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Radiation interception and radiation use efficiency in mixtures of winter cover crops

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A R T I C L E I N F O

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A B S T R A C T

Context: Cover crops are sown in autumn after harvest of a main crop to capture residual nitrogen and to build biomass that will contribute to soil organic matter after being ploughed under. Mixtures are purportedly more productive than pure stands of single species.

Research problem: Dry matter accumulation in field crops can be separated in the processes of resource capture and resource conversion. Here we apply this conceptual approach to analyse whether and how pure stands of single species and stands of species mixtures differ in radiation capture and radiation use efficiency.

Methods: cover crops were sown as pure stands (12 treatments) or mixtures (11 treatments) at two years in four sites, three in the Netherlands and one in northern Germany. Ground cover was measured throughout a growing period of up to twelve weeks to quantify radiation capture while final biomass was determined at harvest. The ratio of biomass and cumulative radiation capture was used to calculate radiation use efficiency.

Results: Oats and crucifers were the most productive species. Crucifers covered the soil quickly and their radiation capture was consequently high (517 MJ m^{-2}) but their radiation use efficiency was low (0.80 g MJ^{-1}). Oats intercepted less radiation (459 MJ m^{-2}) than crucifers but had a higher radiation use efficiency (1.15 g MJ^{-1}). Legumes had low radiation interception (332 MJ m^{-2}) combined with low radiation use efficiency (0.64 MJ m^{-2}) while the group of forb species belonging to other plant families (e.g. Linaceae, Boraginaceae and Asteraceae) had intermediate radiation capture (371 MJ m^{-2}) and radiation use efficiency (0.84 g MJ^{-1}). The radiation capture and radiation use efficiency of mixtures was similar to that of the dominant species in the mixtures, in all cases a crucifer or oats.

Conclusions and implications: The analysis of radiation capture and radiation use efficiency in this study indicates that mixture performance was governed by species dominance within the mixture, with the species capturing most of the light determining to a large extent the radiation use efficiency of the mixture as a whole. Results show the importance of including one or more productive species in a species mixture used for cover cropping, i.e. oats or a crucifer. If species with slow initial growth or low radiation use efficiency are included in a mixture to provide particular services, such as flower resources, atmospheric nitrogen fixation or antibiosis against pests, these species should be included in a large enough proportion to enable their establishment in the mixture.

1. Introduction

Cover crops are grown to provide a wide range of ecosystem services. They are widely used to prevent leaching of nitrogen after harvest of a main crop, to enhance soil quality, control weeds and suppress pests and diseases (Dabney et al., 2001; Sainju et al., 2002; Kruidhof et al., 2009; Steele et al., 2012; Abdalla et al., 2019; Norberg and Aronsson, 2019). Ultimately, growing cover crops is meant to increase the yield of the subsequent cash crop (Chu et al., 2017), and the practice is considered an important component of ecological intensification, a strategy that aims for high system productivity with less agrochemical inputs (Bommarco et al., 2013). The magnitude of the services provided by a cover crop depends on the amount of biomass produced (Blanco-Canqui et al., 2015; Finney et al., 2016). Thus, to assure effective cover cropping, there is a preference for using species that are highly productive.

In late summer and early autumn, the period when winter cover crops are usually cultivated, temperature and solar radiation are steadily decreasing, with serious implications for crop production. This is clearly

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reflected in the potential crop photosynthetic rate of a closed canopy in the Netherlands, which was estimated to gradually decrease from 290 kg CH_2O ha^{-1} in June to 50 kg CH_2O ha^{-1} in December (De Wit, 1959). Therefore, a successful cover crop needs quick soil cover development to allow it to intercept as much as possible of the relatively high amounts of solar radiation during the first weeks after its establishment. Next to radiation interception (RI), the efficiency of converting intercepted radiation into biomass, known as radiation use efficiency (RUE), is an important trait to realize a high crop productivity (Monteith, 1977).

In 2014, the EU implemented regulation 641/2014 that has led to payments to farmers as an incentive to introduce mixtures of cover crops (European-Commission, 2019). This regulation is based on the idea that cover crops composed of more than one species are more productive and provide greater ecological services than a crop composed of a single species. Comparison between the productivity of pure stands and species-mixtures of cover crops was carried out in previous studies e.g. (Finney et al., 2016; Murrell et al., 2017; Wendling et al., 2017; Blesh, 2018; Elhakeem et al., 2019; Florence et al., 2019). In most studies, mixtures of cover crop species were found to produce greater yields than the weighted average of the yields of their component species in pure stand. Frequently, the mixtures produced the same yield as the best performing pure stand species and, in one study, they were even found to produce a greater amount of biomass than the best performing pure stand (Wendling et al., 2017).

It has frequently been suggested that overyielding by species mixtures is due to niche complementarity between the component species (e.g. Vandermeer, 1992). For instance, mixing species with different rooting patterns and/or shoot architecture allows for greater resource capture than pure stand crops (Zhang et al., 2014). Mixing wheat and maize in strips, for instance, increased the amount of intercepted radiation and yield (Wang et al., 2015). The greater amount of intercepted radiation in the strip system was suggested to result from the greater amounts of radiation intercepted by wheat and maize plants in the border rows. A greater radiation use efficiency can be another explanation for overyielding of species mixtures. In this particular example, it was shown that RUE of the two species was indeed changed. Radiation use efficiency of wheat was significantly increased compared to its pure stand, but this increase was offset by a reduction in RUE of maize (Gou et al., 2017). Mixing species can alter both radiation interception and radiation use efficiency of the component species (van Oort et al., 2020).

Information on radiation interception and radiation use efficiency of individual cover crop species is scarce. It is also unknown how mixing cover crop species affects radiation capture and radiation use efficiency. Therefore, the objective of this study was to investigate how radiation interception (RI) and radiation use efficiency (RUE) vary among cover crop species and how RI and RUE of mixtures of cover crop species relate to that of the pure stands of the species they are composed of. In this study, these aspects were studied for a selection of species that are commonly used as cover crops in Northwestern Europe. We hypothesised that 1) RI and RUE differ among species of cover crops, 2) species with quick ground cover intercept the highest amounts of radiation and 3) mixtures intercept higher amounts of radiation and have higher RUE than that of their component species in pure stands.

2. Material and methods

2.1. Site description and experimental design

This study was conducted at four sites in two consecutive years (2017–2018). One site was in the north of the Netherlands (Scheemda), one in the middle of the Netherlands (Wageningen), and a third in the south of the country (Neer), while a fourth site was situated in northern-Germany (Grundhof). Grundhof is about 370 km further north than Neer, the most southern location. Fields in Grundhof were characterized as sandy-clay soils with 2.1 % and 3.4 % of organic matter in 2017 and 2018, respectively. Soil mineral nitrogen in the top 20 cm was 25 and 22 kg ha^{-1} in 2017 and 2018, respectively. In Neer, soil texture was sandy with 2.5 % of organic matter in both years. Mineral nitrogen in topsoil was 46 and 13 kg ha^{-1} in 2017 and 2018, respectively. In Scheemda, soil texture was sandy soil with 8.0 % organic matter and 71 kg ha^{-1} of mineral nitrogen in 2017, and clay soil with 6.9 % organic matter and 33 kg ha^{-1} mineral nitrogen in 2018. In Wageningen, soil texture was sandy in both years with 3.4 % of organic matter and 20 kg ha^{-1} of mineral nitrogen in 2017, and 3.1 % organic matter and 18 kg ha^{-1} of mineral nitrogen in 2018. The details of all sites, including field operations and weather conditions are summarized in Table 1.

In Northwestern Europe, cover crops are used for a range of purposes, like increasing soil organic matter content, nitrogen retention, nitrogen fixation and management of soil-born pests and diseases. Cover crop species used in this study were selected among the species commonly used and officially registered for this purpose (Table 2). The species belong to six botanical families: Brassicaceae, Poaceae, Fabaceae, Boraginaceae, Asteraceae and Linaceae. The selected species were divided into four groups: crucifers (comprising two cultivars of oilseed-radish, white mustard and salad rocket), oats (comprising two cultivars of black oats), legumes (comprising field beans, common vetch and berseem clover) and a clustering of the species belonging to the last three families, and referred to as 'other forbs' (consisting of phacelia, French marigold and linseed). These groups are characterized by different functional traits and architecture. Crucifers are dicotyledons producing large quantities of biomass and capturing considerable amounts of nutrients. Oats produces large quantities of biomass and captures nutrients well, like crucifers, but belongs to the monocotyledons, providing alternative options for crop rotation. Grasses are represented by just two cultivars of black oats, as this species has been adopted widely by farmers during the last decade. Legumes fix atmospheric nitrogen and thus are beneficial to N-poor soils. Species in the 'other forbs' group have in common that they are usually selected to improve soil health, as they contribute to the regulation of plant-parasitic nematodes, like French marigold to manage *Meloidogyne* spp. (Hooks et al., 2010) and soil-born diseases, like linseed and phacelia to help manage *Fusarium oxysporum* (Patkowska et al., 2015).

Based on these four groups, 2-, 3- and 4-species mixtures were composed. Each mixture contained at least one representative from the more productive groups of crucifers and oats. Presence of these two groups was also used to categorize the mixtures in three classes: 1) mixtures with a cruciferous species (Mix_{cruc}); 2) mixtures with oats (Mix_{oats}) and 3) mixtures with a cruciferous and oats ($Mix_{cruc\text{-}oats}$) (Table 2). All mixtures followed a replacement design, with seeds mixed within the row. To create 2-, 3- and 4-species mixtures, we used 50 %, 33 % and 25 % of the seeding rate of each component species, respectively.

The pure stands and mixtures were grown between August and November in a randomized complete block design with either three or four (Wageningen) blocks. In 2017, each block consisted of 10 pure stands and 10 mixture plots. In 2018, two additional pure stands and one additional mixture were included. Plot area was 15.0 m^2 (3.0 m × 5.0 m) in Wageningen, 12.5 m^2 (2.5 m × 5.0 m) in Grundhof and 7.5 m^2 in both Neer (2.5 m × 3.0 m) and Scheemda (1.5 m × 5.0 m). All species were sown in rows with 12.5 cm between rows using a 3 m wide seed planter (Turbo drill, Rape GmbH, Germany) in Wageningen and a 1.5 m wide planter (belt cone planter, Hege GmbH, Germany) in the other sites. Seeding rate followed the recommendation by the seed supplier (Table 1). In both years, the difference between the site with the earliest (Neer) and the latest (Wageningen) sowing date was approximately three weeks.

2.2. Biomass harvesting

Aboveground biomass was harvested at approximately 12 weeks after sowing. In each plot, plants were harvested using a 1.5 m wide harvesting machine (Haldrup F-55, Haldrup GmbH, Germany). The harvested area differed between site-years and varied from 4.5–15 m^2 if

Table 1
Site description, field operations and prevailing weather conditions in 2017 and 2018 at four sites: Wageningen, Neer, Scheemda (all three in the Netherlands) and Grundhof (Germany).

Site characteristics	2017				2018			
	Neer	Wageningen	Scheemda	Grundhof	Neer	Wageningen	Scheemda	Grundhof
	51°15′34″N	51°59′31″N	53°09′15″N	54°46′42″N	51°15′35″N	51°59′28″N	53°09′04″N	54°42′33″N
	5°57′24″E	5°39′15″E	6°57′38″E	9°39′29″E	5°57′45″E	5°39′09″E	6°57′44″E	9°37′48″E
Soil type	Sandy	Sandy	Sandy	Sandy clay	Sandy	Sandy	Clay	Sandy clay
Soil organic matter (%)	2.5	3.4	8.0	2.1	2.5	3.1	6.9	3.4
Soil mineral N (kg/ha) in July	46	20	71	25	13	18	33	22
Soil pH	5.8	5.2	5.7	6.0	5.9	5.2	7.5	6.2
Previous crop	carrots	Winter wheat	Grass	Winter wheat	carrots	Summer barley	Oat	Winter wheat
Sowing date	2nd August	23rd August	17th August	8th August	31st July	23rd August	22nd August	8th August
Harvesting date	26th October	16th November	30th October	2nd November	23rd October	21st November	14th November	6th November
Nitrogen application	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}
Plot size (cm)	250 × 300	300 × 500	150 × 500	250 × 500	250 × 300	300 × 500	150 × 500	250 × 500
Sampled area (m^2)	6.6	4.5	5.0	1.0	7.5	15.0	5.0	12.5
Sum of Precipitation (mm)	181	133	201	421	107	142	123	144
Global radiation sum (MJ m^{-2}) during the growing period	925	679	679	761	1103	774	723	801
Accumulated growing degree days (base temperature: 4 °C)	1022	688	731	825	1077	779	799	905

harvesting was done with machinery (Table 1). In Grundhof in 2017, harvesting was done manually because the wet conditions prevented machine harvesting. In this case, an area of one m^2 was harvested from each plot. Total plot fresh weight was recorded by the harvesting machine. From each plot, a randomly selected and shredded sub-sample was provided by the harvesting machine. Sub-samples were oven dried at 70 °C for 48 h to determine dry matter content. Subsequently, dry weight of each plot was calculated as the product of plot fresh weight and dry matter content. Additionally, from the mixture plots, an area of 0.5 m^2 was hand-harvested just prior to machine harvest. From this sample, species were separated and oven dried (70 °C for 48 h) to determine the relative dry matter contribution of each species in the mixture. In Grundhof in 2017, dry matter contribution of each species was determined from the total harvested area.

2.3. Ground cover

Photos of ground cover were taken to determine the time course of the fraction of soil covered by plants. In Wageningen, such photos were taken eight times during the season while at the other sites, they were taken five times, at 2, 3, 4, 5 and 8 weeks after sowing. A metal frame (1 m × 0.75 m) was fixed to a pole and lowered to the top of the canopy to standardize the pictures. The camera was mounted on the metal frame at a fixed position, 1 m above canopy, and pointed vertically downwards. To analyse the fraction ground cover, photos were analysed using DIP-image toolbox for image analysis in MATLAB (MathWorks, 2013). For pure stands and mixtures, fraction of ground cover of a specific site-year was averaged over replicates. Based on these averaged values a logistic model was fit to the observed ground cover data:

$$GC_T = \frac{GC_{max}}{1 + e^{-s(T - T_{50})}}$$

where GC_T is the fraction ground cover at time T (days after sowing), GC_{max} is the maximum fraction ground cover, T_{50} (DAS) is the time when 50 % of maximum ground cover was reached, while s (DAS^{-1}) is a rate parameter connected to how steep the function rises as it passes through T_{50}. Based on this function and the estimated parameter values, fraction ground cover for each day was estimated for all pure stands and mixtures. Based on these daily values, the cumulative fraction ground cover was calculated as the integration of GC_T over time.

2.4. Radiation interception (RI) and Radiation use efficiency (RUE)

Daily radiation interception (RI) was estimated as the product of the fraction ground cover GC_T and the global radiation on a specific day. Global radiation data for Wageningen, Neer and Scheemda, were obtained from the Royal Netherlands Meteorological Institute (KNMI; De Bilt, the Netherlands). For Grundhof this information was retrieved from "DWD, Aachen-Orsbach, Germany". For all pure stands and mixtures, in each site-year, RI was accumulated over the growing period to arrive at the cumulative radiation interception (CRI; MJ m^{-2}). Radiation use efficiency (RUE; g MJ^{-1}) of pure stands and mixtures was then estimated as the observed biomass at harvest divided by CRI.

2.5. Data analysis

In each site-year, logistic curves for ground cover were fitted in R version 3.4.3 (R Core Team, 2018), using the function drm of the package drc (Ritz et al., 2015). Model parameters were then extracted for all pure stands and mixtures using function ddply of the package plyr (Wickham, 2011).

Linear mixed effect models were used to analyse differences in the estimated parameters of the logistic function for ground cover (T_{50}, GC_{max} and s) as well as biomass, CRI and RUE. The fixed factor was species or species group. In all models, random factors were set as block

Table 2
Seeding rate and thousand seed weight of winter cover crops grown in pure stands and mixtures.

Species group	Latin name	Common name	Cultivar	Seeding rate (kg ha-1)	Thousand seed weight (g)
Crucifers	*Eruca sativa*	Salad rocket	Garden rocket	10	1.97
	Raphanus sativus	Oilseed radish	Valencia	30	10.5
	Raphanus sativus	Oilseed radish	Angus	30	10.2
	Sinapis alba	White mustard	Master	25	5.06
Oats	*Avena strigosa*	Black oat	Exito	90	19.9
	Avena strigosa	Black oat	PRATEX	90	21.5
Legumes	**Vicia faba*	Field beans	Avalon	130	326
	Vicia sativa L.	Common vetch	Jose	110	53.7
	Trifolum alexandrinum	Berseem clover	Laura	35	2.71
Other forbs	*Phacelia tanacetifolia*	Phacelia	Factotum	16	1.80
	Tagetes patula	French Marigold	Ground control	5	3.00
	**Linum usitatissimum*	Linseed	Juliet	35	6.67
Mix_{cruc}	Oilseed radish 'Valencia' + Phacelia				
	Oilseed radish 'Valencia' + Common vetch				
	Oilseed radish 'Valencia' + Salad rocket + Phacelia				
	Oilseed radish 'Valencia' + Berseem clover + Phacelia				
$Mix_{cruc\text{-}oats}$	Oilseed radish 'Angus' + Black oats 'Exito'				
	*Oilseed radish 'Valencia' + Black oats 'PRATEX' + Field beans + Linseed				
	Oilseed radish 'Valencia' + Black oats 'PRATEX'				
	Oilseed radish 'Valencia' + Black oats 'PRATEX' + Berseem clover + Phacelia				
	White mustard + Black oats 'PRATEX' + Berseem clover + Phacelia				
Mix_{oats}	Black oats 'PRATEX' + Common vetch				
	Black oats 'PRATEX' + French marigold				

*treatments used in 2018 only.

nested within site nested within year. Model fitting was conducted using the function lme of the package nlme (Pinheiro et al., 2019). Significance was determined with analysis of variance (ANOVA) in R. The assumption of normality and homogeneity of variances was checked. Following the analysis, pairwise comparisons were conducted using Tukey HSD test.

3. Results

3.1. Ground cover

The logistic function provided an accurate description of the progress in ground cover of the different pure stands and species mixtures (R^2 ranging from 0.78 to 1.00). In all site-years, all pure stands and mixtures reached full ground cover at some point during the growing period (Fig. 1; Supplementary Fig. 1). The time required to cover 50 % of the ground (T_{50}) and the rate parameter *s* differed amongst species groups ($F_{6,156}$ = 53.7; p < 0.001 and $F_{6,156}$ = 20.8; p < 0.001, respectively). Species with the shortest time to reach T_{50} had the largest value for *s* (the fastest increase in ground cover), and vice versa. Averaged over site-years, crucifers, Mix_{cruc} and $Mix_{cruc\text{-}oats}$ were the quickest to reach T_{50}, with average values of 19, 22 and 21 days after sowing, respectively (Table 3). Oats and Mix_{oats} reached T_{50} at 24 and 26 DAS, respectively. Next in rank was the group of other forbs that reached T_{50} at 34 DAS, followed by the legumes that reached T_{50} at 41 DAS.

Groups with a short time to reach T_{50} were also the first to reach full ground cover (Fig. 1). Among pure stands, crucifers (oilseed radish, mustard and salad rocket) were the quickest to reach full ground cover. They reached full ground cover at around five weeks after sowing. Following crucifers, oats reached full ground cover at around seven WAS, whereas the group of other forbs (phacelia, French marigold and linseed) reached full ground cover at around eight WAS. Legumes

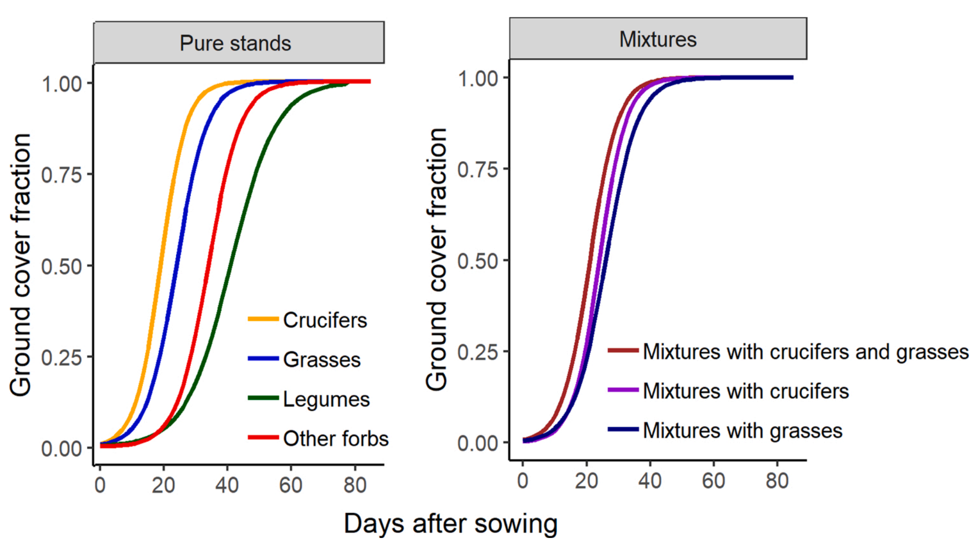

Fig. 1. Time course of fraction ground cover of four species groups of cover crops growing in pure stand (crucifers, grasses 'oats', legumes and other forbs) and three species groups of mixtures with either one dominant component species (crucifer or oats) or with two dominant species (crucifers and oats). Logistic functions are based on individual fits of observed ground cover data in eight site-years. All crops were grown between August and November over eight site-years.

Table 3
Parameter estimates of a logistic function describing the development of ground cover over time (Time to reach 50 % of maximum ground cover (T50 %; DAS), shape parameter s (DAS^{-1}) and maximum ground cover (GC_{max})) in eight site-years. The logistic model was fitted for pure stands and mixtures of cover crop species in each site-year and averaged over site-years. ANOVA was carried out to test the difference between pure stands and mixtures and between species groups. Different letters denote significant differences at P ≤ 0.05; Tukey HSD test.

Latin name	Common name	Cultivar	$T_{50\%}$	s	Species group	T_{50}	s
Raphanus sativus	Oilseed radish	Angus	17 g	0.26 de	Crucifers	19 e	0.25 e
Raphanus sativus	Oilseed radish	Valencia	18 fg	0.25 de			
Sinapis alba	White mustard	Master	19 efg	0.27 e			
Eruca sativa	Salad rocket	Garden rocket	23 defg	0.22 bcde			
Avena strigosa	Black oat	PRATEX	23 defg	0.22 bcde	Oats	24 cd	0.21 bcd
Avena strigosa	Black oat	Exito	25 cdef	0.20 abcd			
Vicia sativa L.	Common vetch	Jose	38 ab	0.16 ab	Legumes	41 a	0.14 a
**Vicia faba*	Field beans	Avalon	39 ab	0.13 a			
Triflolum alexandrinum	Berseem clover	Laura	43 a	0.13 a			
Phacelia tanacetifolia	Phacelia	Phacelia (Pt)	29 bcd	0.24 cde	Other forbs	34 b	0.19 b
**Linum usitatissimum*	Linseed	Juliet	34 abc	0.13 a			
Tagetes patula	French Marigold	Ground control	39 ab	0.17 abc			
Oilseed radish 'Valencia' + Phacelia			21 defg	0.25 de	Mix_{cruc}	22 de	0.24 de
Oilseed radish 'Valencia' + Common vetch			21 defg	0.23 cde			
Oilseed radish 'Valencia' + Salad rocket + Phacelia			22 defg	0.24 de			
Oilseed radish 'Valencia' + Berseem clover + Phacelia			22 defg	0.23 cde			
Oilseed radish 'Angus' + Black oats 'Exito'			19 efg	0.25 de	$Mix_{cruc\text{-}oats}$	21 de	0.23 cde
*Oilseed radish 'Valencia' + Black oats 'PRATEX' + Field beans + Linseed			23 defg	0.24 cde			
Oilseed radish 'Valencia' + Black oats 'PRATEX'			20 defg	0.24 cde			
Oilseed radish 'Valencia' + Black oats 'PRATEX' + Berseem clover + Phacelia			22 defg	0.23 cde			
White mustard + Black oats 'PRATEX' + Berseem clover + Phacelia			23 defg	0.22 bcde			
Black oats 'PRATEX' + Common vetch			26 cdef	0.20 abcde	Mix_{oats}	26 c	0.20 bc
Black oats 'PRATEX' + French marigold			27 cde	0.20 abcde			

*treatments used in 2018 only.

(berseem clover, field beans and common vetch) reached full ground cover only at around nine WAS. Soil cover of mixtures was similar or close to that of the pure stand of the fastest covering component species (oil-seed radish and/or black oats). Mixtures with crucifers (Mix_{cruc}) and those with crucifers and oats ($Mix_{cruc\text{-}oats}$) reached full ground cover at around six WAS while mixtures with oats (Mix_{oats}) reached full ground cover at around seven WAS.

3.2. Cumulative radiation interception (CRI)

Due to the differences in sowing date and global daily radiation pattern during the growing season there was considerable variation in CRI between site-years. For instance, in Neer the sum of global radiation during the growing period was 925 MJ m^{-2} in 2017 and 1103 MJ m^{-2} in 2018. For the other site-years this value ranged between 679 MJ m^{-2} in Wageningen-2017 and Scheemda-2017 and 801 MJ m^{-2} in Grundhof-2018 (Table 1). Averaged over site-years, amongst pure stands, the largest amount of global radiation was intercepted by crucifers (517 MJ m^{-2}; $F_{6,156} = 57.0$; $p < 0.001$; Fig. 2), followed by oats (459 MJ m^{-2}), whereas the lowest amount of global radiation was intercepted by the other forbs (371 MJ m^{-2}) and legumes (332 MJ m^{-2}). Mixtures intercepted more or less the same amount of global radiation as their dominant species. The amount of CRI of $Mix_{cruc\text{-}oats}$ and Mix_{cruc} was 501 and 495 MJ m^{-2}, respectively. Whereas, CRI of Mix_{oats} was 445 MJ m^{-2}.

3.3. Aboveground biomass

The accumulated amount of biomass was strongly affected by site-year. The average biomass yield in Neer was 820 g m^{-2} in 2017 and 733 g m^{-2} in 2018. Yields were much lower in the other site-years, with the average biomass yield ranging from 268 g m^{-2} (Wageningen-2017) to 370 g m^{-2} (Grundhof-2018). Ranking of biomass production of pure stands was site dependent. In Wageningen, Neer and Grundhof, in both 2017 and 2018, the greatest above ground biomass was produced by

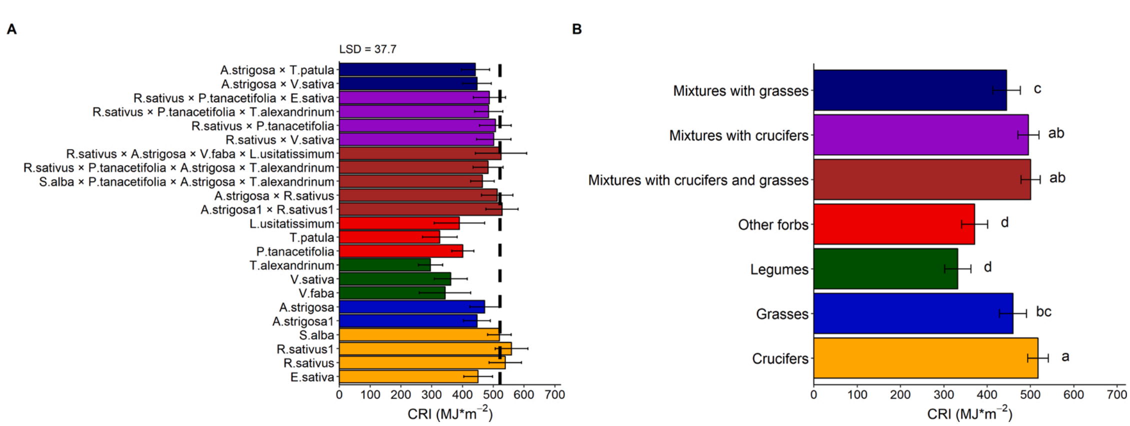

Fig. 2. Cumulative radiation interception (CRI; MJm^{-2}) of 12 pure stands and 11 mixtures of cover crop species. Data presented for pure stands and mixtures (A) and for species groups (B), averaged over site-years. Colour of bars represent species groups. Means were estimated with mixed effect models. Error bars represent ± one standard error. Dotted line represents the highest average minus the least significant difference (LSD). Different letters denote significant differences at P ≤ 0.05; Tukey HSD test.

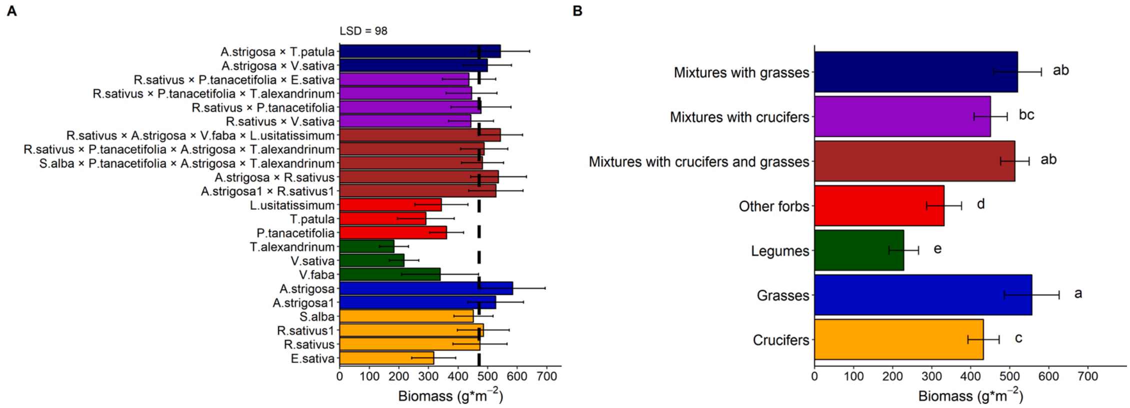

Fig. 3. Biomass (gm^{-2}) of 12 pure stands and 11 mixtures of cover crop species. Data presented for pure stands and mixtures (A) and per species group (B), averaged over site-years. Colour of bars represent species groups. Means were estimated with mixed effect models. Error bars represent ± one standard error. Dotted line represents the highest average minus the least significant difference (LSD). Different letters denote significant differences at P ≤ 0.05; Tukey HSD test.

Table 4
Relative contribution of species and species groups to overall mixture biomass, averaged over site-years. Values are means ± SE.

Species group	Mixture	Crucifers	Oats	Legumes	Other forbs
		%			
Mix_{cruc}	Oilseed radish 'Valencia' + Phacelia	94 ± 5	–	–	6 ± 5
	Oilseed radish 'Valencia' + Common vetch	94 ± 6	–	6 ± 6	–
	Oilseed radish 'Valencia' + Salad rocket + Phacelia	93 ± 7	–	–	7 ± 7
	Oilseed radish 'Valencia' + Berseem clover + Phacelia	90 ± 9	–	2 ± 3	9 ± 7
$Mix_{cruc\text{-}oats}$	Oilseed radish 'Angus' + Black oats 'Exito'	73 ± 18	27 ± 18	–	–
	*Oilseed radish 'Valencia' + Black oats 'PRATEX' + Field beans + Linseed	58 ± 23	32 ± 19	6 ± 6	3 ± 3
	Oilseed radish 'Valencia' + Black oats 'PRATEX'	62 ± 20	38 ± 20	–	–
	Oilseed radish 'Valencia' + Black oats 'PRATEX' + Berseem clover + Phacelia	62 ± 15	31 ± 16	1 ± 1	6 ± 5
	White mustard + Black oats 'PRATEX' + Berseem clover + Phacelia	63 ± 21	31 ± 20	1 ± 1	5 ± 5
Mix_{oats}	Black oats 'PRATEX' + Common vetch	–	92 ± 6	8 ± 6	–
	Black oats 'PRATEX' + French marigold	–	97 ± 4	–	3 ± 4

*treatment used in 2018 only.

Table 5
Cumulative radiation interception (CRI; MJ m^{-2}), radiation use efficiency (RUE; g MJ^{-1}) and biomass (g m^{-2}) of 12 pure stands and 11 mixtures of cover crop species averaged over eight site-years. ANOVA was carried out to test the difference between pure stands and mixtures and between species groups. Different letters denote significant differences at P ≤ 0.05; Tukey HSD test.

Latin name	Common name	Cultivar	CRI	RUE	Biomass	Species group	CRI	RUE	Biomass
Raphanus sativus	Oilseed radish	Angus	559 a	0.84 cd	486 abc	Crucifers	517 a	0.80 c	433 c
Raphanus sativus	Oilseed radish	Valencia	539 ab	0.84 cd	474 abc				
Sinapis alba	White mustard	Master	520 abcd	0.85 bcd	452 abcd				
Eruca sativa	Salad rocket	Garden rocket	451 de	0.66 de	318 def				
Avena strigosa	Black oat	PRATEX	472 bcd	1.18 a	585 a	Oats	459 bc	1.15 a	556 a
Avena strigosa	Black oat	Exito	447 de	1.13 a	527 ab				
Vicia sativa L.	Common vetch	Jose	362 fgh	0.56 e	217 f	Legumes	332 d	0.64 d	228 e
**Vicia faba*	Field beans	Avalon	343 fgh	0.94 abcd	340 cdef				
Triflolum alexandrinum	Berseem clover	Laura	296 h	0.56 e	183 f				
Phacelia tanacetifolia	Phacelia	Phacelia (Pt)	401 ef	0.87 bcd	362 cde	Other forbs	371 d	0.84 c	332 d
**Linum usitatissimum*	Linseed	Juliet	390 efg	0.87 bcd	344 cdef				
Tagetes patula	French Marigold	Ground control	326 gh	0.78 cde	291 ef				
Oilseed radish 'Valencia' + Phacelia			507 abcd	0.89 bcd	477 abc	Mix_{cruc}	495 ab	0.86 c	451 bc
Oilseed radish 'Valencia' + Common vetch			502 abcd	0.85 bcd	443 bcd				
Oilseed radish 'Valencia' + Salad rocket + Phacelia			488 bcd	0.85 cd	437 bcd				
Oilseed radish 'Valencia' + Berseem clover + Phacelia			485 bcd	0.87 bcd	446 abcd				
Oilseed radish 'Angus' + Black oats 'Exito'			528 abc	1.01 abc	537 ab	$Mix_{cruc\text{-}oats}$	501 ab	1.00 b	513 ab
*Oilseed radish 'Valencia' + Black oats 'PRATEX' + Field beans + Linseed			525 abcd	1.05 abc	544 ab				
Oilseed radish 'Valencia' + Black oats 'PRATEX'			513 abcd	0.97 abc	528 ab				
Oilseed radish 'Valencia' + Black oats 'PRATEX' + Berseem clover + Phacelia			484 bcd	0.98 abc	488 abc				
White mustard + Black oats 'PRATEX' + Berseem clover + Phacelia			465 cde	1.01 abc	483 abc				
Black oats 'PRATEX' + Common vetch			447 de	1.08 ab	499 abc	Mix_{oats}	445 c	1.13 a	520 ab
Black oats 'PRATEX' + French marigold			442 de	1.19 a	544 ab				

*treatments used in 2018 only.

black oats. These sites were characterized by a relatively low soil organic matter content (ranging from 2.1%–3.4%). In Scheemda, the site with a relatively high organic matter content (2017: 8.0 % and 2018: 6.9 %), the greatest aboveground biomass was produced by oil-seed radish (2017) and white mustard (2018). Averaged over site-years, amongst pure stands, oats accumulated the greatest amounts of biomass (556 g m^{-2}), followed by crucifers (433 g m^{-2}), the other forbs (332 g m^{-2}) and legumes (228 g m^{-2}; Fig. 3; $F_{6,156} = 41.3$; $p < 0.001$). Among crucifer species, salad rocket produced relatively low amounts of biomass. The average production of 318 g m^{-2}, was considerably lower than that of the other crucifer species (average 471 g m^{-2}).

Biomass of mixtures was largely similar to that of their component species with the greatest biomass in pure stand. Biomass of Mix_{oats} and $Mix_{cruc\text{-}oats}$ was 520 g m^{-2} and 513 g m^{-2}, respectively, whereas, biomass of Mix_{cruc} was 451 g m^{-2}. The highly productive species (crucifers and oats) dominated the mixtures and had the largest share in mixtures biomass (Table 4). In Mix_{oats}, the contribution of black oats to the total biomass ranged from 92 % to 97 %. Similar, in Mix_{cruc}, the contribution of the crucifers was extremely large and ranged from 90 % to 94 %. In three of the total of five mixtures that contained a representative of both oats and crucifers ($Mix_{cruc\text{-}oats}$) there were species from the other two groups included. But also in these mixtures their contribution was marginal and most of the biomass (91–94 %) belonged to two most productive groups. In all $Mix_{cruc\text{-}oats}$, the share of the crucifers (58 %–73 %) was larger than that of the oats (27 %–38 %). In these mixtures, the contribution of legumes and other forbs was thus small and ranged from 1% to 8% for legumes and from 3% to 9% for the other forbs.

3.4. Radiation use efficiency (RUE)

For each species, in each site-year, radiation use efficiency (RUE) was calculated as harvested biomass divided by CRI (Table 5). Averaged over site-years, oats was the most efficient species-group in converting intercepted global radiation into biomass with a RUE of 1.15 g MJ^{-1} ($F_{6,156} = 36.3$; $p < 0.001$). The RUE of oats was followed by that of other forbs (RUE =0.84 g MJ^{-1}) and crucifers (RUE =0.80 g MJ^{-1}). The RUE of legumes (0.64 g MJ^{-1}) was lower than that of all other groups of pure stands. RUE of mixtures with either oats or crucifers was similar to that of the pure stand of these species: Mix_{oats} had an RUE of 1.13 g MJ^{-1}, whereas Mix_{cruc} had an RUE of 0.86 g MJ^{-1}. Mixtures that contained both oats and crucifers had an intermediate RUE of 1.00 g MJ^{-1}.

4. Discussion

4.1. Cover crop species in pure stand

We observed large differences in radiation interception (RI) and radiation use efficiency (RUE) between the four groups of species when grown as pure stands, which confirm our first hypothesis. Crucifers had the greatest RI but a low RUE, whereas oats had the greatest RUE but intermediate RI. Oats produced a significantly greater amount of biomass than the crucifers. RI of the other forbs and the legumes was low. The other forbs combined this with a weak RUE, comparable to that of the crucifers, but for the legumes, the RUE was very low. Similar to our finding, Li et al. (2020) found that RUE of common vetch was approximately half that of oats. Consequently, the biomass production of the other forbs was greater than that of the legumes. These observations confirm that if the purpose of a cover crop is to produce a high amount of biomass, oats or crucifers are to be preferred (Elhakeem et al., 2019).

The differences between the two most productive groups of cover crops are likely to be related to their leaf orientation. Oats, *A. strigosa*, is a typical monocot species with an erect leaf orientation. This results in suboptimal light interception, particularly during the first five weeks after sowing when LAI is still relatively low. On the other hand, crucifers, with a horizontal leaf orientation, have the ability to cover the soil very rapidly. This allows them to intercept a high fraction of incoming radiation during the early stages when LAI is still relatively small. This argument is supported by the fact that crucifers ($T_{50} = 19$, $s = 0.25$) had a quicker development and covered 50 % of the ground faster than oats ($T_{50} = 24$, $s = 0.21$). These results confirm our second hypothesis that species with early development intercept the highest amounts of radiation.

The differences in leaf orientation not only affect RI, but also have implications for RUE. The more vertical leaf orientation results in a better distribution of radiation within the canopy. Hatfield and Dold (2019) reviewed the literature and found that the photosynthetic rate is affected by leaf position and arrangement. Canopies consisting of plants with upright leaf angles allow for penetration of radiation to the lower canopy layers, resulting in a more homogeneous light distribution over canopy layers and therefore higher canopy photosynthesis (Marchiori et al., 2010; Sarlikioti et al., 2011). This better distribution of radiation within the canopy is usually associated with low light extinction coefficient and high biomass (Zhu et al., 2020). For crucifers, the horizontal leaf orientation leads to a high capture of radiation in the top layers of the canopy, resulting in light saturation and comparatively inefficient conversion of light into assimilates. At the same time, this also leads to more shading of the lower layers of the canopy, and a poor contribution of the lower layers to overall canopy photosynthesis. The higher light extinction coefficient and better radiation interception is thus associated with a relatively low RUE (Zhu et al., 2020).

In this study only black oats (*A. strigose*) was used as a representative of the grasses. The reason is that black oats is known for its high biomass production and it is widely used as a cover crop. This quality of black oats was also demonstrated in a pilot experiment, in which we studied the growth characteristics of a wide range of cover crops species (data not shown). Based on the results of the pilot experiment, black oats was the only suitable grass species to be used as winter cover crop that can cover the soil quickly and accumulate large amounts of biomass.

Compared to the other crucifer species, salad rocket was an exception as its ground cover development was slower at the initial growth stage, resulting in lower radiation capture. At the same time, the RUE of salad rocket was relatively low, though not significantly different from that of the other crucifer species. If salad rocket was left out of the comparison between black oats and the other crucifer species (oilseed radish and white mustard) there was no difference in biomass production, despite the lower RUE of the crucifers. In this case, the lower RUE of crucifers was compensated by their greater radiation capture.

Legumes and the 'other forbs', i.e. phacelia, linseed and French marigold had the lowest biomass. Both groups had a much slower soil cover development than crucifers and oats and this resulted in a significantly lower RI. Additionally, legumes and the 'other forbs' had a lower RUE than oats, and lower than both oats and crucifers in the case of legumes. This combination of weak development and low RUE resulted in a lower biomass production than both oats and crucifers. When the purpose of cover cropping is high biomass accumulation, nutrient retention or weed suppression, these species should not be considered as the first choice. These species, however, are useful if the purpose is to fix the atmospheric nitrogen in the soil, as known for legumes (Long, 1989). The other forb species can be used to manage root-lesion nematodes (*Pratylenchus penetrans*) and root-knot nematodes (*Meloidogyne* spp.), as shown in studies on marigold (Pudasaini et al., 2006; Hooks et al., 2010; Adekunle, 2011; Ogundele et al., 2016). Phacelia can stimulate the growth of antagonistic microorganisms, like *Penicillium* spp., that have antagonistic effect against plant pathogens, like *Fusarium oxysporum* (Patkowska et al., 2015).

4.2. Mixtures of cover crops

The species mixtures in this study were categorized according to the presence of representatives of the two most productive species groups. In hindsight, this was a justifiable choice, as the biomass of the mixtures was mostly composed of biomass from these species groups. On average, the crucifer species made up 93 % of Mix_{cruc}, whereas black oats made up 94 % of Mix_{oats}. In mixtures with a representative of either crucifers or oats, the biomass production matched that of the group to which the productive species belonged. Apart from biomass production, this also held for the two components on which biomass production was based: RI and RUE. Mix_{oats} thus had a biomass production that did not differ from that of the group of oats and combined moderate RI with good RUE. Biomass production of Mix_{cruc} was not different from that of the group of crucifers and combined good RI with weak RUE. The performance of these mixtures was thus strongly dependent on the identity of the dominant species. That was also shown in earlier studies on winter cover crops (Wendling et al., 2017; Elhakeem et al., 2019) where highly productive species contributed the most to mixture biomass. Hence, we reject the third hypothesis stating that mixtures intercept higher amounts of radiation and have higher radiation use efficiency than their component species.

Including a high yielding species in a mixture may reduce the risk of obtaining a low yield (Wendling et al., 2019), but these dominant species should not be included in a mixture if the purpose of a cover crop is to provide a specific ecosystem service like pest or disease control and this service is provided by a less competitive species in the mixture. In this case, the targeted species that provides this specific service needs to be protected from being overgrown by its companion species, e.g., by a low seeding rate of the more competitive species in the mixture.

Since the production of the two most productive species groups (oats and crucifers) are based on different traits in terms of RI and RUE, introducing representatives of both species in a mixture could potentially result in the greatest biomass production. This would require that RI would evolve to the level of the crucifers, whereas RUE would reach that of the oats. Our analysis shows that in $Mix_{cruc\text{-}oats}$, RI was indeed taken to the level of the crucifers. However, the RUE stayed behind that of the oats and ended up intermediate between that of oats and crucifers. When reasoning about this in a more mechanistic way, this outcome suggests that 'too much' light was intercepted by the high capturing, but poorly converting crucifers. This high RI by the crucifers was at the cost of RI of the oats, which deprived them of the opportunity to raise the RUE of the mixture to the highest level. This reasoning is supported by the relatively high contribution of crucifers to the total $Mix_{cruc\text{-}oats}$ biomass production (on average, 64 %), while that of black oats was only half of that (32 %). Additionally, the allelopathic potential of crucifiers can negatively affect the surrounding species (Haramoto and Gallandt, 2005) and might also have contributed to the underperformance of oats in the $Mix_{cruc\text{-}oats}$. Despite the lower contribution of oats, the accumulated biomass of $Mix_{cruc\text{-}oats}$ was equal to that of oats or Mix_{oats} (groups with greatest RUE) and greater than that of crucifers (the group with the greatest CRI). These observations suggest that an optimal production of a mixture of oats and crucifers will only be realized if crucifers are dominant during the first stages of crop development, to guarantee a fast soil cover with maximum RI. However, after these initial stages, when the LAI becomes greater than 1–2, productivity could be enhanced if the oats with its more vertical leaf orientation would overtop the crucifers. A dominance of oats during this later stage might result in a more even light distribution and it could prevent light saturation in the top leaves, thus contributing to a greater RUE at crop level. Only such a combination has the potential to combine a high RI with a high RUE and might thus be able to create transgressive overyielding of the mixture.

The results of this study clearly demonstrate that the selection of the most appropriate cover crop species or species mixture is strongly dependent on the purpose of the cover crop. The specific purposes of the group of other forbs (pest and disease suppression) and legumes (N-fixation) seem hard to realize if those species are combined with a high yielding species. The results show that, due to their relatively low RI and RUE, the species are simply outcompeted, making it hard to deliver the ecosystem-services they are intended to provide. Growing them in pure stand seems a better option. If the purpose is to grow a high amount of biomass to contribute as much as possible to the build-up of soil organic matter, the use of mixtures does not comprise such a detriment. Productivity of cover crop species mixtures showed to be comparable to that of the best producing species it contained, but not any better. The inherent trade-off between RI and RUE makes it difficult to realize a species mixture in which both RI and RUE are maximized. Thus, in mixtures that mainly aim to contribute to the build-up of soil organic matter, rather than in quantity, the advantage might be contained in the quality of the produced biomass. This qualitative advantage might evolve from a more diverse composition (Hwang et al., 2015). Risk aversion is also a potential benefit of these mixtures (Wendling et al., 2019), as under extremely adverse conditions certain species might fail. In that situation a mixture acts as insurance against complete failure, as the less affected species will compensate for the poor performance of the sensitive species. Such conditions were not encountered in the eight-site years of the current study, but extreme wet conditions severely hampered the growth of *Raphanus sativus* in a study in 2015 (Elhakeem et al., 2019). Typically, in mixtures with *A. strigosa* and *V. sativa*, complete crop failure was prevented, as these species (partly) compensated the poor performance of oilseed radish under wet and water-logged conditions.

5. Conclusion

We presented here that RI and RUE of winter cover crops are species dependent and differ widely. Oats and crucifers are the two most productive species groups, but their high productivity is based on a different combination of RI and RUE. Oats combine a high RUE with moderate RI, whereas crucifers combine high RI with a lower RUE. Both patterns eventually resulted in much greater biomass production than that of the other forbs and the legumes. Performance of a mixture was highly dependent on the identity of its dominant species. The combination of oats and crucifers did not exceed the productivity of the oats, the species group with the greatest productivity. In the mixture with both oats, a crucifer and other species, the crucifer took a dominant position, due to its superior radiation capture, which in part explains its high early vigour. As a result, the RI of the mixture was as high as that of crucifers, but RUE was only intermediate between that of crucifers and oats. It is argued that to compose a mixture that makes optimum use of the qualities of both oats and crucifers, one should select for a fast developing, but low growing crucifer species that is later overtopped by oats with vertical leaf orientation.

CRediT authorship contribution statement

Ali Elhakeem: Conceptualization, Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Wopke van der Werf:** Conceptualization, Formal analysis, Methodology, Writing - original draft, Writing - review & editing. **Lammert Bastiaans:** Conceptualization, Formal analysis, Methodology, Supervision, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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