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Spatial and genetic crop diversity support ecosystem service delivery: A case of yield and biocontrol in Dutch organic cabbage production

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ABSTRACT

A single focus on yield in agroecosystems comes at the expense of other ecosystem services, for instance, biocontrol of pests. In this study, we investigated the potential of intercropping to improve the delivery of ecosystem services by cropping systems. Intercropping was expected to deliver a higher yield through facilitation and complementarity while simultaneously suppressing pests via pest habitat dilution and habitat provision for natural enemies. Utilizing a network of experiments on crop diversification with different spatial arrangements and different levels of genetic crop diversity across the Netherlands in 2018, we analyzed the effect of seven intercropping designs on crop injury by pests, yield and quality in cabbage. Individual cabbage leaf injury by herbivorous pests was assessed using a newly developed diagrammatic scale. Provisioning services were measured as individual cabbage fresh weight and yield per unit area. We found a significant negative relationship between crop diversity and herbivore feeding injury per cabbage: intercropping designs with more species, accessions and/or cultivars exhibited lower feeding injury. The presence of flower strips significantly reduced overall injury in the adjacent cabbage strip, despite higher injury found in the rows closer to the flower strip. There was no clear relationship between crop diversity and fresh marketable weight per cabbage, however five out of seven intercropping designs were able to maintain total yield per area when compared with the sole crop reference. Our results show that crop diversification can simultaneously support the production ecosystem service by maintaining fresh marketable weight per cabbage plant and productivity per unit area, as well as the regulating ecosystem service of pest control. These results provide a basis for redesigning large-scale arable fields into diversified productive systems, and thereby facilitate the transition towards more sustainable farming systems. A better understanding of crop functionality and management needs in diverse arrangements is relevant for such redesign.

1. Introduction

Agriculture is faced with the challenge of accommodating the twin goals of feeding humanity and operating within planetary boundaries (Rockström et al., 2009; Kahiluoto et al., 2014). This challenge cannot be addressed by an exclusive focus on food production, but requires strategies which also consider ecological intensification, that is, agricultural production supported by biodiversity-mediated ecosystem services (Tittonell et al., 2016; Fischer et al., 2017). Hill and MacRae (1996) proposed a conceptual framework that outlines three (not necessarily sequential) stages necessary for a successful transition towards sustainability in agriculture: efficiency, substitution and redesign. Though reducing and replacing inputs associated with the efficiency and substitution stages, respectively, are important, they argue that true transformative power lies within the redesign stage, which aims for greater resource self-reliance and resilience. Agroecology, "the application of ecological concepts and principles to the design and management of sustainable agroecosystems", offers a redesign approach to address the problems associated with input-intensive agriculture (Gliessman, 1990; Altieri, 1995). It goes beyond yield maximization, emphasizing conservation of natural resources to achieve high-quality food production within a socially and environmentally "just and safe space" (De Schutter, 2014; Wezel et al., 2014; Raworth, 2017). Achieving these aims simultaneously, however, remains a challenge as there are often trade-offs between ecosystem services. For instance, in highly productive agricultural systems improvement in farmland

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biodiversity in terms of species abundance and richness has been found to be associated with roughly proportionate yield loss (Letourneau et al., 2011; Finch and Collier, 2012; Gabriel et al., 2013; Rapidel et al., 2015; Cebrián-Piqueras et al., 2017).

Agroecological practices (e.g. intercropping, crop rotation, cover cropping, minimum tillage, agroforestry) support and enhance the ecosystem services delivered in cropping systems (Wezel et al., 2014). Intercropping – growing more than one crop simultaneously on the same piece of land – is a powerful way to promote agronomic aims by increasing yield per unit input (Coolman and Hoyt, 1993; Brooker et al., 2015; Duchene et al., 2017) and contribute to ecological aims by reducing the need for pesticides through increased biodiversity-mediated pest control (Trenbath, 1993; Pelzer et al., 2012).

In regard to yield, Hector et al. (1999), Yu et al. (2015) and Stomph et al. (2019) demonstrated a positive relationship between crop diversity and ecosystem productivity through niche differentiation, facilitation and complementarity. A meta-analysis of 115 cases by Ponisio et al. (2015) showed that the organic-to-conventional yield gap was reduced from 19 % to 9% when intercropping was applied in organic systems. Productivity in intercropping systems was on average 1.3 times higher than that of sole crops based on a meta-analysis of 14 meta-analyses on intercropping (Beillouin et al., 2019a).

Intercropping has been found to facilitate biological pest control (Khan et al., 1997; Iverson et al., 2014), thus counteracting system vulnerability to pest outbreaks due to the reduction of biodiversity associated with widespread use of monocultures (Altieri and Nicholls, 2004). In natural habitats, bottom-up forces (plant chemistry and morphology) and top-down forces (e.g. natural enemy populations) interact in regulating herbivore abundance (Terborgh et al., 2001; Langellotto and Denno, 2004; Kos et al., 2011). In agricultural settings, presence of non-crop habitats, such as flower strips, provide life-support functions (pollen, nectar, alternative hosts and prey, shelter) for parasitoids and predators that target crop pests (Bianchi et al., 2006). The presence of alternative host plants that are attractive to pests and act as "trap crops" lowers pest pressure on the main crop (Hokkanen, 1991) while plants may also serve as "banker plants", which sustain and subsequently distribute natural enemies to crop plants nearby (Huang et al., 2011). Species diversity in intercropping designs to reduce the habitat for pests and increase resources for natural enemies, is thereby positively correlated with pest suppression (Hatt et al., 2017), though the extent of suppression may be limited by the ability of some pests to use a wide range of plants as alternative hosts (Ratnadass et al., 2012).

Intercropping can be done in different spatial and temporal configurations, and more knowledge on the relation between these configurations and their agronomic and environmental performance is needed to support systems redesign. There are several ways to implement intercropping, such as mixed intercropping (two species grown in the same field without a distinct pattern), row intercropping (two species grown in alternate rows) and strip intercropping (two species grown in alternating strips with at least one strip including more than one row), which can be combined with relay intercropping (various degree of overlap period of intercrops) (Yu et al., 2015). How the spatial, temporal, and genetic diversification dimensions of these designs interact to amplify (or diminish) the ecosystem service gains of intercropping is not well known (Caron et al., 2014). About 80 % of meta-analyses that involve intercropping, cultivar mixtures and/or associated plant species deal with cereals and legumes, with 70 % of these studies reporting yield as the sole outcome (Beillouin et al., 2019b). With four Dutch organic farms as study sites in 2018, we report the effects of crop diversity in different spatial designs on pest attack and productivity of cabbage (*Brassica oleracea* L.) as a model focus crop for which little intercropping research has been conducted. The designs involve growing multiple crops in alternating long and narrow multi-row strips (i.e. strip cropping) or in 50cm × 50cm "pixels" to which crops were allocated randomly (i.e. pixel cropping). In all designs additional levels of within-field crop diversity were created through the inclusion of other crops, cultivars, accessions or flower strips, and compared to a sole crop reference.

Cabbage cultivars are of significant economic importance worldwide due to their nutritional, medicinal and crop rotation benefits and are commonly grown in intensive, single-variety monocultures (Ahuja et al., 2010). The global production area covered more than 3.5 million hectares in 2018 (FAOSTAT, 2020), and pest problems in cabbage and other brassicas in the absence of pesticide application may lead to yield decreases of more than 80 % and subsequent economic losses (Ayalew, 2006). In the Netherlands where this study was conducted, cabbage is an arable broad-acre crop and is the second most important winter crop grown for export, with a national yield of 138 million kg in 2017 (Statistics Netherlands, 2019). In 2016, around 90 % of brassica fields in the Netherlands were treated with pesticides, totalling 33 tons of inputs (Statistics Netherlands, 2019). Biocontrol of pests has the potential to reduce the need for insecticides in various *Brassica* cultivars including cabbage, cauliflower, oilseed rape and turnip rape despite some differences in the major insect pests (Williams, 2010; Balmer et al., 2014). Though still limited, there is a growing body of research reporting positive effects from companion plants and flower strips in cabbage intercropping systems (Gliessman and Altieri, 1982; Géneau et al., 2012; Balmer et al., 2014; Lepse et al., 2017). However, these studies often focus on maximising either provisioning or regulating ecosystem services (Zhang et al., 2007). Given the expectation of multifunctionality in agriculture, optimizing the desired synergies between provisioning and non-provisioning ecosystem services through beneficial interactions among ecosystem properties (Zander et al., 2007; Lavorel and Grigulis, 2012) demands further exploration (Geertsema et al., 2016).

Here, we investigated the potential to simultaneously improve cabbage productivity and reduce pest injury through the implementation of multiple intercropping designs, using 2018 data from, in total, seven intercropping design treatments at four different locations across the Netherlands. We aimed to answer two primary research questions: 1) What is the effect of intercropping design on cabbage leaf injury by herbivorous pests? and 2) How does intercropping design affect cabbage yield and quality? We hypothesized that increasing spatial and genetic diversity in the cabbage cropping system reduces pest injury and therefore contributes to increased productivity per plant and per unit area.

2. Materials and methods

2.1. Experiment sites and designs

The study was conducted on four organic farms, two experimental (the organic experimental and training farm "Droevendaal" (51°59'27.4"N, 5°39'36.0"E) and the Fieldlab Agroecology & Technology at the Broekemahoeve (52°32'29.1"N, 5°34'44.9"E)) and two commercial farms (Mts. Rozendaal (51°45'34"N, 4°25'22"E) and *Exploitatie Reservegronden Flevoland* (ERF B.V.) (52°23'36"N, 5°20'21"E)) in The Netherlands (Fig. 1) from May to November 2018 (Table 1). Soil types were sand at Droevendaal, clay loam at Broekemahoeve, loam at Rozendaal, and heavy clay at ERF. The summer of 2018 was unusually hot and dry with an average temperature of 17.5°C, much warmer than the normal of 15.6°C, and average precipitation of 105 mm, much less than the long-term average of 225 mm (Huiskamp, 2018).

Cabbage (white cabbage (*Brassica oleracea* L. var. *capitata*) or cauliflower (*Brassica oleracea* L. var. *botrytis*)) was grown in strips with neighbouring strips of wheat (*Triticum aestivum* L.) or grass(–clover mixture) (*Lolium multiforum* L., *Trifolium pratense* L. and *Trifolium repens* L.). White cabbage and cauliflower are regarded to be comparable for the purpose of this study as they belong to the same cabbage species, sharing the same growing season, planting density requirements and pests (Hillock, 2016) and are classified as one vegetable product (European Parliament and Council of the European Union, 2013). The crops

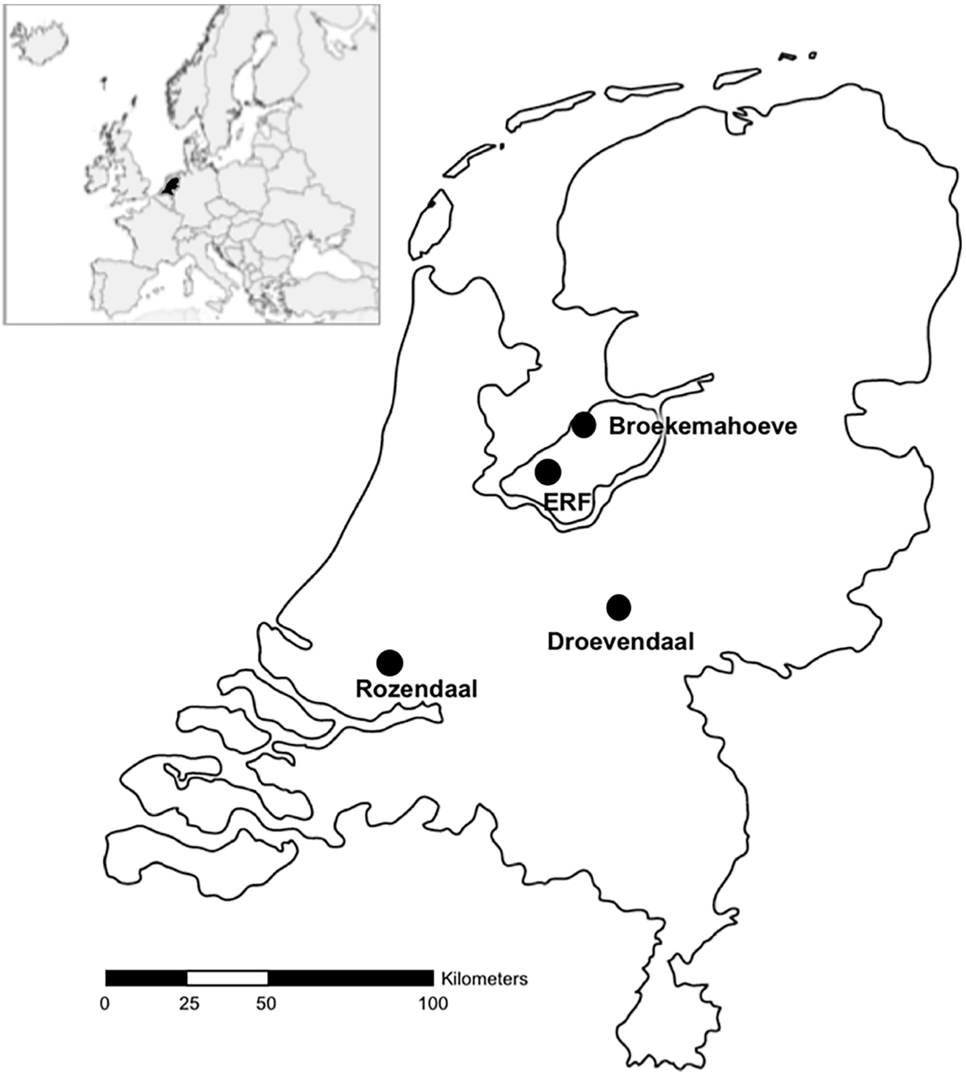


Fig. 1. Overview of the locations in The Netherlands (black area in inset map) of the four organic farms at which the study was implemented.

neighbouring the cabbages are part of a crop rotation commonly applied in the Netherlands and were selected because of their ability to withstand competition from cabbage and their support for natural enemies. Ali et al. (2000) and Khan et al. (2014) found higher productivity and profitability in wheat and *Brassica* intercropping systems when they were grown in alternating strips compared to when mixed seeds of both species were planted together in each row. Tahir et al. (2003) compared interspecific competition in *Brassica*-based intercropping systems and reported that the highest yield advantage was observed when *Brassica* was intercropped in alternating rows with wheat compared to gram, lentil and linseed. Grass–clover was chosen because it has been shown to decrease oviposition and larval densities of various pests when sown under cabbage (Theunissen et al., 1995; Lotz et al., 1997). Grass–clover is also a common 'break' crop in an organic rotation and can be used as a cut and carry green manure. Adding clover as cover crop under white cabbage has been found to result in cabbage yield loss (Lotz et al., 1997).

At one location a flower strip was sown next to the cabbage strip. The presence of flowering plants as sugar sources supports biological control by parasitoids, though its effectiveness depends on attractiveness and nectar accessibility (Wäckers, 2004). The composition of the flower strip was: 16 % *Fagopyrum esculentum* L., 14 % *Triticum aestivum* L., 8% *Trifolium alexandrinum* L., 8% *Agrostemma githago* L., 8% *Gypsophila* sp., 8% *Centaurea cyanus* L., 8% *Medicago sativa* L., 4% *Carthamus tinctorius* L., 3% *Chrysanthemum* sp., 3% *Eleusine coracana* L., 3% *Ammi visnaga* L., 3% *Gilia capitata* L., 3% *Coreopsis grandiflora* 'Early Sunrise', 2% *Cosmos bipinnatus* Cav., 2% *Glebionis segetum* L., 2% *Papaver* sp., 2% *Helianthus annuus* L., 2% *Phacelia tanacetifolia* L., 1% *Linum usitatissimum* L.

Management was based on the conditions at each farm (Table 1). Weekly irrigation of 15−25 mm was applied at all locations during the month of July. Pixel cropping at Droevendaal was mistakenly not fertilized in early season, while the reference at Rozendaal was mistakenly fertilized twice.

Seven intercropping designs of cabbage were tested against a sole crop reference (Fig. 2). The experimental setup, including design of the strips (spatial dimension) and choice of crop species, accessions and cultivars (genetic dimension) was informed by a combination of literature review and expert consultation. The choice of white cabbage or cauliflower was decided by the farmers at each location. In the STRIP design (Fig. 2A) strips of a standard cabbage accession were sown next to strips of a single cultivar of wheat, grass or grass–clover. Strip widths tested included 3, 6, 12 and 24 m, depending on location. In the STRIP_VAR design (Fig. 2B) an accession mixture of cabbage was grown next to a 50:50 mixture of two wheat cultivars, Lennox and Lavette. The cabbage accession Christmas Drumhead was combined with the standard accession Rivera at a 1:8 planting ratio. Christmas Drumhead is more susceptible to cabbage aphid (*Brevicoryne brassicae* L.) (Broekgaarden et al., 2008) and lepidopteran herbivores (Poelman et al., 2009), and thus was expected to reduce pest intensity on the target

Table 1
Locations of the studied intercropping designs and their management. FYM is cattle farmyard manure.

Location	Intercropping design and number of replicates	Planting and harvest dates	Cultivars (main and substitute)	Fertilizer application	Pesticide application
1. Droevendaal (51°59’27.4”N, 5°39’36.0”E)	A. STRIP: 3 m (9 reps) B. STRIP_VAR (9 reps) C. STRIP_ADD (9 reps) D. STRIP_ROTATION (2 reps) E. STRIP_ROTATION VAR (2 reps) F. STRIP_ROTATION ADD (2 reps) G. Pixel cropping (2 reps) H. Sole crop reference	Cabbage: June – Nov, 2018 Wheat: May – Aug, 2018 Potato: May – Sep, 2018 Leek: Aug, 2018 – Jan, 2019 Grass–clover: May, 2018 – May, 2020	Cabbage : Rivera (main), Christmas Drumhead (subs) Wheat: Lennox (main), Lavett Potato: Agria (main), Carolus, Alloutte Leek: Pluston (main), Vitaton Grass–clover: Italian rye grass, English rye grass (70 % Melbolt, 15 % Sputnik, 15 % Humbi 1), red clover (Salino)	Cabbage: 20−25 t/ha FYM + 2 t/ha OPF 11-0-5 Wheat: 25 t/ha liquid manure Potato: 35 t/ha FYM Leek: 20−25 t/ha FYM + 2 t/ha OPF 11-0-5 Grass–clover: none	None
2. Broekemahoeve (52°32’29.1”N, 5°34’44.9”E)	A. STRIP: 3 m (3 reps) B. STRIP_VAR (3 reps) C. STRIP_ADD (3 reps)	Cabbage: June, 2018 – Nov2018 Wheat: April – August, 2018	Cabbage: Rivera (main), Christmas Drumhead Wheat: Lennox (main), Lavett	Cabbage: 8 t/ha chicken manure Wheat: 8 t/ha chicken manure	None
3. Rozendaal (51°45’34”N, 4°25’22”E)	A. STRIP: 3 m (3 reps) H. Sole crop reference	Cabbage: May, 2018 – Oct, 2018 Grass–clover: April, 2017	Cabbage: Storema Grass–clover: di-tetraploid English rye grass, lucerne, tall fescue, white and red clover (cultivar data unavailable)	Cabbage: 30 t/ha liquid manure (5.93 kg/ton N and P) Grass–clover: none	Cabbage: Spinosad, 0.2 L: 500 L /ha July 9, 2018
4. ERF (52°23’36”N, 5°20’21”E)	A. STRIP: 6 m (3 reps), 12 m, 24 m (2 reps each) H. Sole crop reference: 48m	Cauliflower: July, 2018 – October, 2018 Grass–clover: April 2018	Cauliflower: Adamello Grass–clover: English rye grass (30 % Romark, 35 % Polim, 35 % Maurice), red clover (Vesna)	Cauliflower: 35 t/ha liquid manure Grass–clover: none	Cabbage: Xentari (Bt), 1 kg/ha Sep 17, 2018

accession Rivera. The STRIP_ADD design (Fig. 2C) comprised a single standard accession of cabbage grown alongside strips of broad bean (*Vicia faba* L., cv. Pyramid) and wheat cultivar Lennox. With its extrafloral nectar, broad bean constitutes a food source for parasitoids of cabbage pests (Géneau et al., 2012). The designs STRIP_ROTATION, ROTATION VAR and ROTATION ADD (Fig. 2D-F) comprised strips with one or two accessions of cabbage grown alongside four other crops or mixtures. For the STRIP_ROTATION a single accession of cabbage was grown alongside single cultivar of wheat and grass, with single cultivar of potato (*Solanum tuberosum* L., cv. Agria), and leek (*Allium porrum* L., cv. Pluston) completing the cropping plan typical for a six-year rotation. Comprising the same crops as in the STRIP_ROTATION, broad bean and red clover were added to wheat and grass respectively in the STRIP_ROTATION ADD. The STRIP_ROTATION VAR design differed from the STRIP_ROTATION design in that instead of one cultivar, three cultivars of potato and two cultivars of each of the other crops were grown per strip (Table 1). The Pixel cropping design (Fig. 2G) included six crops with a total of eleven cultivars – single cultivars of broad bean and red clover, two accessions of cabbage, two cultivars of wheat and leek, and three cultivars of potato – randomly allocated to 0.5 m × 0.5 m “pixels”. The sole crop reference (Fig. 2H) comprised a single accession of cabbage. Experimental layouts at the four locations are shown in the Supplementary Materials (Figs. A1–A4).

At each location an incomplete block design was implemented, with between two and nine replicates for each treatment, except for the unreplicated large-field monoculture reference which was not present at Broekemahoeve. STRIP was present at all sites; STRIP_VAR and STRIP_ADD were implemented at Droevendaal and Broekemahoeve; and the rest of the designs were implemented at Droevendaal only (Table 1). The ERF site is comparable to the other locations as it compares strips of different widths (i.e. STRIP of 6, 12, 24 m) with a sole crop reference (48 m), both with neighbouring flower strips. The results presented here are from one year but from multiple locations and are the start of a long-term study examining effects of spatial and genetic crop diversification.

2.2. *Data collection*

2.2.1. *Injury assessment tool*

To the best of our knowledge, and according to the website SADBank (http://emdelponte.github.io/sadbank/) developed by Del Ponte et al. (2017), a standardized approach to measuring herbivore feeding injury on cabbage has not yet been developed. To this end, we developed an injury assessment tool adapting the standard area diagram procedure suggested by Nuñez et al. (2017). Our tool uses a diagrammatic scale that encompasses six injury interval scales with unequal steps to visually assess the severity of injury on cabbage leaves. The scale was created by assessing 84 cabbage leaves with various injury levels. Each sampled leaf was photographed, and total and estimated missing leaf areas were determined using image recognition software [ImageJ 1.49v; (Rasband, 1997)]. As estimating uninjured total leaf area becomes increasingly difficult as injury increases, estimation was done by superimposing an uninjured leaf with a similar size and shape. The accuracy of the assessment tool was tested by enlisting ten external evaluators, all inexperienced in assessing cabbage leaf injury, to use the scale and assess eleven preselected cabbage leaves with different levels of injury. Two rounds of assessments were performed: the first round without the aid of the scale, the second round with the aid of the scale. The results of estimated injury of both rounds were compared to the actual feeding injury and linear regressions were plotted to assess estimation accuracy.

2.2.2. *Feeding injury and fresh marketable weight of individual cabbages*

At physiological maturity whole cabbage plants were selected at random from each row in a strip and harvested by cutting the stem at the soil surface. Two random samples were collected per row from each design, except for STRIP (24 m) where one plant was collected per row for reasons of feasibility. Border strips and plants within 10 m-distance from the end of the strip were not sampled to avoid border effects. In the sole crop reference plants were only collected from rows in the middle of the field. In the pixel design five non-random samples neighbouring various plants were collected per replicate. Upon harvesting, each cabbage plant was wrapped in plastic to secure pests present on the cabbage and kept in a cold storage unit at 6.0°C for subsequent fresh marketable weight analysis. Feeding injury by herbivorous pests and fresh marketable weight of the individual cabbage heads were assessed within two weeks of cabbage collection. Using the injury assessment scale, feeding injury was calculated as mean percentage injury of the wrapper leaves and of the outer layer of injured head leaves per cabbage for white cabbage, and of only wrapper leaves for cauliflower. Fresh marketable weight was found by weighing the cabbage heads after trimming off the injured head leaves. Pests found on each cabbage were collected and

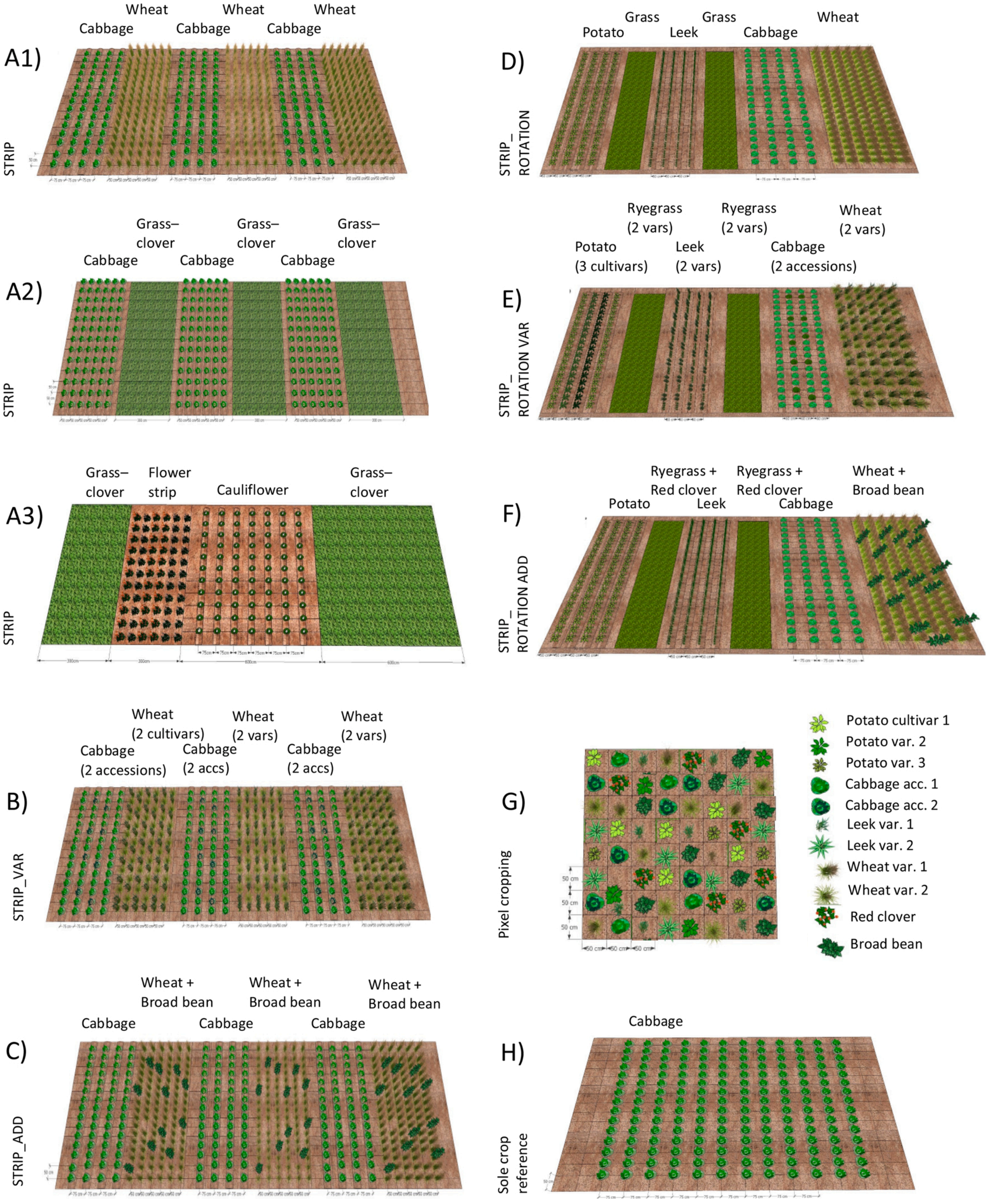


Fig. 2. Experimental design illustrations: A: STRIP at Droevendaal and Broekemahoeve (A1), Rozendaal (A2) and ERF (A3); B: STRIP_VAR at Droevendaal and Broekemahoeve; C: STRIP_ADD at Droevendaal and Broekemahoeve; D: STRIP_ROTATION at Droevendaal; E: STRIP_ROTATION VAR at Droevendaal; F: STRIP_ROTATION ADD at Droevendaal; G: Pixel cropping at Droevendaal; and H: Sole crop reference at Droevendaal, Rozendaal and ERF. Strips within 15 m radius from the middle of a cabbage strip are shown to illustrate the spatial unit of observation for the crop diversity measure.

preserved in 70 % ethanol for identification. Pest identification was focused on caterpillars because they are considered a major pest in cruciferous plants that directly affect both yield quantity and quality (Talekar and Shelton, 1993). For samples from Droevendaal and Broekemahoeve where no pesticide was applied, total number of caterpillars and the number parasitized caterpillars was recorded for the four major caterpillar species: *Pieris rapae* L., *Pieris brassicae* L., *Plutella xylostella* L. and *Mamestra brassicae* L.

2.2.3. Relative yield and quality class

At physiological maturity, cabbage heads were harvested for relative yield analysis. At Droevendaal, all cabbage heads were harvested per row in each design including the sole crop reference, and per replicate in the pixel design; the total number of heads and their fresh weight were recorded on the field. At the other locations, cabbage heads within a random sampling area of 6 m × row width (0.5 m at Rozendaal; 0.75 m at Broekemahoeve and ERF) were harvested per row in each design. Per sampling area, the number of cabbage heads were counted and their total fresh weights were measured using a field scale, from which yield per unit area was calculated. Fresh weight refers to the weight of the cabbage head without trimming off the outer layer of injured head leaves. Relative yield, the ratio of intercrop to sole crop yields, was calculated to evaluate the effect of each design on cabbage productivity. Using the individual cabbage samples, quality assessment was performed (see 2.2.2) to evaluate the effect of the design. Cabbage productivity was expressed as weight per unit area and number of marketable cabbage heads per unit area, for each of the four quality classes that determine the return to the farmer. Productivity was expressed in terms of revenue per unit area to capture the combined effect of cabbage quantity and quality (see Eq. (1)). The fraction of cabbage heads in each quality class was based on the data from the individual cabbage samples (see 2.2.2). Quality assessment was based on fresh marketable weight of individual cabbage heads using size quality classification standards adapted from the United Nations Economic Commission for Europe (UN/ECE) (OJ L 112, 26.4.2006, p. 3–8) and an interview with a farmer.

$$\text{Revenue X } = (a + b) \times N \times €0.35 + (c \times N \times €0.25) \tag{1}$$

where X is experiment design; a, b, c are proportions of cabbage heads in market class I, industry, and market class II, respectively; N is number of marketable cabbage heads per m^2; € 0.35 is the farm-gate price of market class I and industry cabbage, and € 0.25 is the farm-gate price of market class II. These prices apply specifically to the Netherlands in 2018 based on an interview with a farmer on market prices in the journal for Dutch farmers (boerderij.nl).

2.3. Statistical analyses

Linear mixed-effect models (LMMs) were used to evaluate the proposed injury assessment tool and to assess the effects of the intercropping designs on several response variables: feeding injury, fresh weight, fresh marketable weight, relative yield, and caterpillar number. Feeding injury was log-transformed to follow a normal or near-normal distribution. In the presentation of results, model-predicted feeding injury was back-transformed and thereby reported on the scale of the observation. Weighted averages of feeding injury and fresh marketable weight for design comparison between Droevendaal and Broekemahoeve were calculated by multiplying the response variables with the number of heads at the respective locations, and then dividing them by the total number of heads at both locations. To evaluate the relationship between crop diversity of the design and feeding injury and fresh marketable weight, another LMM was fitted. Crop diversity refers to the number of species, accessions and cultivars within 15 m radius from the middle of a cabbage strip (e.g. in the STRIP_VAR design two cabbage accessions plus two wheat cultivars equals a total crop diversity of four). Grass and clover mixture, despite its composition of four to five cultivars or species depending on the study site, and flower strip, despite its composition of 19 flowering plant species (Table 1), were assigned crop diversity of two and one, respectively, for practical reasons of accounting for its combined effects instead of the effects of individual cultivar or species. Another LMM was fitted to evaluate the effects of crop diversity and the composition of direct neighbour (i.e. plant species, accession and cultivar within 0.75 m of the sampled plant) on feeding injury and fresh marketable weight at individual plant level. As composition of neighbouring plants can differ despite having the same crop diversity value, the effects of both were tested separately. Generalized additive models (GAMs) were used to assess injury and marketable weight across the different widths of the STRIP designs at ERF.

As experiments were conducted at four different locations, the variable ‘location’ was included as random effect in the LMMs to account for the variation of the responses among and within locations. Nested in ‘location’ were ‘field’, ‘block’, ‘strip’, and ‘row’ (Supplementary Material D). Harvest occurred at peak maturity at each location, rendering timing confounded with location. Therefore, sampling date or days after planting was not included as a random effect. In each model, either design or crop diversity was included as a fixed effect. To evaluate the effects of direct neighbours on feeding injury and fresh marketable weight, the neighbouring plant diversity or composition was included as a fixed effect.

LMMs with a Restricted Maximum Likelihood (REML) algorithm for variance parameter estimation are appropriate for analysis of multi-site incomplete block designs of field experiments (Gilmour et al., 1995). Normality of data was assessed by a Shapiro-Wilk test on the residuals and statistical analyses were performed using one-way analysis of variance (ANOVA) and Tukey’s honestly significant difference (HSD) as a post-hoc test. All analyses were conducted using the statistical program R, version 3.5.1 (R Core Team, 2018) and the ‘nlme’ package (Pinheiro et al., 2018).

3. Results

3.1. Injury assessment tool for cabbage

Use of the diagrammatic scale (Fig. 3) was found to result in more accurate injury severity estimates compared to unsupported visual assessment ($F_{1,218} = 10.67$, $p < 0.001$, Fig. 4). Use of the scale by external evaluators increased the accuracy of prediction as described by the increase in R^2 (from 0.73 to 0.81) and by the decrease in the root-mean-squared error from 11 % to 2%. When no scale was used, on average, the predictions overestimated actual values by 96 % and underestimated them by 27 %, whereas with the scale, overestimation was reduced to 26 % and underestimation to 23 %.

3.2. Effects of intercropping designs at the four locations

3.2.1. Feeding injury

Feeding injury of the 476 individual cabbages sampled across the four locations varied from 0 to 24 % per plant. Strip designs tended to perform better than sole crops at Droevendaal and Rozendaal, but not at ERF. At Droevendaal, the sole crop showed greater injury than the intercropping designs (Table 2). Comparing the three strip designs at Droevendaal and Broekemahoeve, weighted average feeding injury in STRIP_VAR at the two locations (3% ± 1) was intermediate between STRIP_ADD (3% ± 1) and STRIP (4% ± 1). At ERF, the presence of flower strips next to cabbage strips reduced feeding injury significantly by more than 50 % ($F_{1,14} = 22.47$, $p < 0.001$). However, the narrower the strip width, the higher the feeding injury. Within the strip, significantly higher injury was found in the rows closer to the flower strip ($F_{1,87} = 7.01$, $p < 0.01$), indicating that cabbage rows closer to flower strips suffered greater pest infestations. Despite the high injury at the edges of the strips, the strips adjacent to the flower strips performed better overall than the strips without neighbouring flowers.

A total of 586 lepidopteran instars, including larvae and pupae, were collected at the end of the growing season at Droevendaal and Broekemahoeve where no pesticide was applied. The number of caterpillars per plant varied between zero and five at both locations. In all designs, the number of parasitized caterpillars was twice the number of non-parasitized ones at the end of the season. However, we did not find significant differences in caterpillar abundance or parasitism rate between designs. Additionally, there was no correlation between caterpillar abundance or parasitism and feeding injury.

3.2.2. Fresh marketable weight

Fresh marketable weight across the four locations varied from 0.09 to 2.90 kg (Table 3). Strips tended to have plants of greater weight than the sole crop at Droevendaal and Rozendaal, but not at ERF. Significantly lower weight was observed in the Pixel cropping design. Comparing the strip cropping designs at Droevendaal and Broekemahoeve, the weighted average of fresh marketable weight in the STRIP_VAR design at the two locations (1.29 ± 0.17 kg) was intermediate between STRIP_ADD (1.13 ± 0.17 kg) and STRIP (1.32 ± 0.16 kg). Similar to injury, the narrower the strip width, the lower the marketable weight. Significantly lower marketable weight was found in the rows

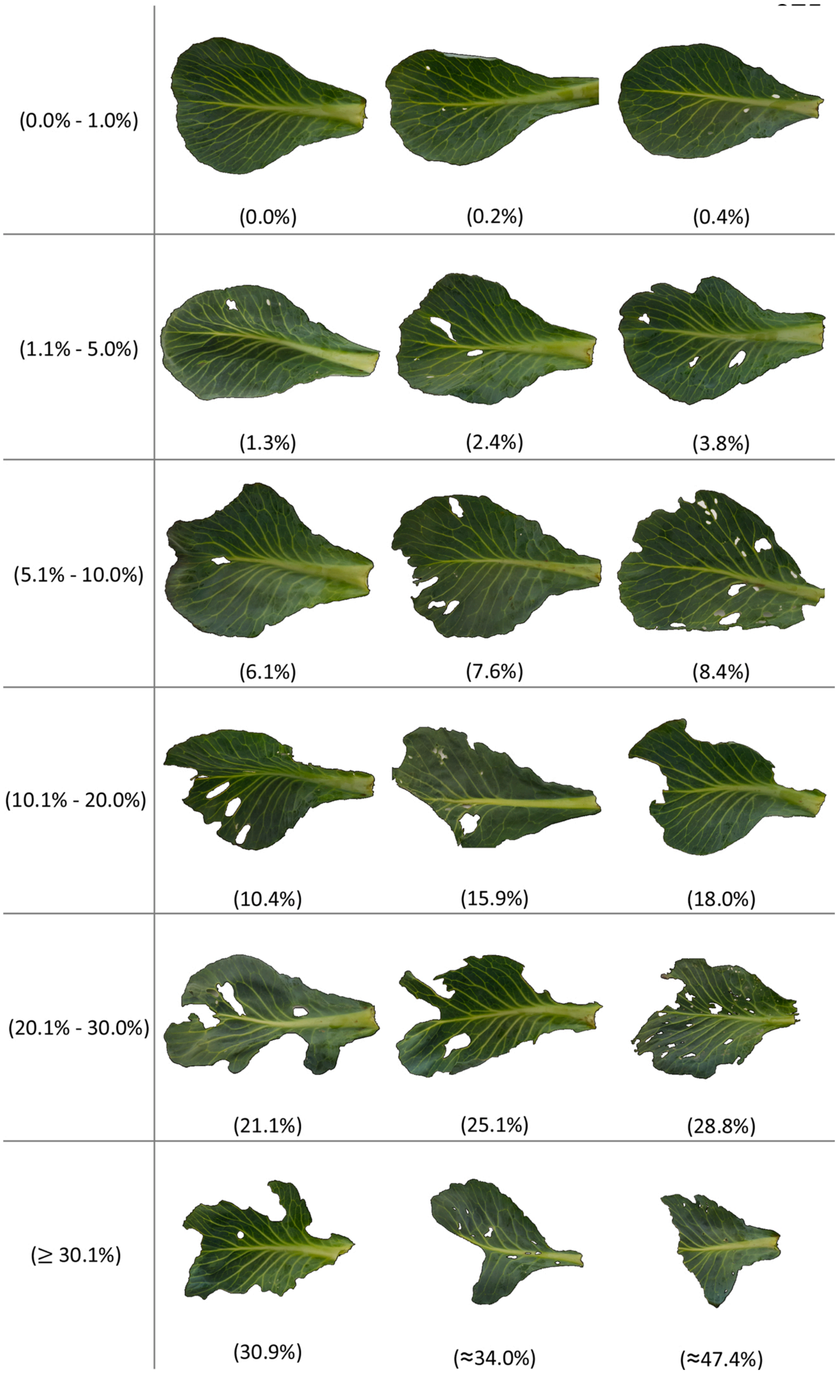


Fig. 3. Diagrammatic scale of cabbage wrapper leaves used to quantify the herbivore leaf-chewing injury. The numbers to the left of each row indicate levels of injury, and the numbers below each image indicate the real percentage of missing leaf area.

closer to the flower strip ($F_{1,104} = 6.20$, $p = 0.01$).

3.3. *Trends across locations*

3.3.1. *Effect of direct neighbour*

Neither crop diversity around the sampled plants nor the composition of the direct neighbours (i.e. plant species, accession and cultivar within 0.75 m of the sampled plant) were found to have a significant effect on injury or marketable weight of individual plants (Supplementary Materials, Fig. B). Design had a significant effect, suggesting that it exerted greater influence than direct neighbours did.

3.3.2. *Effect of design*

3.3.2.1. Effects of crop diversity on feeding injury and fresh marketable weight. We found a significant negative relationship between crop diversity of a design (i.e. the number of species, accessions and cultivars within 15 m radius from the middle of a cabbage strip) and feeding injury. For every additional species, accession or cultivar, crop injury was reduced by 7% ($F_{1,288} = 12.45$, $p < 0.001$, Fig. 5A). At the same time crop diversity appeared to negatively affect fresh marketable weight ($F_{1,288} = 9.82$, $p < 0.05$, Fig. 5B). Disregarding the Pixel cropping design (in which the first fertilizer application was erroneously missed) confirmed the negative relation between diversity and injury ($F_{1,279} = 6.84$, $p < 0.05$) but no longer revealed a relation between crop diversity

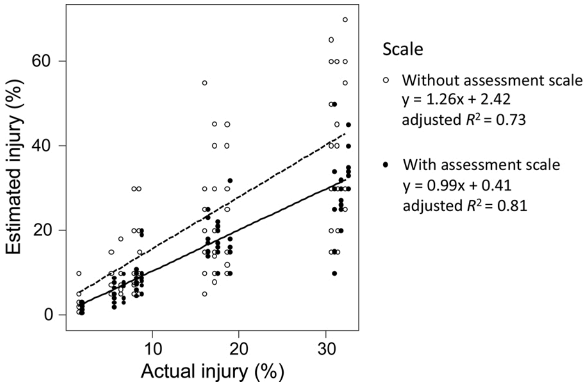


Fig. 4. Relation between leaf injury visually estimated by 10 external evaluators without (black dotted line) and with (black solid line) the diagrammatic scale, and actual injury.

Table 2
Effects of intercropping designs on feeding injury of individual cabbage leaves at the four experimental sites in 2018. Means (± standard error) followed by the same letter in the same column are not significantly different, Tukey HSD, 0.95 confidence level. F-tests on the effect of designs were performed with Satterthwaite's method. *p*-Values were derived from Type II Wald chi-square tests.

Design	Feeding injury (%)			
	Droevendaal	Broekemahoeve	Rozendaal	ERF
Sole crop reference with flower strip	–	–	–	2 ± 1 ^{a}
Sole crop reference	6 ± 1 ^{ab}	–	13 ± 2 ^{a}	–
STRIP (3 m)	3 ± 1 ^{b}	6 ± 1 ^{a}	11 ± 2 ^{a}	–
STRIP (6 m) with flower strip	–	–	–	3 ± 1 ^{a}
STRIP (12 m) with flower strip	–	–	–	2 ± 1 ^{a}
STRIP (24 m) with flower strip	–	–	–	1 ± 1 ^{a}
STRIP (24 m)	–	–	–	7 ± 1 ^{b}
STRIP_VAR (3 m)	3 ± 1 ^{ab}	3 ± 1 ^{a}	–	–
STRIP_ADD (3 m)	2 ± 1 ^{ab}	4 ± 1 ^{a}	–	–
STRIP_ROTATION (3 m)	2 ± 1 ^{ab}	–	–	–
STRIP_ROTATION VAR (3 m)	1 ± 1 ^{ab}	–	–	–
STRIP_ROTATION ADD (3 m)	2 ± 1 ^{ab}	–	–	–
Pixel cropping (0.5 × 0.5 m)	1 ± 1 ^{a}	–	–	–
	$F_{7,132} = 5.01$	$F_{2,21} = 1.64$	$F_{1,15} = 1.30$	$F_{4,101} = 9.46$
	$p = 1.08e^{-5}$	$p = 0.19$	$p = 0.25$	$p = 1.20e^{-7}$

and fresh marketable weight ($F_{1,279} = 0.13$, $p = 0.27$, Fig. 5).

3.3.2.2. Relative yield and quality class. At Droevendaal, Rozendaal and ERF where sole-crop cabbage was implemented, productivity of strip cropped cabbage was expressed as fresh weight and number of marketable heads and revenue per unit area. All of the strip cropping designs, except STRIP at Rozendaal ($p \leq 0.05$, Supplementary Materials C), were able to maintain productivity relative to the sole crop (Fig. 6A–B). Pixel cropping was not included due to its unusually poor yield, which was at least in part associated with lack of fertilization (see 3.3.2.1).

4. Discussion

Our study shows that a higher crop diversity through the addition of plant species, accessions, cultivars and a flower strip, reduced the magnitude of caterpillar herbivory in individual cabbage plants. Moreover, our data show that five out of seven intercropping designs were able to simultaneously support the production ecosystem service (by maintaining fresh marketable weight per cabbage plant and productivity per unit area) and the regulating ecosystem service of pest control. However, we did not find evidence that reduced crop injury translated into an increase in cabbage head weight.

Table 3
Effects of intercropping designs on fresh marketable weight of individual cabbage at the four experimental sites in 2018. Means (± standard error) followed by the same letter in the same column are not significantly different, Tukey HSD, 0.95 confidence level. F-tests on the effect of designs was performed with Satterthwaite's method. *p*-Values were derived from Type II Wald chi-square tests.

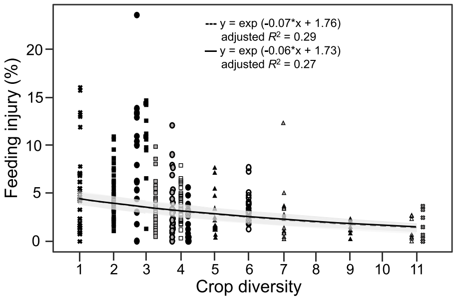
Design	Fresh marketable weight (kg)			
	Droevendaal	Broekemahoeve	Rozendaal	ERF
Sole crop reference with flower strip	–	–	–	0.82 ± 0.12 ^{a}
Sole crop reference	0.97 ± 0.35 ^{ab}	–	0.79 ± 0.13 ^{a}	–
STRIP (3 m)	1.42 ± 0.18 ^{b}	0.94 ± 0.10 ^{a}	0.93 ± 0.11 ^{a}	–
STRIP (6 m) with flower strip	–	–	–	0.65 ± 0.10 ^{a}
STRIP (12 m) with flower strip	–	–	–	0.68 ± 0.10 ^{a}
STRIP (24 m) with flower strip	–	–	–	0.81 ± 0.12 ^{a}
STRIP (24 m)	–	–	–	0.81 ± 0.12 ^{a}
STRIP_VAR (3 m)	1.37 ± 0.19 ^{ab}	1.02 ± 0.10 ^{a}	–	–
STRIP_ADD (3 m)	1.15 ± 0.19 ^{ab}	1.06 ± 0.10 ^{a}	–	–
STRIP_ROTATION (3 m)	1.03 ± 0.21 ^{ab}	–	–	–
STRIP_ROTATION VAR (3 m)	0.91 ± 0.34 ^{ab}	–	–	–
STRIP_ROTATION ADD (3 m)	1.10 ± 0.23 ^{ab}	–	–	–
Pixel cropping (0.5 × 0.5 m)	0.54 ± 0.24 ^{a}	–	–	–
	$F_{7,132} = 2.45$	$F_{2,21} = 0.61$	$F_{1,15} = 1.63$	$F_{4,101} = 2.27$
	$p = 0.02$	$p = 0.54$	$p = 0.20$	$p = 0.06$

4.1. *Injury by pest infestation*

Our analysis at Droevendaal, Broekemahoeve and Rozendaal indicates that intercropping of cabbage significantly decreased individual plant injury (Fig. 5A), a finding in line with previous studies (Theunissen et al., 1995; Bukovinszky et al., 2004). At ERF, this result was not observed, possibly because the effect of the design (STRIP with various strip widths) was hidden by the effect of the flower strip. Possible mechanisms leading to less injury with greater within-field crop diversity include reduced ability of pests to locate host-plants through host dilution (Finch and Collier, 2000, 2012) and "trap crops" (Cook et al., 2007), and increased abundance and diversity of natural enemies (Bianchi et al., 2006; Letourneau et al., 2011). The importance of the effects may depend on location.

Christmas Drumhead acting as a "sacrificial" plant (Altieri, 1994) due to its attractiveness to both specialist and generalist lepidopteran herbivores and aphids (Poelman et al., 2009), may have caused the observed lower feeding injury in the target accession Rivera in the STRIP_VAR design. This effect may be enhanced by optimizing the planting ratio of the two accessions and the distances between Christmas Drumhead and the target accession (Aartsma et al., 2019) to minimize the likelihood of pest spill-over. In the STRIP_ROTATION design, a greater number of plant diversity may have increased the chance of pests

(A) Feeding injury



(B) Fresh marketable weight

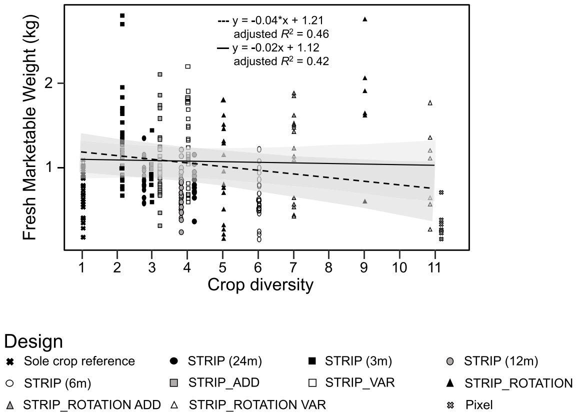


Fig. 5. Relationship between crop diversity and (A) feeding injury and (B) fresh marketable weight. The feeding injury was log back-transformed. Crop diversity was measured by adding the number of species, accessions or cultivars in the design. For example, it is 1 in Sole crop reference, 2 in STRIP, and 4 in STRIP_VAR. In each graph, regression lines including (dotted line) or excluding (solid line) the Pixel cropping design data are shown; the respective equations are shown in the graphs. Asterisks in regression equations indicate a significant fixed effect of crop diversity. Symbols indicate intercropping designs.

landing on non-host plants, thereby further reducing feeding injury on the main cabbage accession, as suggested by Finch and Collier (2000).

The sacrificial accession Christmas Drumhead has been reported to be highly attractive to parasitoid wasps as they respond to the herbivore-induced plant volatiles released upon herbivore attack (Poelman et al., 2009). Following the "banker plant" method applied mostly for biological control in greenhouses (Huang et al., 2011), in an open field context a similar spill-over effect of parasitoid wasps in the STRIP_VAR design may have played a role in lowering the overall feeding injury in the target cabbage accession. The inclusion of floral elements across the growing season within a crop field has been reported to sustain the natural pest control function (Bianchi et al., 2008; Balzan and Moonen, 2014), thereby lowering feeding injury (Albrecht et al., 2020). However, mere presence of flowering plants is not sufficient to guarantee adequate biocontrol; the potential effectiveness of within-field flower strips in suppressing pests is influenced by several factors. These factors include the composition of flower species and their flowering times, parasitoid mobility and spatial within-field arrangement. Species vary considerably in their attractiveness (or even repellence) to parasitoids, thereby significantly influencing larval and egg parasitism of herbivores (Wäckers, 2004; Wäckers and Van Rijn, 2012; Balmer et al., 2014). Matching the flowering time of non-crop plants with the cabbage growing season is one way to enhance the effectiveness of insectary flower strips on biological control (Johanowicz and Mitchell, 2000).

Despite some evidence that the number of parasitoids and parasitism rates are highest closest to flower strips (Lavandero et al., 2005; Balzan and Moonen, 2014), there is also a risk of non-crop habitat acting as reservoirs for pests that invade crops (Van Emden, 1965; Frank, 1998; Géneau et al., 2012). This edge effect could explain the high feeding injury observed in this study in the rows closer to flower strips. Given the single flight capacity of female parasitoids that can easily exceed 100 m especially in the presence of a sugar source (Wanner et al., 2006), future experiments should explore the potential to increase the effectiveness of the design by placing the flower strip a few meters away from the crop strip to avoid pest contamination.

In this study, feeding injury was used as a measure of overall pest infestation. Caterpillar sampling, which was only conducted once at the end of the growing period, was not sufficient to capture caterpillar population dynamics or to show any correlation with the observed leaf injury. Multiple caterpillar and parasitism sampling rounds, starting from the early head formation stage during which caterpillar infestation may start to affect yield (Andaloro et al., 1983), would provide complementary insights to explain the observed feeding injury.

4.2. *Yield quantity and quality*

Our results indicate a general trend that strip cropping delivered higher fresh marketable weight of individual cabbages at Droevendaal, Broekemahoeve and Rozendaal. The improvement in fresh marketable weight can be explained by spatial-temporal niche complementarity and facilitation between cabbage and companion crops that resulted in enhanced resource-use efficiency (Hector et al., 1999; Li et al., 2014; Yu et al., 2015; Duchene et al., 2017). This trend was not observed at ERF, possibly due to the overriding effect of the flower strip and pesticide application late in the season compared to the effect of the other design attributes (STRIP with various strip widths).

The number of crops included in the system was not the major factor affecting fresh marketable weight, as no clear trend was observed (Fig. 5B). Design may be considered as a stronger factor influencing interspecific competition. The unusually low individual fresh marketable weight found in the Pixel cropping design at Droevendaal is partially attributable to the fertilizer management error (missed first manure application). In addition, the fully randomized allocation of six crop species in the Pixel cropping design may have intensified interspecific competition for water and nutrients. Elucidating the potential of the Pixel cropping design will require investigation across multiple years. Lower fresh marketable weight was also observed in STRIP with narrower strip widths at ERF. Cauliflower in rows close to flower strips seemed to suffer from water stress throughout the very hot and dry growing season, resulting in slower growth and lower fresh marketable weight. Though a certain degree of shading by taller flowering plants might help crops cope with high soil water tension by reducing transpiration (Wolff and Coltman, 1990), this effect appeared insufficient to contend with soil moisture competition. Increasing the distance between flower strips and crop strips in the STRIP design, and optimizing crop composition and spatial allocation in Pixel cropping, could reduce interspecific competition and thus the extent of related abiotic stress.

Five out of seven intercropping designs simultaneously promoted apparent biological pest control and maintained fresh marketable weight per cabbage plant and productivity per unit area. These designs were STRIP_ADD, STRIP_VAR, STRIP_ROTATION, STRIP_ROTATION ADD, and STRIP_ROTATION VAR. No significant difference in terms of head count and fresh weight was observed, except at Rozendaal, where the significantly lower number of heads formed in the strips led to lower total fresh weight. This might be partially attributed to fertilizer application which was erroneously doubled in the reference field. At Droevendaal, on the other hand, a lower number of cabbage heads might have allowed extra space for growth and contributed to greater individual cabbage weight and higher fresh weight per unit area than the reference (Fig. 6A and B). Since fresh cabbage is usually sold per individual head instead of per kilogram, the quality class it belongs to (i.e. market class I, industrial, market class II and unmarketable) is regarded as more important than its absolute weight. Productivity in terms of revenue (Fig. 6C), which captures the interaction between number of

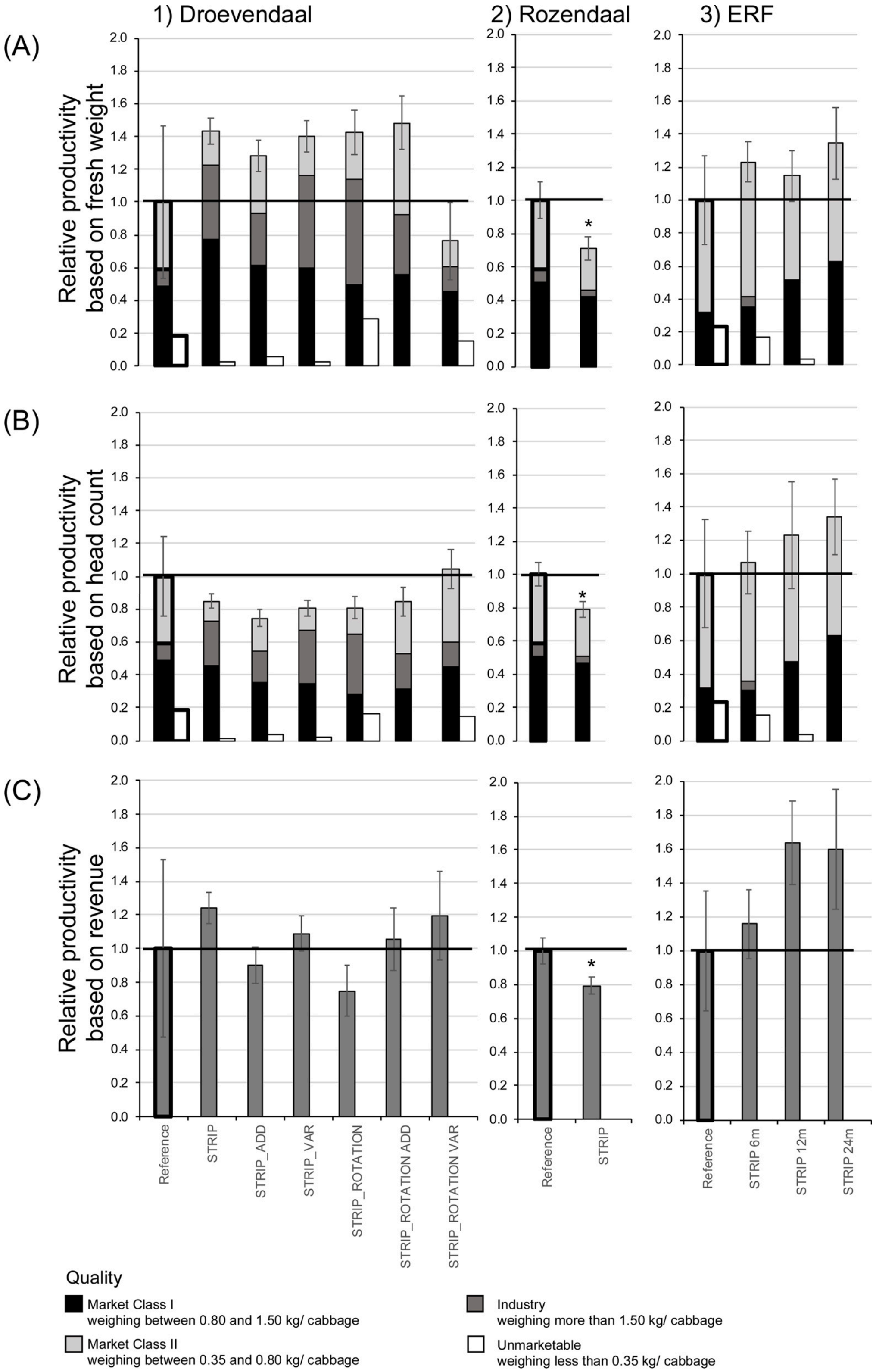


Fig. 6. Productivity of strip cropped cabbage relative to that of the sole crop reference in terms of (A) weight per unit area, (B) number of marketable cabbage heads per unit area and (C) revenue per unit area under different intercropping schemes at 1) Droevendaal, 2) Rozendaal and 3) ERF. Bars with thick circumference indicate the reference design. If relative yield value exceeds 1 (indicated by the horizontal solid line), response variables of the intercropping designs exceeded the reference. Bar shading indicates product quality classes and their contributions to total cabbage productivity (Supplementary Material C). Asterisks indicate significant differences compared to the reference ($p < 0.05$). Error bars indicate standard errors of marketable cabbage. The unmarketable class (white bar) is included to illustrate its importance relative to the marketable classes.

heads (yield quantity) and quality class (yield quality), is most relevant for farmers if they were to consider the adoption of strip cropping designs. Yield quality at Droevendaal and ERF was able to compensate for lower quantity resulting in revenues equal to those in the reference fields. This highlights the potential of the strip cropping designs to increase quality in addition to quantity as previously found (van Oort et al., 2020).

4.3. Limitations and suggestions for future study

We did not find evidence that reduced crop injury translated into an increase in individual head weight, as postulated by Iverson et al. (2014). Possible explanations for the limited impact of injury on yield are that pest pressure was not high enough to cause significant reduction in damage and subsequent yield, that prevailing parasitism rates by natural enemies were already sufficient so there was little room for improvement (Balmer et al., 2014), and that the application of pesticides at ERF and Rozendaal confounded the effect.

Under field conditions, plants are exposed to various factors which influence the functioning of ecosystem services. The ecological stress gradient hypothesis (Brooker et al., 2008) suggests that environmental context may alter the net balance of interactions occurring within a given intercropping system (Brooker et al., 2015). For instance, attainable yield is determined by both yield-protecting and yield-increasing factors (Van Ittersum and Rabbinge, 1997) and the interactions among them. In this study, these interactions within the environmental context were considered as random effects capturing variation between and within individual fields. These random effects may explain the absence of significant difference in feeding injury between the sole crop reference and strip designs at Droevendaal (Table 2). In future experiments, the incorporation of soil nutrient status (e.g. soil organic material and nitrogen content) and parasitoid population dynamics as covariates in model fitting may better explain the observed results.

At Droevendaal and Broekemahoeve, parasitized caterpillar counts at the end of the growing period were twice those of non-parasitized, which was high but still within the range (minimum and maximum values of 4.0 % and 94.1 %) reported by Bianchi et al. (2008). This high parasitism rate may indicate that the natural parasitoid population was already sufficient to suppress herbivore infestation without pesticide application. In contrast, we suspect that the effect of the (organic) pesticide affecting both pest and natural enemies at Rozendaal and ERF might have masked the effect of biological control (Veres et al., 2013). Interference by farm management, for instance through pesticide application, hinders the system from developing natural control mechanisms that build ecological resilience and adaptability (Van Apeldoorn et al., 2011). Future research enabling systems to develop natural control mechanisms would allow unravelling of the complex multi-trophic interactions and the potential of the designs in optimizing natural biological control.

This research was conducted in the first year of a long-term study at several locations, testing if the effect of the intercropping designs is consistent across locations. With temporal effects becoming apparent in the following years, future research can examine the combined effects of spatial, genetic and temporal dimensions of crop diversification on production and regulating ecosystem services. Improving the designs tested here would benefit from more knowledge on complementarities and trade-offs among characteristics of neighbouring crops. A better understanding of results across four different soil types at each location would contribute a basis to encourage a wider network of farmers to adopt diversification practices. Finally, a cost-benefit analysis to calculate profits is necessary to assess feasibility for the actual adoption of these intercropping designs.

5. Conclusions

Farm management in an ecological intensification paradigm aims to deliver sustainable crop production by enhancing ecosystem services that minimize the need for external inputs to control pest infestation and sustain yield. Results of this study support the hypothesis that increasing system diversity reduces the magnitude of pest injury. While we did not find a correlation between feeding injury and attainable yield, five out of the seven tested intercropping designs were able to improve individual cabbage fresh marketable weight and maintain yield per unit area compared to a sole crop reference. The improvement in individual quality of intercropped cabbage was considered to be as important as the total yield per unit area because selling price is determined by the quality of each cabbage head. The results provide a starting point for understanding how spatial crop diversification can be utilized to promote synergies between ecosystem services and facilitate a transition towards system redesign for sustainable agriculture. In the case of cabbage, spatial and genetic crop diversification designs contribute to agroecological farming systems that support production and regulating ecosystem service of pest control.

Author statement

All authors have read and agreed to the submitted version of the manuscript.

CRediT authorship contribution statement

Stella D. Juventia: Conceptualization, Methodology, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Walter A.H. Rossing:** Conceptualization, Funding acquisition, Project administration, Writing - review & editing. **Lenora Ditzler:** Conceptualization, Project administration, Writing - review & editing. **Dirk F. van Apeldoorn:** Conceptualization, Methodology, Funding acquisition, Project administration, Writing - review & editing.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fcr.2020.108015.

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