | | Pot biomass | | Ind. biomass | | RMF | | LMF | | SMF | | SSL | | SRL | |
	df	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Nutrients (N)	1	293.83	**<0.001**	286.84	**<0.001**	140.68	**<0.001**	2.00	0.165	57.05	**<0.001**	55.31	**<0.001**	2.89	0.091
Density (D)	1	225.14	**<0.001**	1,239.14	**<0.001**	71.01	**<0.001**	15.76	**<0.001**	20.87	**<0.001**	143.39	**<0.001**	21.26	**<0.001**
N × D	1	41.66	**<0.001**	44.42	**<0.001**	0.18	0.675	5.40	**0.025**	6.85	**0.012**	32.90	**<0.001**	16.08	**<0.001**

Notes: Density, biomass per pot biomass, individual biomass, specific stem length and specific root length were log10-transformed before analyses. Statistically significant values ($p < 0.05$) are in bold-face.

FIGURE 1 The effect of density and nutrients on (a) total biomass per pot and (c) mean individual biomass per pot, and the effect of density and functional group of a species (grass, legume or non-leguminous forb) on (b) total biomass per pot and (d) mean individual biomass per pot. Shaded areas indicate 95% confidence intervals. Note the log-scales for density, pot biomass and individual biomass

3.2 | The effect of nutrients and density on biomass allocation

Plants strongly adjusted their biomass allocation in response to both nutrient level and density (Table 2). The proportion of biomass allocated to roots (root mass fraction, RMF) was much higher at low than at high nutrient levels and increased with density, but there was no interaction between nutrient level and density (Figure 2a). Allocation of biomass to leaves (leaf mass fraction, LMF) and stems (stem mass fraction, SMF) in response to density showed the opposite pattern, that is, a reduction with density (Figure 2b,c). However, while the reduction in LMF with density was stronger at low than at high nutrient levels (Figure 2b), the opposite was the case for SMF (Figure 2c).

The species differed strongly in their biomass allocation to roots (RMF: $df = 1$, chi-square = 252.47, $p < 0.001$) and in the response of RMF to density and nutrients ($df = 4$, chi-square = 11.76, $p = 0.019$). For example, the RMF of individually grown plants at high nutrient levels varied from 14% in *Galium verum* to 55% in *Lathyrus pratensis*. Density influenced the effects of species characteristics on biomass allocation (Table 3). In general, the RMF of grasses was higher than that of legumes and forbs. In response to density, grasses and forbs strongly increased their RMF, but legumes hardly responded at all (Figure 2d). In forbs, the increase in RMF was at the expense of both leaves and stems, whereas in grasses it was only at the expense of stems (Figure 2e,f).

Perennial plants invested more biomass into leaves and roots than annuals, while annual plants invested more biomass into stems

TABLE 3 Mixed model analyses of variance of the effects of nutrients, density and species characteristics on biomass production per pot and per individual and biomass allocation to roots (root mass fraction, RMF), stems (stem mass fraction, SMF) and leaves (leaf mass fraction, LMF), and on the morphology of stems (specific stem length, SSL) and roots (specific root length, SRL)

	df	Productivity				Biomass allocation						Morphology			
		Pot biomass		Ind. biomass		RMF		LMF		SMF		SSL		SRL	
		F	p	F	p	F	p	F	p	F	p	F	p	F	p
Nutrients (N)	1	40.14	**<0.001**	38.94	**<0.001**	36.74	**<0.001**	1.74	0.194	9.77	**0.003**	8.54	**0.009**	2.34	0.129
Density (D)	1	43.72	**<0.001**	352.86	**<0.001**	22.66	**<0.001**	0.12	0.730	19.38	**<0.001**	110.73	**<0.001**	9.14	**0.005**
N × D	1	3.21	0.081	3.34	0.075	0.02	0.881	0.62	0.437	0.89	0.351	1.94	0.186	4.35	**0.019**
Functional group	2	12.83	**<0.001**	12.75	**<0.001**	7.65	**0.001**	17.44	**<0.001**	1.86	0.168	4.29	0.057	5.01	**0.031**
N-value	1	0.25	0.618	0.26	0.610	0.04	0.848	3.90	0.055	3.02	0.090	4.10	0.063	4.58	**0.038**
Life span	1	0.13	0.718	0.15	0.703	3.36	0.074	3.78	0.059	9.00	**0.004**	4.08	**0.045**	11.08	**0.001**
N × Fungroup	2	0.02	0.982	0.02	0.981	2.90	0.066	1.09	0.344	1.58	0.218	5.17	**0.035**	3.30	**0.039**
D × Fungroup	2	10.32	**<0.001**	10.78	**<0.001**	7.79	**0.001**	4.22	**0.022**	12.62	**<0.001**	4.13	0.063	8.80	**0.001**
N × N-value	1	0.49	0.486	0.50	0.483	0.89	0.351	0.47	0.497	<0.01	0.969	0.40	0.534	6.44	**0.012**
D × N-value	1	1.84	0.182	1.22	0.275	0.60	0.444	5.03	**0.031**	5.93	**0.019**	8.65	**0.012**	0.53	0.471
N × Life span	1	0.07	0.787	0.08	0.774	0.45	0.507	0.02	0.879	0.14	0.714	1.15	0.297	1.93	0.167
D × Life span	1	0.01	0.908	<0.01	0.982	16.69	**<0.001**	0.74	0.393	7.42	**0.009**	2.47	0.140	2.60	0.114
N × D × Fungroup	2	0.95	0.395	1.03	0.365	1.41	0.258	2.47	0.097	0.59	0.559	0.09	0.764	0.05	0.948
N × D × N-value	1	1.12	0.295	1.23	0.274	<0.01	0.984	<0.01	0.991	<0.01	0.975	0.45	0.502	3.57	0.059
N × D × Life span	1	<0.01	0.984	<0.01	0.949	1.76	0.193	0.49	0.486	3.25	0.079	0.06	0.801	0.46	0.497

Notes: Density, biomass per pot biomass, individual biomass, specific stem length and specific root length were log10-transformed before analyses. The effect of species characteristics was investigated for plants of different functional groups (grasses, forbs and legumes), lifespan (annual vs. non-annual) and their realised niche with respect to nutrients (N-value). The SSL-values were only calculated for non-rosette species other than grasses (*n* = 14, see Section 2); the number of functional groups was thus only 2 for SSL and the *df* for functional group and its interactions only 1. Statistically significant values (*p* < 0.05) are in bold-face.
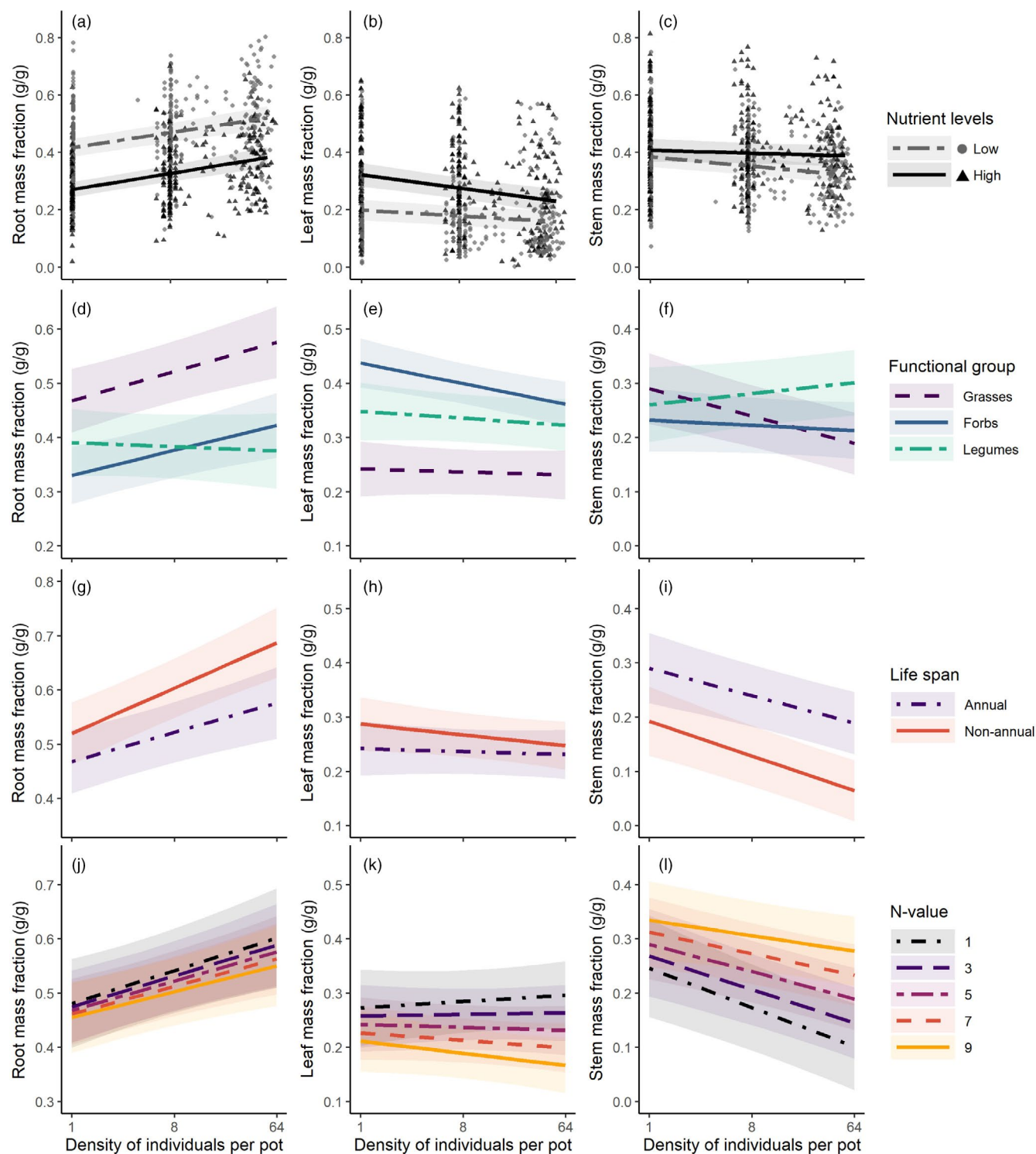
FIGURE 2 The influence of nutrients (a–c), functional group (d–f), life span (g–i) and nutrient indicator value (j–l) on the effect of density on biomass allocation to roots (a, d, g, j), leaves (b, e, h, k) and stems (c, f, i, l). Shaded areas indicate 95% confidence intervals. Note the log-scale for density

(Figure 2g–i). In response to density, perennials further increased their RMF at the expense of leaves and stems (Table 3). Species from nutrient-poor habitats, that is, with low N-indicator values, allocated in general more biomass to leaves than species from nutrient-rich habitats (Figure 2k), which instead invested more biomass into stems (Figure 2l). This difference became even stronger at high densities,

while biomass allocation to roots was not affected by N-indicator values (Figure 2j, Table 3). Nutrient levels did not influence the effects of species characteristics on allocation, with the exception of some evidence for a stronger reduction of the RMF of grasses (56.4% to 36.6%) than forbs (41.9% to 29.0%) or legumes (43.1% to 32.9%) in response to high nutrient levels (Table 3).

3.3 | The effect of nutrients and density on stem and root morphology

Plants also adjusted their specific length of stems (SSL) and roots (SRL) in response to nutrient supply and density (Figure 3). The stems of plants were elongated in particular at low nutrient levels and at high densities. However, there was an interaction between these two factors, as the increase in SSL with density was stronger at high than at low nutrient levels (Table 2, Figure 3a). Conversely,

the SRL decreased more strongly with density at high nutrient levels (Figure 3b).

Species strongly differed in their stem and root morphology and in their response to nutrients and density. Stems of non-leguminous forbs were more elongated than those of legumes, particularly at low nutrient levels (Figure 3c) and in response to density, non-leguminous forbs elongated their stems more strongly than legumes (Figure 3e). The SRL of forbs was higher than that of legumes and grasses (Figure 3d). While SRL was similar for legumes and grasses
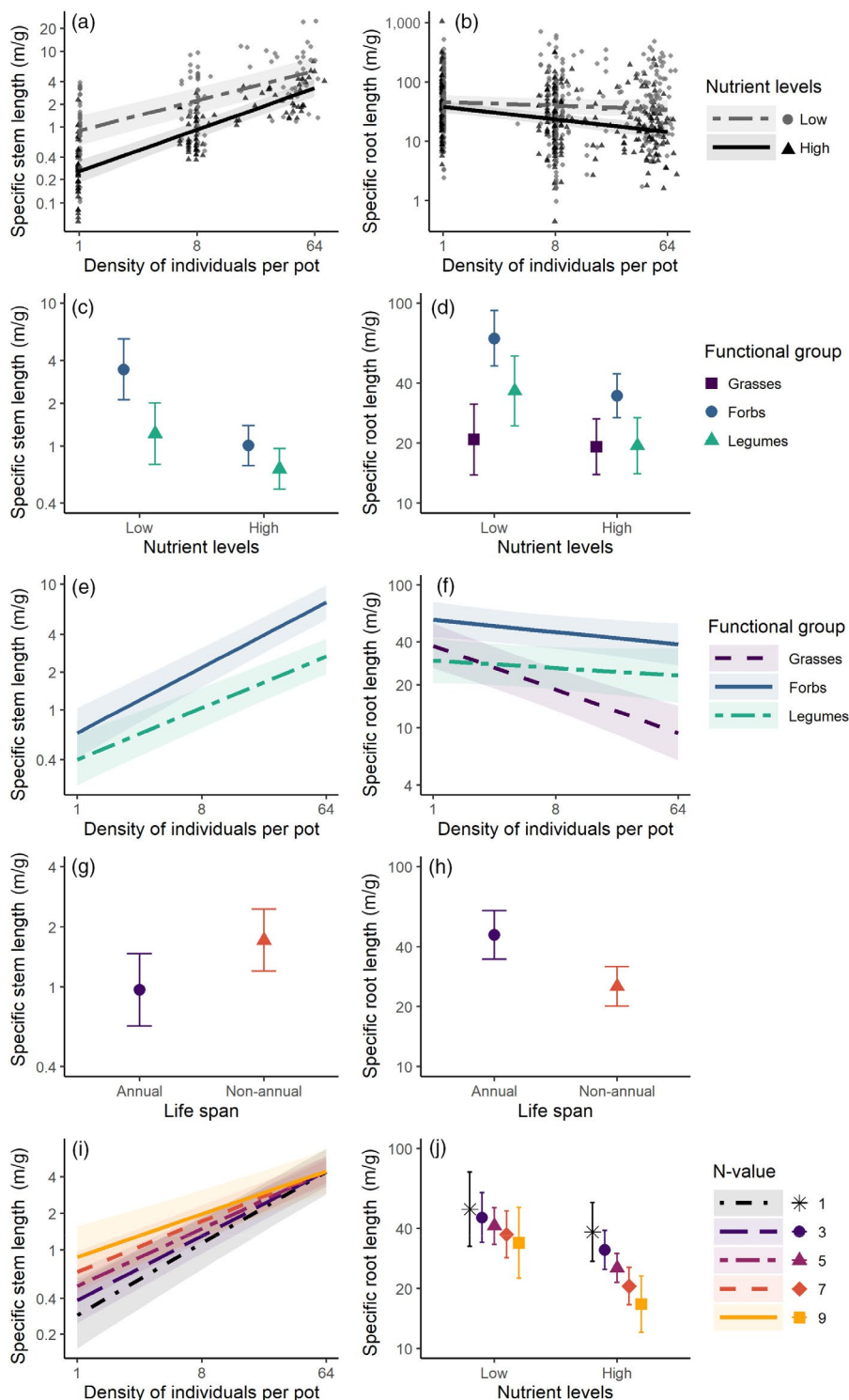
FIGURE 3 The influence of density, nutrients and species characteristics on the specific length of stems (a, c, e, g, i) and roots (b, d, f, h, j). (a, b) Interactive effects of density and nutrients, (c, d) interactive effects of functional group and nutrients, (e, f) interactive effects of functional group and density, (g, h) effects of life span, (i) interactive effects of N-value and density and (j) interactive effects of N-value and nutrient levels. Specific length of stems was only calculated for a subset of 14 species (see Section 2). Note the log-scales for density, specific stem length and specific root length. Error bars and shaded areas indicate 95% confidence intervals

at high nutrient levels, only legumes and forbs increased their SRL in response to nutrient scarcity and the SRL of legumes was thus higher than that of grasses at low nutrient levels (Figure 3d). In response to density, however, grasses decreased their SRL, while legumes and non-leguminous forbs hardly responded (Figure 3f). The life span of a plant did not affect plant responses in SSL or SRL to nutrients or density (Table 3), but overall annual plants had higher SSL and lower SRL than perennial plants (Figure 3g,h). The stems of plant species from highly productive habitats, that is, with high N-indicator values, were more elongated than those of plants from nutrient-poor habitats, that is, with low N-indicator values, at low densities, but not at the highest density (Figure 3i). The SRL of species with low N-indicator values was generally higher than that of species with high N-indicator values. In response to high nutrient levels, species from highly productive environments were most plastic and reduced their SRL more strongly than species from nutrient-poor habitats (Figure 3j).

4 | DISCUSSION

Fertilisation strongly increased intraspecific competition as individual biomass decreased more strongly with density at high than low nutrient levels. Simultaneously, nutrient addition increased the mortality of individuals at the highest density ('self-thinning', Westoby, 1984; Yoda et al., 1963). The slope of a regression between biomass per pot and density was lower at high than at low nutrient levels indicating that plants were closer to the maximum total biomass per pot at high nutrient levels ('constant final yield'; Farazdaghi & Harris, 1968). The effects of nutrients and density on biomass production differed among species, but of the studied characteristics only the functional group explained some of the variation among species. Legumes were more productive at the highest density and, thus, suffered less from increasing competition than grasses and non-leguminous forbs. This may have been due to their mutualistic symbiosis with rhizobia that buffered the negative effects of intraspecific competition on nitrogen availability, although high plant density may reduce the formation of nodules by legumes (Menéndez et al., 2017).

4.1 | Effects of nutrients and density on biomass allocation

According to the optimal partitioning theory, plants balance the allocation of biomass to leaves, stems and roots in order to increase the uptake of the most limiting resources (Bloom et al., 1985; Brouwer, 1963). In our study, more than 95% of the plant species grown without competitors (vs. 75% of cases reviewed in Reynolds & D'Antonio, 1996) allocated more biomass to roots at low than at high nutrient levels, thus supporting the optimal partitioning theory (Poorter et al., 2012). However, when plants are competing, light and nutrients may be limiting at the same time. The relative

importance of above- and below-ground competition is thought to depend on the amount of nutrients available (DeMalach et al., 2016; Grime, 1977; Tilman, 1982). In our study, plants growing at high densities allocated more biomass to roots, indicating that competition was more intense for below-ground resources than for light, even at high nutrient levels. In contrast, a recent meta-analysis found that at high densities most plants allocate more biomass to stems, and concluded that higher density predominantly increases competition for light (Postma et al., 2020). There are several possible explanations for these conflicting results. Approximately half of the studies on stem mass fraction reviewed by Postma et al. (2020) were carried out in the glasshouse, where light availability is lower than in the field, whereas our experiment was performed in a common garden during summer. In three studies, below-ground competition had explicitly been prevented (Aphalo & Rikala, 2006; Casper et al., 1998; Maliakal et al., 1999). These factors probably increased the importance of light limitation through increased density in these studies. Similar patterns have been found in agricultural systems (Hecht et al., 2016, Shao et al., 2018, but see Kamel, 1959), where biomass allocation to roots (Jackson et al., 1996) and below-ground competition is strongly reduced by the addition of high amounts of fertiliser. Similarly, Postma et al. (2020) suggested that the high levels of soil fertility in agronomic field experiments were responsible for the fact that in their review they found a reduction of RMF in response to density only in crops but not in wild species.

A possible cause of the increase in RMF with density at high levels of nutrients in our experiment could have been water shortage which intensifies below-ground competition relative to light competition (Foxx & Fort, 2019). However, plants in our experiment were watered regularly and showed no signs of drought stress. Moreover, a more detailed analysis showed that legumes in contrast to forbs and grasses did not show an increase in RMF with density, suggesting that, even at the high nutrient levels, scarcity of nitrogen might have been responsible for the increased allocation to roots. We applied amounts of fertiliser typical for agriculture practice (c. 220 kg/ha in this study vs. (50-)191–300 kg N/ha for *Zea mays* in Roy et al., 2006; 240 kg N/ha in Shao et al., 2018), but used nutrient-poor sand as substrate. The low nutrient retention capacity of the sand might have contributed to a scarcity of nutrients through leaching by precipitation. Our results may be typical for ecosystems which are characterised by high-light availability and a moderate availability of nutrients or water, such as grasslands and tundras which show on average the highest RMFs of all biomes (Jackson et al., 1996; Mokany et al., 2006; Poorter et al., 2012).

Plants can respond to changes in environmental conditions in traits other than biomass allocation, for example, through changes in morphology or plant architecture (Kleyer & Minden, 2015; Kleyer et al., 2019). In the current experiment, plants strongly increased their specific stem length (SSL) in response to density. Such a response is often interpreted as a mechanism of shade avoidance by which plants aim to position their leaves above those of their competitors

(Franklin, 2008; Maliakal et al., 1999; Poorter et al., 2016, 2019). In addition, the increase in SSL may also have been due to the necessity to increase RMF in response to density and a subsequent reduction in resources available for above-ground growth, as plants also elongated their stems at low nutrient levels. Increasing SSL with density may then have been a mechanism to reach similar heights with less investment into biomass than at low density conditions. However, the fact that in our experiment SSL, but not RMF, increased more strongly with density at high than at low nutrient levels suggests that competition for light became stronger at high nutrient levels. Other studies have also found that changes in above-ground morphological traits are important responses of plants to density (Poorter et al., 2012, 2016; Postma et al., 2020) or light availability (Freschet et al., 2015; Poorter et al., 2019).

In contrast, several recent studies on the relative strength of below-ground responses to changes in nutrient levels found weak responses in morphological traits compared to those in RMF (Bennett et al., 2016; Freschet et al., 2015; Kramer-Walter & Laughlin, 2017). This has led to the suggestion that plasticity in below-ground morphological traits may be genetically constrained (Kramer-Walter & Laughlin, 2017) and less important for plant resource acquisition than plasticity in above-ground morphological traits (Freschet et al., 2015). A key root morphological trait is SRL, which is thought to reflect the efficiency of soil resource uptake (Freschet et al., 2021; Hong et al., 2018; Ostonen et al., 2007; Ryser, 2006), but conflicting relationships between SRL and nutrient uptake have been found in studies across species (see Freschet et al., 2021 and references therein). Corrected for phylogeny, SRL was found to increase among species with habitat fertility (Fort & Freschet, 2020) because high SRL may be important for plants to compete in nutrient-rich environments (Mommer et al., 2011). However, we found significant increases in SRL in response to low nutrient levels, and only in forbs and legumes and for plant species from highly productive environments. These differences among species with different characteristics may help to explain the large variation of responses in SRL to nutrient shortage found among different studies (Ryser, 2006). In response to density, we had expected either no response (due to genetic constraints) or an increase in SRL (as observed for some species in response to low nutrients or competition). However, plants at high nutrient levels even reduced their SRL with density. Such a response could be interpreted as a mechanism to avoid competition with conspecific individuals (Bennett et al., 2016; Novoplansky, 2009). However, an alternative explanation could be that at high densities the volume of rooting space for each individual was strongly reduced, restricting the lateral growth of roots.

4.2 | The effect of species characteristics on biomass allocation and morphology

Plants from the three functional groups differed strongly in their allocation patterns. Overall, grasses invested most of their biomass into roots, whereas legumes and non-leguminous forbs allocated more biomass to leaves, underlining the structural differences between these functional groups (Poorter et al., 2015; Roumet et al., 2016). It has been suggested that the larger RMF of grasses could be a compensation for a lower frequency of mycorrhizal symbioses (for C3 grasses; Wilson & Hartnett, 1998) or the lower protein concentration and nitrogen uptake per mass (Poorter et al., 2015; Roumet et al., 2016). Furthermore, responses in biomass allocation and morphology to increased density and nutrient shortage differed among functional groups. Forbs increased both their RMF and SRL in response to both treatments, which may be thought of as mechanisms to increase nutrient uptake of the plants (Ryser, 2006). Legumes responded also with higher SRL and RMF to low nutrients, but did not change their RMF with density. Instead, legumes always invested a large fraction of their biomass into above-ground organs, which may be necessary to support growth and respiration of root-inoculating rhizobia with photosynthetic carbon. The lack of an increase in RMF with density further suggests that, in contrast to the other functional groups, legumes were not nutrient limited at high densities. While the root biomass per pot decreased in absolute terms in response to lower nutrients, it increased with density, which may in the case of legumes have resulted in higher total numbers of nodules and thus total N-fixation per pot. The RMF of grasses increased in response to both nutrient scarcity and density, but their SRL did not change with nutrient level and decreased much more strongly with density than that of other plants. Such a missing response in SRL to nutrients by grasses has also been reported by other studies (Boot & Mensink, 1990). SRL is only one of several root traits which can be adjusted independently, and it is possible that grasses responded in traits we did not measure, like root hair density (Boot & Mensink, 1990) or root tissue density (Bergmann et al., 2020; Kramer-Walter et al., 2016). The strong decrease in SRL with density, however, might have been due to their intensive root system (Craine et al., 2001; Roumet et al., 2016) and their generally high RMF, which could have increased the negative effect of root crowding on lateral growth of roots at high densities.

The life span of species also influenced their biomass allocation and morphology. Perennial species tended to allocate more biomass to leaves and roots and less to stems than annuals and their specific stem length was higher and their SRL lower. While the higher RMF of perennial species may increase their chances of survival over winter, annuals must complete their life cycle and reproduce within one growth period and thus allocate their resources accordingly, resulting in a low RMF (Eziz et al., 2017). Although we harvested most plants before flowering, the larger SMF of annuals may have been due to a switch to reproduction. The increased SRL of annual plants may then be a mechanism to compensate for the low RMF to obtain a root surface similar to that of perennial plants. The different trade-offs between survival and fecundity for annual and perennial plants may also explain their different responses to density in terms of biomass allocation, as to increase their RMF annuals reduced their LMF, while perennials reduced mainly their SMF.

A further characteristic that may influence the response of species to density and nutrient levels is their realised niche with respect to nutrient availability, which we assessed by their N-indicator value

(Hellegers et al., 2020; Schaffers & Sýkora, 2000). In highly productive environments above-ground competition for light is particularly strong (DeMalach et al., 2016; Grime, 1977), which may explain why plants adapted to these habitats have higher growth rates (Poorter & Remkes, 1990), are typically taller, have higher stem mass fraction (SMF; Craine & Dybzinski, 2013) and higher specific root length (SRL; Fort & Freschet, 2020). In contrast, in nutrient-poor habitats investment into leaves may be more beneficial than investment in mechanical tissues like stems (Yan et al., 2016). In line with this, in our experiment species with low N-indicator values had higher leaf mass fractions (LMF) than species with high N-indicator values. In response to density, all species increased their biomass allocation to roots, but species with high N-indicator values reduced their LMF, whereas species with low N-indicator values reduced their stem mass fraction. The observed differences in the morphological responses to increased density and nutrient level suggest that different strategies have been selected in nutrient-poor and highly productive habitats. The SSL of species from highly productive habitats was higher than that of species from low-nutrient habitats and reduced less strongly in response to low density conditions, reflecting their adaptation to environments where competition for light is most important. In contrast, the SRL of species with low N-indicator values was higher than that of species from high productivity habitats and less strongly reduced in response to high nutrients, reflecting their adaptation to environments where competition for nutrients is more important than competition for light. Our result of lower SRL for species of highly productive habitats is in contrast to the positive correlation between SRL and N-indicator value found using a global database of root traits (Fort & Freschet, 2020). However, this database includes many studies of whole communities of species competing with each other in various habitats, while we studied a set of plants growing under the same environmental conditions.

5 | CONCLUSIONS

In our study of 43 herbaceous plants species, we found that the proportion of biomass allocated to roots generally increased with density, suggesting that competition for below-ground resources may be more important than previously thought, even at relatively high nutrient levels. Moreover, this study shows that plants not only change their patterns of biomass allocation but also the morphology of roots and stems in response to nutrient availability and density. These responses depend on a plant's functional type, life span and the realised niche with regard to nutrients. Attempts to explain the biomass allocation or competitive ability of plants should thus take growth conditions, species characteristics and their interactions into account.

AUTHORS' CONTRIBUTIONS

F.R., T.M.S. and D.M. conceived and designed the experiments. F.R. conducted a pilot study and performed the experiments. All authors analysed the data. F.R. wrote the first draft of the manuscript. All authors contributed substantially to revisions and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data from this study are available from Dryad Digital Repository https://doi.org/10.5061/dryad.n02v6wwwf (Rehling et al., 2021).

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