

Effects of strip intercropping of potatoes with non-hosts on late blight severity and tuber yield in organic production

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The effects of strip cropping of potatoes with cereals or a grass-clover mix in and perpendicular to the main wind direction on foliar late blight severity and tuber yield were studied in large-scale field experiments in Germany. Disease progress was assessed in 12–18 sections per plot and yields determined from the same sections. In 2000, plot size was 3×10 m and there were no disease reductions apparently due to interplot interference. In 2001 and 2002, with plot sizes of 6×18 and 6×36 m in strip-cropped potatoes, disease was significantly reduced by 9–20% and 4–12%, respectively, compared to pure stands of potato, with the greatest reductions in plots planted perpendicular to the wind and neighboured by grass-clover. The most important factors contributing to disease reduction were loss of inoculum outside of the plots and barrier effects of neighbouring non-potato hosts. Only 0–20% of the overall yield variation could be explained by the area under the disease progress curve, depending on cultivar and year. In one year disease effects on the yield of a moderately resistant cultivar were higher than on the yield of a susceptible cultivar. This was probably caused by differences in bulking behaviour. Nutrient limitation appeared to be more important than disease in reducing yields. Yields in the edge potato rows directly neighboured by cereals were significantly reduced in all 3 years, but competition by cereals did not change the disease–yield-loss relationship. Strip intercropping might be a useful component in an overall management strategy to reduce incoming late blight inoculum.

Keywords: diversification strategies, epidemiology, organic farming system, *Phytophthora infestans*, *Solanum tuberosum*, yield-loss relationship

Introduction

The only effective fungicides against late blight, caused by *Phytophthora infestans*, in organic farming are copper-based with a maximum permitted application of 3 kg pure copper per ha and season in Germany (Tamm *et al.*, 2004). Copper is a heavy metal that remains in the environment (Brümmer *et al.*, 1986) and only 200–300 g per ha and year are taken up by plants as a micronutrient (Filipinsky, 1989). Therefore, copper fungicides are totally prohibited in the Netherlands and Scandinavia, the EU is aiming to prohibit copper in the foreseeable future and hence there is a need for alternative strategies for disease control (Tamm *et al.*, 2004).

To date, alternative treatments such as plant or compost extracts or mineral-based products have failed to reliably reduce late blight under conducive natural field

conditions (Stephan & Koch, 2002; Dorn *et al.*, 2007). However, when disease pressure was lower, some alternative treatments were reported to reduce disease (Monkos & Gruber, 1998; Dorn *et al.*, 2007). These results suggest that if it were possible to reduce disease pressure with preventive strategies, such as resistance, field hygiene and the removal of infected seed tubers before planting, and also if microclimatic conditions in the field could be improved, alternative treatments might become more reliable (Kessel *et al.*, 1993).

Diversity of crops and varieties is known to reduce many airborne diseases and pests (Mundt, 2002; Finckh & Wolfe, 2006) and cultivar mixtures are highly effective in cereals (Finckh *et al.*, 2000). However, with respect to late blight in potatoes results are not straightforward. Although it was reported that mixtures and alternating rows of differently susceptible potatoes work better under reduced disease pressure (Garrett *et al.*, 2001; Andrivon *et al.*, 2003; Pilet *et al.*, 2006), it is also the case that in mixtures as well as in alternating rows, higher disease severity on the resistant component and lower severity on the susceptible one has occurred (Beuermann *et al.*, 2000; Garrett & Mundt, 2000; Garrett *et al.*, 2001; Andrivon

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et al., 2003; Finckh *et al.*, 2003; Phillips *et al.*, 2005; Pilet *et al.*, 2006). This is because differences in susceptibility in most of the currently used cultivars are quantitative and an increase of disease pressure resulting from a susceptible neighbour will reduce quantitative resistance effects. Therefore, mixture effects were greater in experiments where highly qualitatively resistant cultivars were used (Pilet *et al.*, 2006).

To reduce overall disease pressure in the system and to avoid negative effects on resistant cultivars it might therefore be more effective to diversify the farming system by arranging different non-host crops with potatoes. This was suggested theoretically by Skelsey *et al.* (2005), who showed that the efficiency of mixtures was greatest in smaller fields surrounded by non-hosts ('padded' fields). In the modelling approach of Skelsey *et al.* (2005) disease was assumed to disperse evenly in all directions. However, wind serves as the main dispersal agent for *P. infestans* sporangia (Waggoner, 1952; Harrison & Lowe, 1989; Aylor *et al.*, 2001). The simulations of Skelsey *et al.* (2005) also predict that disease will travel along strips of susceptible potatoes if potatoes are planted in alternating rows. Planting potato strips perpendicular to the main wind direction should lead to inoculum being blown outside the field (Waggoner, 1952) and reduce the chance of spores spreading along the rows (Waggoner, 1962; Harrison & Lowe, 1989).

When considering strip cropping, the choice of the neighbouring crop will be important. Generally, taller crops might provide a barrier to incoming inoculum. However, shading and turbulence effects (Van Arsdell, 1967) may also play a role. Thus, spore loss, reduced spread within rows, and an overall reduced density of potatoes within the farming system through strip intercropping might altogether reduce regional inoculum pressure.

Only a few data on the effects of late blight on yield are available for conventionally grown potato crops (Large, 1952, 1958; James *et al.*, 1972; Rotem *et al.*, 1983) and even less for organically grown crops (Finckh *et al.*, 2006; Möller *et al.*, 2006). When comparing sprayed and non-sprayed plots with diseased leaf areas ranging between 12 and 65% Rotem *et al.* (1983) reported a coefficient of determination (R^2) of 0.91 between disease and yield. Multiple regression of yield on weekly disease increments in plots subjected to different fungicide spray schedules resulted in estimated yield losses ranging between 23 and 55%, compared with 24–52% actual yield losses over 9 years (James *et al.*, 1972). In conventional systems in Germany, potato tuber growth duration usually lasts until late August if the crop is not killed by disease. In contrast, in organic farming, because of limited N supply, final yields are usually reached by early to mid-August (Schulte-Geldermann *et al.*, 2005; Möller *et al.*, 2006) and recent analyses showed that in Germany late blight often starts so late that its effects on organic yields may be less than commonly thought (Finckh *et al.*, 2006; Möller *et al.*, 2006).

The primary objective of this study was to determine if strip intercropping could be used as a strategy to reduce late blight pressure within an organic farming system.

From 2000 to 2002, field experiments were conducted at the organic experimental farm of the University of Kassel, in central Germany. Plots of different cultivars were planted in line with and perpendicular to the main wind direction and with different neighbour crops to investigate: (i) the effects of intercropping of potatoes with crops of different architecture (cereals or a grass-clover mix) on late blight epidemics and tuber yield and (ii) interactions between varietal resistance, planting direction and late blight. As the ultimate goal of this work was to help achieve stable yields, special attention was paid to possible effects of the neighbour crops on potato yields and the interactions of these effects with yield losses attributed to disease.

Materials and methods

Field experiments were conducted at the organic experimental farm of the University of Kassel, which is located 10 km north of Kassel in central Germany. The experimental site is characterized by deep rich silty loam soils. The annual mean precipitation is around 720 mm and mean annual temperature is 8.1°C. Temperature, humidity, hours of sunshine, and wind direction were recorded at the experimental site in 2001 and 2002 with a datalogger of type Combilog 1020 (T. Friedrichs & Co). In 2000, data were taken with semiautomatic devices and completed with data obtained from a German weather service station 5 km away.

For all experiments, fields with a legume pre-crop were chosen (Table 1). Soils were ploughed after the pre-crop in early spring and the seedbeds prepared shortly before planting. Hilling was performed twice before canopy closure. Depending on the year and field conditions, planting dates varied by 3 weeks (Table 1). Potatoes were planted in all plots in rows 75 cm apart, with an overall planting density of 40 000 tubers ha⁻¹.

Experimental design

All experiments were arranged as split-plot trials with four replications. In 2000, planting direction was assigned to the main plots to simplify field operations. Potato cultivar and neighbour crop were assigned to the subplots (Table 1). Two potato cultivars, Secura and Simone (susceptible and moderately resistant to late blight, respectively) were planted with four different neighbour crops: spring oats, potatoes, and mulched and unmulched grass-clover mix.

Subplots were arranged in four long rows in a north-south direction, each row accommodating one replication. The rows were separated by 12 m consisting of 6 m of spring barley with 3 m of regularly mulched grass-clover on either side. Subplots were 10 m long with a central plot of four rows (3 m) of potatoes and two 3-m-wide plots of the respective neighbour crop on either side. If the neighbour crop was potatoes, 3 m of grass-clover were inserted before the next subplot to ensure that the distance between potatoes in the subplots was always 6 m. The experimental size was in total 1.5 ha (220 × 72 m).

Table 1 Field parameters and experimental design of potato strip intercropping experiments, 2000–02

Field parameters	2000	2001	2002
pre-crop	faba beans	peas	grass-clover (GC)
planting of potatoes	26 April	6 May	16 May
harvest	2nd week Sep.	3rd week Sep.	1st week Sep.
Experimental design	2000	2001/2002	
main factor	planting direction	potato cultivar	
subplot factors	cultivar × neighbour	neighbour × (plot size × planting direction)	
planting direction	east–west (= in) and north–south (= perpendicular to wind)		
susceptible cultivar	Secura	Linda	
mod. resistant cultivar	Simone	Agria	
neighbour crops ^a	potatoes, spring cereals, mulched GC		
plot size ^a	unmulched GC 3 m × 10 m	– 6 m × 36 m (in wind) 6 m × 18 m (perpendicular to wind)	
distance between blocks ^b	6 m GC + 6 m cereal	12 m GC + 12 m cereal	
total no. of plots	64	56	

^aIn 2001 and 2002, the smaller plots planted perpendicular to the main wind direction were arranged crosswise as downwind and upwind plots (see Fig. 1).

^bBlocks were arranged perpendicular to the main wind direction: from upwind (replicate I) to downwind (replicate IV) in 2000 and 2001 and as two-by-two pattern in 2002 with two replicates upwind and two downwind.

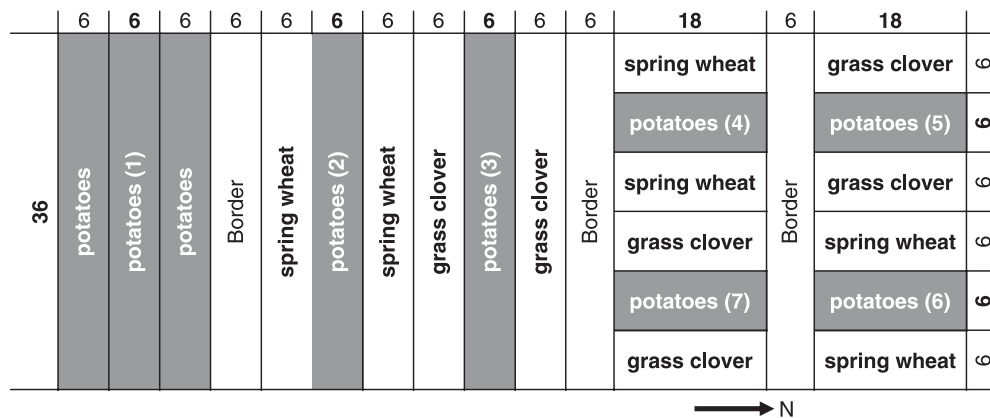


Figure 1 Schematic arrangement of experimental treatments in 2001 and 2002, representing one cultivar. Neighbours were either potatoes (dark grey), mulched grass-clover, or spring wheat. Borders were inserted to ensure a minimum distance of 12 m between potato strips and were also planted to grass-clover. The main wind direction was along the long plots (treatments 1–3), while perpendicularly planted plots were arranged upwind (4 and 5) and downwind (6 and 7). Plot sizes and distances are marked in metres.

In 2000, disease severity in the field increased significantly from NW to SE and plots of the more resistant cv. Simone neighbored by the more susceptible cv. Secura were more diseased than when neighbored by Simone. This suggested that interplot interference was large, especially between the two cultivars. Also, the plots were too small to clearly see epidemic patterns within plots. Therefore, in 2001 and 2002, cultivar was designated a main-plot factor and plot sizes and distances were increased (Table 1).

From the 2000 data it was estimated that the 12-m distance between replicates was not enough to prevent interplot interference in the wind direction. Therefore, in 2001 and 2002, subplots within replicates were arranged in long rows in a north–south direction with 12 m between

potato strips (Fig. 1). In the east–west direction, the distance was increased to 24 m with 12 m of spring wheat in the centre. The different distances were justified because of the relatively steady westerly wind direction during the epidemics (see Table 2). Plot size in the wind direction was increased to 6 m (eight rows) wide and 36 m long. The number of neighbour crops was reduced to three – potatoes, spring wheat and mulched grass-clover.

In 2001 and 2002, for the plots perpendicular to the wind, there were several problems that had to be dealt with simultaneously. If a single strip 6 m wide had been planted perpendicular to the 36-m-long plot, the distance between replicates would have varied between 15 and 30 m. In addition, the experiment would have become impossibly large. By arranging two strips in parallel, the

Table 2 Monthly mean air temperature (°C), precipitation (mm), hours of sunshine (h) and mean wind direction recorded at German weather station in Calden, located 5 km from the experimental site (2000), and from the weather station located at the experimental site (2001 and 2002)

	2000			2001				2002			
	°C	mm	h	°C	mm	h	°wind ^a	°C	mm	h	°wind ^a
March ^b	6.0	72	83	4.0	90	44	159	5.6	41	114	199
April	10.7	34	161	7.5	49	116	233	7.6	13	167	191
May	15.0	47	229	14.2	25	252	190	13.2	49	129	208
June	16.9	83	224	14.9	79	151	257	16.5	43	181	219
July	14.9	102	–	18.4	59	223	204	16.9	106	133	220
August	17.8	71	209	18.6	48	205	198	18.5	35	171	215

^aWind direction varying from north (0/360°) to south (180°). Measurements were recorded every 10 min and means were calculated per day (data not shown) and per month. Only data for 2001 and 2002 are shown.

^bBold values within rows (months) indicate extreme values of climatic parameters, either maximum or minimum, compared among years. Dash indicates missing data.

distances between the strips within a replicate were reduced to 12 m, a distance that based on the previous year's experience might be prone to interplot interference. Therefore, after thorough discussion with the statistician and exploratory data simulations, the perpendicular plots with neighbouring grass clover and wheat were split in two halves that were placed up- and downwind of the two halves of each other in case the different neighbours affected spore dispersal in and out of the plots differently (Fig. 1). To reduce size, it was decided to omit the 18 × 36-m pure potato treatment perpendicular to the wind.

Even with these reductions, the total potato area of the experiments was about 1.2 ha. The susceptible cv. Linda and the moderately resistant cv. Agria were chosen to match the cultivars grown on the organic farm to avoid logistical problems.

Experimental size was 4.5 and 4.2 ha in 2001 and 2002, respectively. In 2001, the four replicates were arranged in four rows. In 2002, a sufficiently long field was available to allow for two long rows of plots accommodating two replicates each.

Assessments

Late blight from natural infections was assessed as percentage diseased leaf area (DLA) following the scheme of James (1971). In 2000, each potato row was divided into three equal sections (12 assessments per plot) which were individually assessed every 3–4 days once late blight symptoms appeared. In the following years, assessments were performed in 6-m sections. In 2001, each plot was divided into the left and right half with four potato rows each, resulting in a total of 12 and six observations for the large and small plots, respectively. In 2002, the edge rows of the plots were assessed separately and the four central (inner) rows of each plot together, resulting in a total of 18 and nine observations in the large and small plots, respectively. After detection of the first late blight lesions in at least one experimental plot, assessments were made 12, 11 and 11 times in 2000, 2001 and 2002, respectively.

Harvest and sorting of tubers

In 2000, potato tubers were harvested per row, i.e. in 10-m sections. In 2001 and 2002, tubers were harvested from the same 6-m sections where late blight had been assessed. From each plot, the two outer potato rows and two randomly selected inner rows were harvested. The tubers were separated into the size classes (i) < 30 mm, (ii) 30–60 mm (marketable yield) and (iii) > 60 mm, and weighed separately.

Data processing and analysis

Each field experiment was analysed separately. The area under the disease progress curve (AUDPC) was calculated according to Kranz (1996) for each assessment location within the plots. Because late blight assessments in 2002 were carried out for the outer rows separately, for the calculated plot mean the values of the two inner row assessments were weighted threefold to represent the six inner rows in contrast to the single outer rows.

Tuber yields were calculated in t ha⁻¹. As a high proportion of edge rows result from strip cropping, their yield was included in the yield analysis. With two inner and two outer rows in 2000, the mean of all four rows was used. In 2001 and 2002, mean tuber yield was calculated using one quarter of the outer and three quarters of the inner rows.

All statistical analyses were carried out with Statistical Analysis Systems (SAS Institute). In 2000, late blight and yield were analysed with the GLM procedure as a split plot with wind as main plot and cultivar by neighbour crop as subplots. If significant effects were detected, means were compared with the Duncan test.

With the increased plot size and distance in 2001 and 2002, the spatial distribution of disease across the experimental area became very uneven. Therefore, each assessment section in the field was assigned east–west and north–south coordinates on a grid covering the whole experimental field. In a separate study, the spatial patterns of disease development in the field were modelled to

adjust treatment effects for spatial trends (Büchse *et al.*, 2005; unpublished data). This spatial adjustment process was incorporated into the ANOVA of the AUDPC data in the present study. The modelling of the large-scale spatial trends of the experiment revealed that the block effect could be neglected in both years. However, errors attributable to the main factor (cultivar), subplot, and autocorrelation among neighbouring assessment points were included into the final ANOVA model (equation 1) used to evaluate AUDPC data:

$$y_{ijb} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + f_{ib} + g_{ibk} + \gamma(\text{NS,EW}) + \lambda_1(\text{EW_P}) + \lambda_2(\text{EW-P})z + e$$

with α_i = main effect of i^{th} cultivar
 β_j = main effect of j^{th} treatment (i.e. planting pattern \times neighbour crop)
 $(\alpha\beta)_{ij}$ = interaction of cultivar \times treatment
 f_{ib} = main error (cultivar \times block)
 g_{ibk} = subplot error (cultivar \times subplot \times block)
 $\gamma(\text{NS,EW})$ = large-scale trends of the field in north–south and east–west direction
 $\lambda_1(\text{EW_P})$ = east–west gradient within a potato plot
 $\lambda_2(\text{EW_P})z$ = east–west gradient among treatments (s_plot and ss_plots, see below)
 e = error of individual assessment points with spatial variance-covariance matrix.

In a separate analysis, AUDPC from the easternmost and westernmost sections within a plot were compared in a two-factorial design with treatment and section as the two factors. Cultivar \times planting direction \times neighbour were included in the factor treatment.

Yield was analysed using PROC MIXED (SAS) with a model that did not include the adjustments for the spatial

trends of disease. By using the repeated statement in PROC MIXED, the error variance was calculated separately for the different plot sizes. The plot error was divided into two parts: s_plot (subplot) error (large versus small plots) and ss_plot (subsubplot) error (small plots arranged crosswise upwind and downwind to each other). The large plots had one s_plot and one ss_plot each, while the two crosswise small plots with the same neighbour crop shared one s_plot, but had different ss_plots. The upwind and downwind plots in 2001 and 2002 with the same neighbours were thus combined for the analysis (i.e. a total of 10 different treatments in 2001 and 2002). The SAS code can be obtained from the authors.

For estimation of competition effects of neighbour crop on tuber yield the data of inner (central) and outer (edge) potato rows were analysed with factors either wind or cultivar \times neighbour \times row (outer/inner). As no interactions were detected, the GLM model was reduced to neighbour \times row. In case of significant differences, LSMeans were compared pairwise with *t*-tests. Simple linear regression analyses (PROC REG) were used to determine the relationship between late blight severity (AUDPC) and potato tuber yield.

Results

Disease development

As a result of severe rainfall events in mid-July 2000 (Table 2) late blight progressed rapidly in susceptible cv. Secura, resulting in around 75% DLA within only 1 week and the highest AUDPC among cultivars and years (Table 3). In contrast, on the moderately resistant cv. Simone, the steepest disease increase started 10 days later, in late July, and the disease progressed more slowly.

Table 3 Effects of potato cultivar, planting pattern and neighbour crop on area under disease progress curve (AUDPC) of late blight epidemics, 2000–02

	2000	2001	2002
Potato cultivar			
susceptible	2471 A ^a	1459 A	1767 A
moderately resistant	1053 B	723 B	1308 B
Planting direction \times neighbour crop ^b			
in wind			
potatoes	1786 a	1264 a	1654 a
cereals	1813 a	1076 b	1564 bc
grass-clover (GC), mulched	1751 a	1105 b	1513 cd
GC, unmulched	1773 a	–	–
perpendicular			
potatoes	1756 a	–	–
cereals (upwind)	1766 a	1025 b	1519 bcd
cereals (downwind)		1005 b	1588 ab
GC, mulched (upwind)	1747 a	1016 b	1475 de
GC, mulched (downwind)		1147 ab	1449 e
GC, unmulched	1703 a	–	–

^aData for 2001 and 2002 are cleared of spatial trends (Büchse *et al.*, 2005). Different letters within columns indicate significant differences between mean values for cultivars or treatments [2000: cultivar effect $P < 0.01$, $F = 1175$ (GLM); 2001 and 2002: cultivar effect $P < 0.01$, $F = 35.5$ and 62.3 , respectively; treatment effect $P < 0.01$, $F = 3.85$ and 9.27 , respectively (PROC MIXED with pdiff)].

^bIn 2000, all plots were 3×10 m, while in 2001 and 2002 plot size varied between 6×36 and 6×18 m when planted in or perpendicular to the prevailing wind direction, respectively (see Fig. 1).

While the first lesions in the experimental plots were detected on 11 July in 2000 and 2002, in 2001, the first late blight lesions were found on 28 June. However, disease did not progress rapidly until mid-July and 1% DLA was observed for both cvs Agria and Linda at the same date in both 2001 and 2002. Due to long-term hot and dry weather conditions from mid-July to mid-August 2001 (Table 2), late blight development in 2001 was slow and before 100% DLA was reached on Agria the crop started senescing by mid-August. Agria was killed by late blight in 2002, however. As a result of regular rainfall events in mid-July 2002 (Table 2), disease severity increased rapidly from 25 to 30 July, resulting in an increase from 25% to about 80% DLA on Linda within 5 days. Consequently, AUDPC on Agria in 2002 was nearly twice that of 2001 (Table 3).

In 2000, a random accumulation of cv. Secura plots in the northwestern corner of the experiment promoted late blight development in the neighbouring plots of cv. Simone. AUDPC increased from 1707 in replicate I upwind to 1807 in replicate IV downwind ($P < 0.01$). Also, there was a discernible pattern across the experimental area: in the least diseased first replicate located upwind AUDPC in susceptible plots neighboured by potatoes was 37–44% higher than in plots neighboured by other crops. The differences between treatments became smaller from replicate I to replicate IV (data not shown) resulting in no significant differences overall in disease severity between treatments (Table 3).

With main factor potato cultivar and expanded barrier strips between plots and blocks in 2001 and 2002, interferences between cultivars, blocks and plots were much reduced. Semivariograms (Finckh *et al.*, 2005) suggested that interference between neighbouring assessment areas became negligible beyond 12 and 20 m in NS and EW directions, respectively. Geostatistical analyses (Büchse *et al.*, 2005; Finckh *et al.*, 2005) revealed spatial trends in 2001 and 2002, with the highest disease severity in 2001 in a slightly lower-lying eastern part of the field, resulting in increased severity from west to east. In 2002, symptoms of late blight first appeared approximately in the middle of the north–south transect, resulting in a more complex spatial pattern. After removal of the overall spatial trends there were no more significant replication effects in 2001 and 2002 (Büchse *et al.*, 2005).

In 2001 and 2002, the highest AUDPC was observed in the large potato plots planted in line with the wind direction and neighboured by potatoes (Table 3). In both years, AUDPC in the large plots planted in the wind direction was significantly higher than in the small plots perpendicular to the wind located upwind. While in 2002 disease was lowest in plots with mulched grass-clover as the neighbour crop (relative AUDPC 0.88–0.91), in 2001 the reduction was greatest with neighbour cereals (relative AUDPC 0.80–0.85). There were no significant differences in AUDPC between the small upwind (plots 4 and 5, Fig. 1) and downwind (plots 6 and 7, Fig. 1) plots with the same neighbour in both years (Table 3).

Disease severity was usually higher in the downwind eastern sections than in the upwind western sections of the

36-m-long plots planted in the wind direction (west–east) in 2001 and 2002 (Fig. 2b,c). No clear gradients were observed in the 10-m-long plots in 2000 planted west–east (Fig. 2a). Except for the cv. Simone plots (Fig. 2a, right) in 2000, in which overall severity was quite low, disease severity was higher in the east than in the west row in the plots planted north–south perpendicular to the wind with neighbour grass-clover in all 3 years. In contrast, when neighboured by cereals, the gradients were reversed in 2000 and 2002 and not discernible in 2001. In 2001, assessments were not carried out in the edge rows separately. While the differences were clearly visible in the field, unfortunately only data of the left and right half of the plots were taken. These did not show these differences.

No tuber blight was found in any of the 3 years within 4 weeks after harvest, when potatoes were graded.

Potato tuber yields

Total tuber yields were similar in 2000 and 2001, while that in 2002 was less than half that of the years before. In 2002, the proportions of non-marketable small tubers (< 30 mm) were 44% and 20% of the total yield of cvs Linda and Agria, respectively (Fig. 3).

While there were no differences in marketable yield between Secura and Simone in 2000, marketable yield of Agria was significantly higher than that of Linda in 2001 and 2002 (Table 4). In all 3 years, the highest yields were obtained in one of the treatments with neighbouring grass-clover, while the lowest yields were observed in plots neighboured by cereals. Overall, these differences were rarely significant, however (Table 4).

A more detailed analysis comparing the yields of the potato rows neighboured by the different crops (outer rows) with the yields of the central rows in the plots revealed that differences between the whole plots were mostly attributable to significant yield reductions in the rows neighboured by cereals (Table 5).

Yield loss relationships

Yield loss relationships were calculated for total tuber yield. The effects of disease on total tuber yield varied between cultivars and years (Fig. 4). About 20% of the variation in yield in 2000 and 2001 could be related to AUDPC, but not in 2002. Although in 2000 AUDPC was much higher for Secura, the slope of the regression line was much shallower (–0.06) than for Simone (–0.19). Slopes were more similar for Agria and Linda in 2001.

The negative effects of the cereals on yield in the edge rows could be caused by competition or increased disease in the edge rows. In addition, competition could lead to changes in yield loss as a result of additional stress on plants already suffering from disease. When considering the mean of both outer rows, on average, disease in inner and outer rows was not different in the plots bordered by cereals (data not shown). Also, comparing the regressions of yield on AUDPC between rows neighboured by potatoes versus cereals or grass-clover did not result in a clear

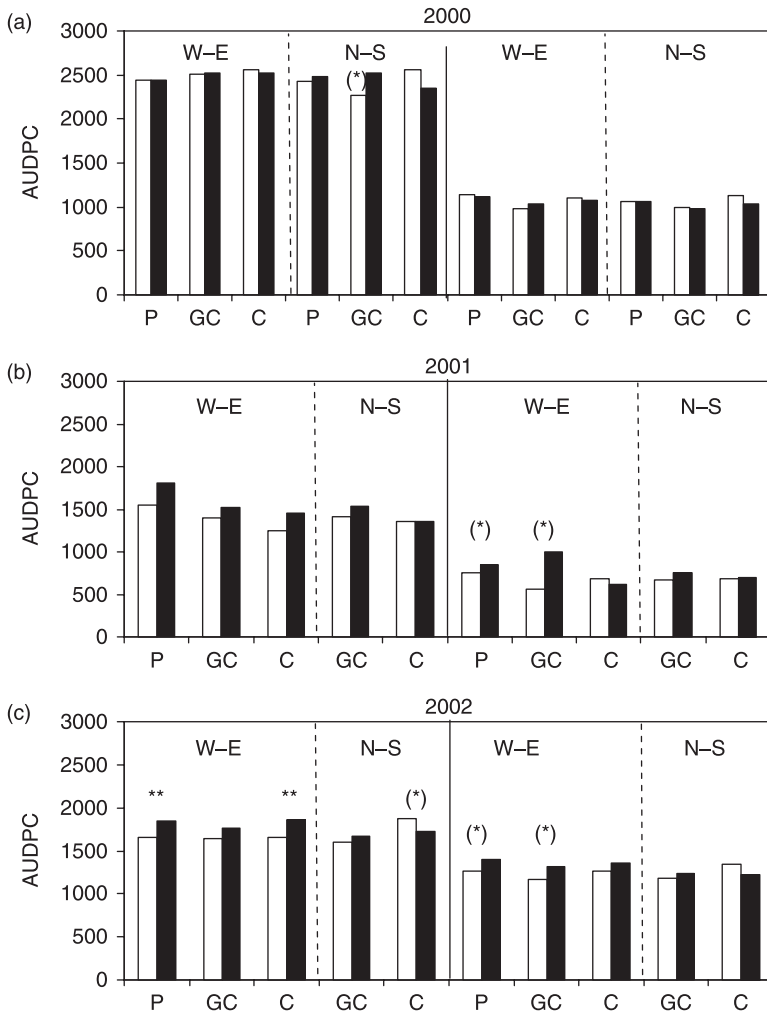


Figure 2 Area under disease progress curve (AUDPC) of late blight in (a) 2000, (b) 2001 and (c) 2002 in upwind (west, white bars) or downwind (east, black bars) rows/sections within potato plots of a susceptible cultivar (left half of graphs) and a moderately resistant cultivar (right half). Plots were planted east-west (W-E = in main wind direction) and north-south (N-S = perpendicular to the main wind direction) and arranged with neighbour crops of potatoes (P), grass-clover (GC) or cereals (C). The western or eastern sections for the W-E plots represent the 3-m end sections in 2000 and the 6-m end sections in 2001 and 2002. For the plots planted N-S (perpendicular to the wind) data for the edge rows are presented for 2000 and 2002. For 2001, only the data for two halves of the plots were available. (*) and ** indicate that differences between eastern and western sections were significant at $P < 0.10$ or $P < 0.01$, respectively (t-test).

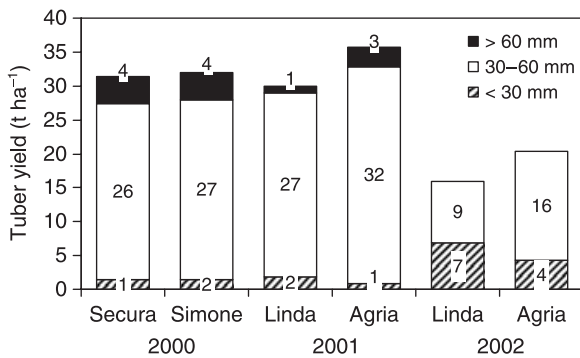


Figure 3 Total yield ($t\ ha^{-1}$) subdivided into different tuber size classes, ranging from $< 30\ mm$ to $> 60\ mm$, of potato cvs Secura and Simone (2000) and Linda and Agria (2001 and 2002).

pattern (Table 6). While in 2000, with cereals the slope became somewhat steeper for the susceptible Secura and R^2 increased, the pattern was reverse for the moderately resistant Simone. With susceptible Linda and moderately resistant Agria the patterns in 2001 were again different. Generally, R^2 values were even lower for the regression

of marketable yield on AUDPC than for total yield. For susceptible/moderately resistant cultivars they were: 0.16/0.17 (2000), 0.23/0.13 (2001) and 0.00/0.11 (2002).

Discussion

When tested in large experimental plots of $6 \times 36\ m$ in 2001 and 2002, strip intercropping generally reduced potato-late blight disease pressure as well with grass-clover as with cereals as the neighbour crop. Planting the strips perpendicular to the wind in smaller plots in most cases led to further disease reductions. No such effects could be observed in 2000, when the plots were only $3 \times 10\ m$ in size.

The neighbour crops greatly affected the spatial patterns in late blight development when the crop was planted perpendicular to the wind. While disease was most severe in the downwind parts of plots when neighboured by grass-clover the opposite pattern was observed in plots neighboured by wheat.

While varietal resistance was the strongest factor affecting disease, cropping pattern and neighbour crop did not interact with cultivar. Overall yield levels were strongly

Table 4 Effects of potato cultivar, planting pattern and neighbour crop on marketable potato tuber yield (t ha⁻¹) in intercropping experiments, 2000–02

		2000	2001	2002
Potato cultivar				
	susceptible	26.1 A ^a	27.0 B	8.9 B
	moderately resistant	26.5 A	32.0 A	15.6 A
Planting direction × neighbour crop ^b				
in wind	potatoes	25.8 a	29.9 ab	12.5 ab
	cereals	25.3 a	29.5 abc	10.7 c
	grass-clover (GC), mulched	26.2 a	29.8 ab	12.8 ab
perpendicular	GC, unmulched	27.1 a	–	–
	potatoes	26.7 a	–	–
	cereals (upwind)	26.0 a	30.3 a	12.1 b
	cereals (downwind)		27.7 c	12.1 b
	GC, mulched (upwind)	26.4 a	30.6 a	12.4 ab
	GC, mulched (downwind)		28.6 bc	13.3 a
	GC, unmulched	26.7 a	–	–

^aDifferent letters within columns indicate significant differences between means of cultivars or treatments [2000: no significant effects (GLM); 2001 and 2002: cultivar effects: $P < 0.01$, $F = 112$ and 477 , respectively; treatment effects $P = 0.031$ and < 0.01 , $F = 2.65$ and 4.10 , respectively (PROC MIXED with pdiff)].

^bIn 2000, experimental potato plots were uniformly 3×10 m. See Fig. 1 for plot sizes and arrangement in 2001/02.

Table 5 Total tuber yield (t ha⁻¹) of potato plots planted with different neighbour crops in strip intercropping experiments, 2000–02

Neighbour crop	2000		2001		2002	
	inner rows ^a	outer rows ^a	inner	outer	inner	outer
Potatoes	30.8	29.9 b ^c	33.4	33.5 a	18.1	17.9 a
Grass-clover, mulched	30.4	32.1 a	33.5	32.7 a	18.9	18.3 a
Cereals ^b	30.7**	28.0 c	33.6**	28.7 b	19.0**	15.7 b

^aTotal tuber yield (t ha⁻¹) of inner (central) and outer (edge) potato rows, i.e. in direct contact to the neighbour crop.

^bSpring oats (2000) and spring wheat (2001–02) were sown as the cereal neighbour crop.

^cNumbers within columns followed by different letters are statistically different at $P < 0.01$ (LSMeans/pdiff).

**Differences between inner and outer potato rows were significant at $P < 0.01$ (linear contrast).

Table 6 Parameters of linear regression^a of tuber yield on area under disease progress curve (AUDPC) of late blight of susceptible and moderately resistant potato cultivars^b neighboured by different crops, 2000–02

Neighbour crop × row ^c	Susceptible			Moderately resistant		
	b	y_0	R^2	b	y_0	R^2
2000						
potatoes	-0.005	42.1	0.15**	-0.022	51.4	0.30**
cereals	-0.007	44.0	0.73**	-0.003	32.0	0.02
grass-clover	-0.007	47.7	0.23	-0.042	76.0	0.22
2001						
potatoes	-0.006	40.3	0.39**	-0.011	44.8	0.33**
cereals	-0.005	33.7	0.14**	-0.009	37.3	0.33**
grass-clover	-0.008	41.3	0.50**	-0.011	43.6	0.31**
2002						
potatoes	+0.001	18.8	0.01	+0.000	14.8	0.05
cereals	-0.002	17.3	0.03	-0.003	21.1	0.01
grass-clover	-0.002	20.1	0.01	+0.006	12.7	0.06

^aLinear regression function $y = bx + y_0$ with b = slope of regression function and intercept y_0 . Coefficients of determination R^2 are shown. ** indicates that regression was significant at $P < 0.001$.

^bIn 2000 Secura and Simone, and in 2001 and 2002 Linda and Agria were planted as susceptible and moderately resistant potato cultivars, respectively.

^cTuber yield of inner potato rows (neighbour potato) in contrast to outer rows with non-potato host as neighbour, i.e. cereals or grass-clover.

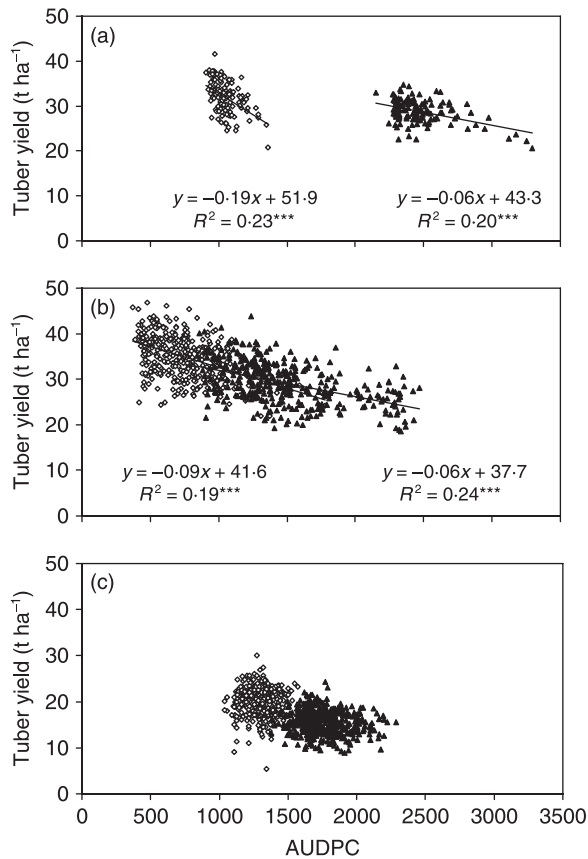


Figure 4 Regression of area under disease progress curve (AUDPC) of late blight and tuber yield (t ha^{-1}) in potato plots planted with susceptible cvs Secura in 2000 and Linda in 2001 and 2002 (black) or moderately resistant cvs Simone in 2000 and Agria in 2001 and 2002 (white). (a) 2000, (b) 2001 and (c) 2002.

affected by year and cultivar and there were clear competitive effects of cereals as a neighbouring crop on potatoes. Depending on the year, late blight had moderate to no discernible effects on yield of marketable tubers.

The effects of strip intercropping, especially with grass-clover, on late blight can at least partially be explained by reduced spore interchange between potatoes planted in strips, as predicted by the model for the isolated diversified situation (i.e. the 'padded' one) by Skelsey *et al.* (2005). However, the disease reductions observed were much smaller than predicted by the theoretical model. This was probably caused by a combination of several factors. First, semivariograms based on the geostatistical analyses of Büchse *et al.* (2005) and Finckh *et al.* (2005) indicated that the influence between points in the present study only became negligible at distances of around 20 m in the prevailing wind direction and at about 12 m perpendicular to the wind. These distances imply a relatively shallow dispersal gradient. Skelsey *et al.* (2005) used dispersal radii of 6, 4 and about 3 m. With a shallower disease gradient mixtures are expected to be more effective than with a steeper one (Garrett & Mundt, 1999; Mundt, 2002).

However, this is most important if the genotype unit area (GUA) is small, e.g. for cereals. In potato strips, in contrast, the GUA is rather large, allowing for much more autoinfection. For strip intercropping to be effective, it seems logical that the distance between strips should exceed the dispersal radius, if possible. The west-east effects are enhanced by the fact that during wet weather westerly winds prevail in central and western Europe, increasing the distance of spore dispersal in that direction.

Secondly, in the simulation model, epidemics were only simulated up to a disease severity of 20–40% (Skelsey *et al.*, 2005), while the present results take complete epidemics into account. With increasing epidemic duration mixture effects tend to decrease (Mundt, 2002). The apparent infection rate r in the present experiments was best estimated by a non-symmetrical Richards function (Richards, 1959), with a slow-down once 50% DLA was reached; only for the susceptible cv. Linda in 2002 was a logistic growth model within the confidence limits (unpublished data). Considering only epidemics up to 40% DLA to determine a logistic r -rate leads to an overestimation of mixture effects across the complete epidemic. Therefore, the predictions of Skelsey *et al.* (2005) can only be compared with data on early epidemics and more moderate disease reductions are to be expected in the field.

The third and probably most important factor making a direct comparison with the results of Skelsey *et al.* (2005) impossible is the scale. In the model, single susceptible rows (0.75×75 m) were separated by one (0.75 m) to seven (5.25 m) resistant rows. In the experiments here strips of eight rows (6×36 m) were separated by at least 12–24 m of non-host tissue. It would be very interesting to see the predictions of the model for this experimental setup integrating the effects of wind, r -rates and dispersal gradients.

Disease in 11 of the 12 long plots (36 m) in 2001 and 2002 increased from west to east as expected. The lack of gradient in the moderately resistant cv. Agria neighbored by cereals in 2001 (Fig. 2b) might have been caused by the low disease pressure in 2001 as a result of less favourable climatic conditions (Table 2). Differences among treatments were smaller overall in that year (Table 3).

Besides loss of spores, disease reduction in smaller potato plots might also be the result of barrier effects and a reduction of initial infections. While the intercropped neighbour (barrier) crops may catch or filter out some of the spores, the chances of incoming spores falling onto a plot are also reduced. In experiments comparing disease dynamics in potato plots of different sizes separated by 10–40 m of cereals disease reductions were observed in the smaller plots mostly as a result of delayed onset of the epidemic in the small plots, while epidemic rates were almost the same in all plots once they had started (Beuermann *et al.*, 2000). Also, disease in the 18×36 -m potato plots was significantly higher than in the smaller plots in 2001 and 2002 (Table 3). Similar observations were made by Phillips *et al.* (2005), who found that disease in larger potato plots was significantly higher than in smaller plots, despite higher epidemic rates in smaller plots.

The opposite spatial patterns within the potato plots perpendicular to the wind when neighboured either by grass-clover or cereals may have been caused by a combination and interaction of mechanisms such as microclimatic changes and turbulences as influenced by architecture of the neighbour crop. In 2001, relative humidity and temperature were measured in the edge rows of one plot per cultivar neighboured by wheat and one neighboured by grass-clover. The duration of conducive conditions within the canopy (i.e. minimal 90% relative humidity and 15–19°C) during the period from 14 July to 16 August 2001 in plots neighboured by cereals was 156 h in the upwind rows compared to 134 h in the downwind rows. When neighboured by grass-clover, the overall number of conducive hours was lower and the pattern reversed, with 114 h upwind and 130 h downwind. Generally, the same tendencies were observed in both potato cultivars (unpublished data). As cereals are taller than potatoes it is possible that turbulences will arise causing incoming air currents to fall faster into the crop than would be expected. That could lead to an increased deposition of spores in the upwind row. Effects of plants of different heights on spore deposition were observed with white pine blister rust along forest edges (Van Arsdel, 1967). Such effects would be synergistic with the more conducive microclimatic conditions in the upwind rows neighboured by wheat.

The low yields in 2002 and the high percentage of tubers below 30 mm in diameter were mostly the result of climatic conditions. Because in organic farming no soluble mineral fertilizers can be applied, the potato cropping system depends very much on warm soil temperatures with adequate moisture to allow mineralization of organic matter. The low precipitation from March to June combined with cool temperatures in May apparently resulted in low nutrient availability. These effects were probably exacerbated by delayed planting. In a parallel experiment about 40 km east of the experimental site in this study, soil nitrogen levels below normal were recorded in 2002, also resulting in very low tuber yields (Schulte-Geldermann *et al.*, 2005; Finckh *et al.*, 2006). Similar conditions were reported to be responsible for low tuber yields in the experiments of Rotem *et al.* (1983). Based on sequential harvests in experiments parallel to the ones reported here, Schulte-Geldermann *et al.* (2005) found that as a result of limited nutrients, even when potatoes were protected from late blight to a certain degree by copper fungicides, final yields were usually reached by the end of July. This was confirmed for southern German conditions by Möller *et al.* (2006). With severity of blight levels over 75% occurring only late in July in the present experiments under organic conditions, a lack of strong yield effects was to be expected, although without a control treatment completely protected from disease no final conclusion can be made.

While nitrogen supply and availability are probably very important in limiting yields, the varietal properties with respect to timing of tuber initiation are probably the next most important factor. This could be seen in 2000,

when comparing the effects of late blight on cvs Simone and Secura. Although much less diseased, Simone suffered relatively more yield loss through late blight than Secura, as indicated by a threefold steeper negative regression slope (Fig. 4). This discrepancy can be explained by the fact that Simone is later bulking than Secura and thus Secura had a chance to accumulate much of its tuber yield before the onset of heavy disease. As Agria and Linda have similar bulking behaviour, no such differences were seen in 2001 and 2002. However, similar results were obtained in parallel experiments in 2002 and 2003 when cultivars of different bulking behaviour were compared (Schulte-Geldermann *et al.*, 2005) and also in southern Germany in the 1990s (Möller & Reents, 2007). Therefore, recommendations in organic farming stress the importance of early bulking cultivars (Möller & Reents, 2007) and of planting sprouted (chitted) tubers (Karalus & Rauber, 1997). Chitting not only speeds up overall development but also facilitates removal of infected potatoes before planting.

Tuber blight did not play a role in this study and over the years only a little tuber blight has been observed on potatoes produced (among others for certified organic seed potatoes) on this experimental farm. However, tuber-borne inoculum in general does play a role [it was shown that the population structure of *P. infestans* at the farm in this study was determined by the origin of the seed potatoes, especially from other sites (Bouws & Finckh, 2007)].

While competition from wheat led to significantly reduced yields in the edge rows of the plots, the influence of this additional stress was not translated into greater effects of disease on yield. This was a further indication that overall yields were only partially limited by late blight in the experiments.

The results of this study indicate that growing potatoes in narrow strips perpendicular to the wind and separated by non-potatoes may in general reduce epidemic pressure within this type of farming system. Grass-clover as a neighbour crop appears to be a more useful choice than cereals as there will not be excessive competition in the edge rows. It would be interesting, however, to test other crops with different architecture, such as faba beans, for example, as intercrops.

While late blight often appears very severe, nutrient availability may still be of greater importance than commonly thought. Selection of potato cultivars with moderate resistance against late blight and/or early tuber initiation is of prime importance for organic farmers. As an additional preventive strategy, chitting of seed tubers should allow for the removal of blight-affected tubers, reducing initial inoculum. It will also lead to earlier emergence of potato plants and hence partial escape from effects of late blight. Such a strategy might on first sight be more attractive to small farmers as their fields are already smaller and smaller amounts of seed potatoes will need to be chitted. However, on larger farms it might be easier to divide fields in the right direction and possibly arrange for a rotation that accommodates alternating strips of potatoes and grass-clover in a field over 2 years.

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