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Selection for *Phytophthora* field resistance in the F_2 generation of organic outdoor tomatoes

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Abstract Tomatoes are the most important vegetable, globally as well as in Germany. Outdoor tomato production is seriously impaired due to increasing infections with evolving late blight (*Phytophthora infestans*) populations. Within organic agriculture, research is being conducted to develop regionally adapted and open pollinated cultivars of outdoor tomatoes with late blight field resistance. In the present experiment, three crosses, including wild, cocktail, and beefsteak tomatoes, were selected for field resistance against late blight in F_2 at one location per cross. The comparison of positive and negative selection in F_3 revealed the selection of single F_2 plants to be efficient in all three crosses. F_2 selection has proved to be a robust and efficient tool for breeding programs. The correlated response to selection in other traits, including yield, fruit weight, days to maturity, harvest period, and plant height, depended on the cross. It was evident that selection for desired traits combined with field resistance against late blight is promising, even in wide crosses. The most undesired attribute of wild tomatoes is the formation of shoots on leaves and in inflorescences. No correlation was observed between field resistance and shoot formation, allowing the selection of genotypes with improved field resistance and yield, but without morphological disadvantages.

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Introduction

Tomatoes are the most important vegetable on the global scale. In 2008, approximately 130,000,000 t were produced (FAO 2010). Germany imported approximately 660,000 t in 2008. Commercial horticulture produced approximately 63,000 t (FAO 2010) while approximately the same amount was harvested in home gardens (unpublished data). As in most neighboring regions, tomatoes intended for processing (canning, etc.) are imported in large quantities, while the domestic crop is almost exclusively used for the fresh market. In Germany, cheap and resource-efficient outdoor tomato production has almost ceased to exist due to increasing infections with late blight (*Phytophthora infestans* (Mont.) de Bary). Analysis of *Phytophthora* isolates from both host species, the tomato and the potato, collected during 1967–2000 revealed massive changes in population structure, resulting in more aggressive pathogen genotypes (Rullich et al. 2002). Similar changes were observed in France (Lebreton et al. 1998) and England (Day and Shattock 1997). Many populations collected since the 1980s belonged to 'new' populations, which are characterized by the presence of both mating types in France and by new haplotypes in England. Prior to this time, only the A1 mating type was observed outside Mexico. The presence of the A2 mating type outside Mexico created the opportunity for sexual reproduction and the creation of new, more aggressive genotypes (Foolad et al. 2008). A2 outside of Mexico was first reported in Western Europe, but was observed worldwide soon after (Fry et al. 1993). The occurrence of oospores has been reported in many parts of the world, including Europe (Rullich et al. 2002; Drenth et al. 1995), North America (Gavino et al. 2000), Israel (Rubin et al. 2001), and Taiwan (Deahl et al. 2008). Recently, Klarfeld et al. (2009) have shown experimentally that known sources of resistance can easily be overcome by recombinant *Phytophthora* genotypes derived from oospores.

The experiment presented here is part of the Organic Outdoor Tomato Project, which was started in 2003 as a participatory selection and breeding program in Germany. A screening based on 3,500 accessions identified cultivars to improve amateur gardening (Horneburg 2007). The best parent cultivars were chosen to develop breeding strategies to be carried out in the breeding program in three organic market gardens in Central and Northern Germany. The first open pollinated cultivars resulting from the Organic Outdoor Tomato Project were released in 2010.

The accelerated recombination of *P. infestans* must be balanced by continuous resistance breeding in the target environments. Knowing in which segregating generation selection can be done under field conditions is of crucial importance for the development of an efficient breeding strategy. In the present experiment, the selection efficiency in F_2, the first segregating generation after crossing, was tested. The use of genotypes not adapted to present production techniques was also considered. In wide crosses, we have used 'wild tomatoes' as sources for important traits, including earliness, high field resistance against *Phytophthora*, and fruit quality. However, these positive attributes are often combined with less-desired traits, like strong vegetative growth, rapid succession of short internodes, and abundant shoot formation on leaves and in inflorescences. The correlated response to selection in undesired traits when selecting desired traits was investigated.

Materials and methods

Three crosses were used in the present experiment, including wild, cocktail, and beefsteak tomatoes.

Cross 1: Wild tomato 'Rote Murmel' × cocktail tomato 'Zuckertraube'.
Cross 2: Wild tomato 'Golden Currant' × beefsteak tomato 'Paprikaförmige'.
Cross 3: Cocktail tomato 'Celsior' × beefsteak tomato 'Paprikaförmige'.

The pedigrees of the parent genotypes are unknown. These genotypes were chosen due to their different susceptibilities to late blight infection in earlier field trials (Table 2). Information about resistance to specific late blight races was not available. In 2009, Rote Murmel was resistant against *Phytophthora* race US-11 in a test with detached leaflets from field-grown plants (Miles et al. 2010). One cross per location was grown and selected in central or northwest Germany. Typical to the research area, plants were grown as staked tomatoes and pruned to one main shoot. Locations are characterized in Table 1 and genotypes in Table 2. The term "wild" tomato is used for genotypes with very small fruits and heavy side shoot formation. "Wild" tomato is not a botanical term, as we do not know the history of the genotypes used in the experiment. Wild tomatoes have a very low yield if grown as staked tomatoes; however, fruits are abundant when the plants are grown with little or no pruning.

In 2004, 10 parent plants, 10 F_1 plants, and 30 F_2 plants were grown from each cross in two replications. The plants at Schönhagen and Ellingerode were damaged by late frosts shortly after being transplanted to the field plots. Early growth was severely impaired and it was not possible to determine yield level. The five best and five worst F_2 plants per cross were selected according to the scores for *Phytophthora* leaf and fruit infections, general plant health, and fruit set at the end of the season. In 2005, F_3 progenies of the 10 selected F_2 plants and their parents were grown in a randomized block design with three replications and two plants per plot. *Phytophthora* infections were scored according to Table 3 at intervals of 5–28 days during periods of infection. The area under the disease progress curve (AUDPC) was calculated according to Kranz (1996):

Table 1 Description of the experimental sites

	Experimental sites		
	Schönhagen	Ellingerode	Rhauderfehn
Management	Bio-dynamic	Organic	Organic
Geographical location	51°19′60″ N, 10°1′0″ E	51°19′60″ N, 9°49′0″ E	53°16′51″ N, 7°53′71″ E
Altitude	300 m	140 m	2 m
Soil	Loamy clay	Sandy loam	Sand
Fertilizer	150–180 dt/ha composted cattle manure	150–180 dt/ha composted sheep manure	150–180 dt/ha sheep manure
Pre-crop 2004	Winter wheat	Oats	Clover grass
Pre-crop 2005	Malva verticillata	Crimson clover	Clover grass

Table 2 Attributes and origin of the genotypes used

	Genotypes				
	Rote Murmel	Golden Currant	Celsior	Zuckertraube	Paprikaförmige
Fruit type	Wild tomato	Wild tomato	Cocktail	Cocktail	Beefsteak
Approx. fruit weight (g)	2	7	14	23	200–250
Growth type	Indeterminate	Indeterminate	Indeterminate	Indeterminate	Indeterminate
Fruit infection[a]	61	81	73	Susceptible	155
Leaf infection[a]	135	130	179	Susceptible	229
Origin	Dreschflegel[b]	Dreschflegel[b]	SamenArchiv[c]	Commercial cultivar released 1994 by Reinsaat KG[d]	Private seed saver B. Rumkowski

[a] Area under disease progress curve. Mean value 2003 Schönhagen and Rhauderfehn

[b] In der Aue 31, 37213 Witzenhausen, Germany

[c] Waldstraße 40, 90596 Schwanstetten, Germany

[d] 3572 St. Leonhard am Hornerwald 69, Austria

$$AUDPC = \sum_{i=1}^{n-1} \left(\frac{x_{i+1} + x_i}{2} \right) (t_{i+1} - t_i)$$

with x_i is the score at time i, t_i is the day of the ith observation, and n is the number of scores. High AUDPC values indicate high infection levels.

The tomatoes were sown on 18 March 2004 and 31 March 2005 in the greenhouse. They were transplanted to the fields on 19 May 2004 and 25 May 2005, respectively. The number of inflorescences with at least one flower in bloom was counted 91–101 days after transplanting. Plant height was measured 49–51 days after transplanting. Shoot formation on leaves and shoot formation in inflorescences were scored 75–101 days after transplanting; 1 = no shoots, 9 = maximum shoot formation. Planting to maturity indicates the period between the establishment of the field plots and full maturity of the first fruit. The total amount of healthy fruit produced per plant, or yield per plant, was determined in intervals of 14 days. The size of the fruit produced in each cross was calculated as the average fruit weight for the entire season. The highest truss with at least one mature and healthy fruit was counted. Harvest period is the period between the date the first healthy mature fruit was observed and the date the last healthy mature fruit was harvested.

Data were analyzed with Plabstat, Version 3A-pre (Utz 2005). Deviation of F_2 from the parent mean was tested using the t-test. Mean values of F_3

Table 3 Key for the assessment of damages by late blight (*Phytophthora infestans* (Mont.) de Bary) on leaves and fruits of tomatoes in field experiments

	Leaf infections
1	No infections
2	First symptoms as grey-green to brown leaf spots[a]
3	Symptoms obvious. Yellowing or browning of some leaves or small leaf spots to 50% of plant height
4	Increased yellowing or browning, or small leaf spots to 75% of plant height
5	Plant severely affected
6	Yellowing or browning to 50% of plant height
7	Yellowing or browning to 75% of plant height
8	Entire plant yellow to brown, all leaves infected
9	All leaves dead
	Fruit infections including small, immature fruits
1	No infections
2	Up to 12.5% of the fruits with grey-green to brown spots
3	Up to 25% of the fruits with typical dark spots
4	Up to 37.5% of the fruits with typical dark spots
5	Up to 50% of the fruits with typical dark spots
6	Up to 62.5% of the fruits with typical dark spots
7	Up to 75% of the fruits with typical dark spots
8	More than 75% of the fruits with typical dark spots
9	All fruits infected

[a] At a low level of infection, discerning between late blight and early blight (*Alternaria solani* (Ell. & Mart.) L. R. Jones & Grout) is not always possible

progenies from positive and negative selection were compared using the *t*-test.

Results

In 2004, the average late blight fruit infection of F_2 plants from crosses 1 and 3 differed significantly from parent mean values and was closer to the more resistant parent (Tables 4, 5, 6). In all crosses, the genotypes with smaller fruits (Rote Murmel, Golden Currant, and Celsior) were less susceptible to *Phytophthora* infections. The F_2 plants from the positive and negative selections were clearly distinguishable by the level of fruit and leaf infections. Leaf infections in all three crosses differed significantly from the parent mean values and were closer to the more resistant parent. In crosses 1 and 3, F_1 was less infected than F_2 and both parents. In crosses 2 and 3, plant height decreased from F_1 to F_2. The wild tomatoes in crosses 1 (Rote Murmel) and 2 (Golden Current) produced a higher number of inflorescences than the other parent (Tables 4, 5). F_2 plants, on average, produced an intermediate number of inflorescences. Plant height of the F_2 populations from crosses 1 and 2 was intermediate between the parent genotypes, but closer to the height of the wild tomato parents (Rote Murmel and Golden Currant). In cross 3 (Table 6), F_2 plants surpassed the height of the less vigorous parents (Celsior and Paprikaförmige). For both wild tomato parents, abundant undesired shoot formation in inflorescences and on leaves (Golden Currant only) was observed, while the F_2 populations displayed intermediate levels (Tables 4, 5).

In 2005, F_3 progenies of the F_2 plants selected in 2004 were grown. In all three crosses, the positive selection had a higher field resistance against late blight than the negative selection (Tables 4, 5, 6). Differences were highly significant, the one exception being leaf infection in the cross Celsior × Paprikaförmige. As in the previous year, differences in fruit infection were more pronounced than differences in leaf infection.

Selection for *Phytophthora* field resistance had an effect on morphology, phenology, and agronomic traits. Significant differences between positive and negative selection were observed for plant height in

Table 4 Effect of the selection for *Phytophthora* field resistance in cross 1 'wild tomato Rote Murmel × cocktail tomato Zuckertraube' in Schönhagen, 2004 and 2005

Schönhagen	Fruit infection[a]	Leaf infection[a]	Number of inflorescences[b]	Plant height (cm)[c]	Shoot formation on leaves[d]	Shoot formation in inflorescences[d]	Planting to maturity (days)	Highest truss	Harvest period (days)	Fruit weight (g)	Yield (g)
2004											
Rote Murmel	31	131	3.6	200	1.3	4.7					
Zuckertraube	68	150	0.6	100	1.0	1.7					
F_1	35	112	2.9	191	1.3	3.8					
F_2	35***	115***	2.3	195	1.4	2.4					
Positive selection F_2	31	100	2.8	193	1.0	2.0					
Negative selection F_2	44	121	2.4	192	2.6	1.8					
2005											
Rote Murmel	57	142	4.2	187	2.8	2.8	63.0	8.0	77.0	2.2	172
Zuckertraube	271	322	3.0	146	1.8	1.8	71.8	4.0	38.8	22.5	342
Positive selection F_3	107	170	4.2	193	3.0	3.0	64.1	7.5	72.2	11.1	681
Negative selection F_3	185***	276***	4.1	177***	3.4	3.4	67.2*	6.4	55.3***	8.6***	418***

*, *** Significant deviation from the parent mean (2004) or differences between positive and negative selection (2005) in the *t*-test at $p = 0.05$, or $p = 0.001$, respectively

[a] Area under disease progress curve

[b] 9 July 2004 and 13 July 2005

[c] 26 August 2004 and 25 August 2005

[d] 3 August 2004 and 8 August 2005

Table 5 Effect of the selection for *Phytophthora* field resistance in cross 2 'wild tomato Golden Currant × beefsteak tomato Paprikaförmige' in Ellingerode, 2004 and 2005

Ellingerode	Fruit infection[a]	Leaf infection[a]	Number of inflores-cences[b]	Plant height (cm)[c]	Shoot formation on leaves[d]	Shoot formation in inflorescences[d]	Planting to maturity (days)	Highest truss	Harvest period (days)	Fruit weight (g)	Yield (g)
2004											
Golden Currant	47	94	4.5	185	7.0	8.5					
Paprikaförmige	56	205	2.7	116	1.0	1.0					
F_1	50	111	4.3	186	2.2	3.7					
F_2	55	111**	3.4	163	3.3	4.5					
Positive selection F_2	44	90	4.6	178	4.2	5.8					
Negative selection F_2	74	181	2.8	174	1.8	5.0					
2005											
Golden Currant	45	108	6.7	194	9.0	8.3	70.0	7.3	64.0	6.7	473
Paprikaförmige	174	176	3.5	145	1.0	1.0	86.3	1.7	23.5	248.4	1877
Positive selection F_3	76	109	4.8	190	4.3	5	77.0	6.0	56.5	31.7	1072
Negative selection F_3	130***	162***	4.7	194	3.9	4	82.1*	5.3	44.6**	59.8***	1316

*, **, *** Significant deviation from the parent mean (2004) or differences between positive and negative selection (2005) in the *t*-test at $p = 0.05$, $p = 0.01$, or $p = 0.001$, respectively

[a] Area under disease progress curve

[b] 9 July 2004 and 14 July 2005

[c] 24 August 2004 and 25 August 2005

[d] 12 August 2004 and 3 September 2005

Table 6 Effect of the selection for *Phytophthora* field resistance in cross 3 'cocktail tomato Celsior × beefsteak tomato Paprikaförmige' in Rhauderfehn, 2004 and 2005

Rhauderfehn	Fruit infection[a]	Leaf infection[a]	Number of inflores-cences[b]	Plant height (cm)[c]	Shoot formation on leaves[d]	Shoot formation in inflorescences[d]	Planting to maturity (days)	Highest truss	Harvest period (days)	Fruit weight (g)	Yield (g)
2004											
Celsior	363	395	3.0	131	1.2	1.7	80.9				
Paprikaförmige	402	438	3.9	162	1.0	1.5	79.8				
F_1	368	389	3.5	200	2.1	2.2	76.9				
F_2	386**	403*	3.3	186	1.1	2.1	80.0				
Positive selection F_2	346	394	3.6	191	1.0	1.1	81.7				
Negative selection F_2	439	422	2.8	169	1.2	2.5	76.3				
2005											
Celsior	315	380	3.8	106	5.0	3.5	85.7	3.3	35.8	13.8	177
Paprikaförmige	406	406	4.2	143	2.0	2.0	87.8	0.0	0.0	–[e]	0
Positive selection F_3	319	345	3.6	126	4.2	3.2	95.5	1.9	21.5	40.6	124
Negative selection F_3	350**	358	4.2	141***	4.0	2.5	86.2	1.7	9.3*	47.5	119

*, **, *** Significant deviation from the parent mean (2004) or differences between positive and negative selection (2005) in the *t*-test at $= p$ 0.05, $p = 0.01$, or $p = 0.001$, respectively

[a] Area under disease progress curve

[b] 8 July 2004 and 13 July 2005

[c] 25 August 2004 and 24 August 2005

[d] 4 August 2004 and 21 August 2005

[e] Fruit weight approx. 200–250 g

Table 7 Correlation of traits between ten F_3 progenies in three crosses. Top line cross 1, middle line cross 2, bottom line cross 3

	Fruit infection	Leaf infection	Number of inflores-cences	Plant height	Shoot formation on leaves	Shoot formation in inflores-cences	Planting to maturity	Highest truss	Harvest period	Fruit weight
Leaf infection	0.92***									
	0.91***									
	0.71**									
Number of inflorescences	−0.64**	−0.54								
	−0.57	−0.34								
	−0.78***	−0.49								
Plant height	−0.50	−0.53	0.66**							
	−0.04	−0.09	−0.29							
	0.48	0.67**	−0.06							
Shoot formation on leaves	−0.10	0.10	0.27	0.42						
	−0.18	−0.02	0.61	0.13						
	−0.45	−0.30	0.60	−0.40						
Shoot formation in inflorescences	−0.10	0.10	0.27	0.42	1[a]					
	−0.49	−0.30	0.74**	−0.69**	0.23					
	−0.61	−0.49	0.48	−0.69**	0.73**					
Planting to maturity	0.72**	0.64**	−0.78***	−0.27	0.20	0.20				
	0.68**	0.46	−0.82***	0.29	−0.21	−0.69**				
	−0.22	−0.02	−0.08	−0.29	0.32	0.12				
Highest truss	−0.72**	−0.69**	0.72**	0.80***	0.24	0.24	−0.46			
	−0.57	−0.34	0.94***	−0.26	0.42	0.64**	−0.85***			
	−0.63	−0.14	0.87***	0.17	0.56	0.24	0.25			
Harvest period	−0.95***	−0.93***	0.76**	0.55	0.04	0.04	−0.79***	0.79***		
	−0.72**	−0.53	0.82***	−0.27	0.17	0.60	−0.95***	0.87***		
	−0.58	−0.63**	0.57	−0.18	0.26	0.52	−0.11	0.27		
Fruit weight	−0.16	−0.41	−0.11	−0.22	−0.87***	−0.87***	−0.32	−0.02	0.25	
	0.61	0.27	−0.84***	0.27	−0.39	−0.69**	0.90***	−0.84***	−0.86***	
	0.71**	0.17	−0.59	0.13	−0.43	−0.34	−0.58	−0.69**	−0.09	
Yield	−0.59	−0.70**	0.47	0.15	−0.59	−0.59	−0.77***	0.40	0.68**	0.80***
	0.27	0.12	−0.10	0.18	−0.15	−0.35	0.20	0.11	−0.17	0.39
	−0.40	−0.21	0.85***	0.27	0.46	0.24	−0.18	0.79***	0.47	−0.26

, * Significant differences between positive and negative selection in the *t*-test at $p = 0.05$ or $p = 0.01$, respectively

[a] Combined score for shoot formation on leaves and in inflorescences

crosses 1 and 3 (Tables 4, 6). In cross 1, the more resistant parent (Rote Murmel) grew taller than the less resistant parent (Zuckertraube) and the positively selected F_2 grew taller than the negatively selected F_2. In cross 3, the opposite was observed (and again, the plant height of the positive selection more closely resembled that of the more resistant parent). Earliness was improved in the positive selection of crosses 1 and 2 by 3.1 and 5.1 days, respectively (Tables 4, 5). The parents of cross 3 did not differ much in earliness (Table 6). The harvest period of the positively selected offspring of all crosses was prolonged by at least 11.9 days. Fruit weight of the F_3 populations did not reach the mean fruit weights of the parents. Positive selection for field resistance led to lower fruit weight in crosses 2 and 3; the opposite occurred in cross 1. Significant differences in yield were observed in cross 1, where positive selection improved yield by more than 50%.

Correlations of the observed traits between the F_3 progenies are presented in Table 7. In all crosses, fruit and leaf infection were positively correlated. No correlation was observed between level of infection and shoot formation in inflorescences and on leaves. In cross 3, leaf infection and plant height were correlated and a correlation was also observed between shoot formation in inflorescences and on leaves. Days to maturity and harvest period were negatively correlated in crosses 1 and 2, while in cross 3 the parent genotypes differed in days to maturity by only 2.1 days. In most cases, fruit and/or leaf infection were negatively correlated with harvest period. Surprisingly, a positive correlation between harvest period and yield was observed only in cross 1. Yield and fruit weight were positively correlated only in cross 1. A positive correlation between number of inflorescences and highest truss existed in all crosses, although highest truss and yield were only positively correlated in cross 3. A positive correlation between fruit infection and fruit weight occurred only in cross 3. A positive correlation between plant height and infection level was only significant for leaf infections in cross 3.

Discussion

Despite difficult experimental conditions, the selection for *Phytophthora* field resistance in F_2 was successful in all three crosses investigated. Frost damage at two sites had resulted in uneven, delayed, and atypical development of the tomato plants. Therefore, this technique proved to be a robust and efficient tool for breeding programs.

A key for the assessment of damages by late blight was developed by the Organic Outdoor Tomato Project for the rapid scoring of large numbers of field-grown tomato plants. The assessment keys for late blight of potatoes were insufficient for this purpose. Keys scoring the percentage leaf area covered (e.g., James 1971) are only suitable for limited numbers of plants or laboratory assays. While it is possible to score the percentage of necrotic tissue in potatoes (e.g., Cruickshank et al. 1982), tomato late blight can develop in different ways. Symptoms either spread from older to younger leaves (resulting in die-off of entire leaves), or they spread more evenly over large parts of the plant (causing multiple of leaf spots).

We scored leaf infections in addition to fruit infections for two reasons. First, the level of leaf infection will influence the vitality and photosynthetic activity of the plant (and as a consequence, yield). Second, in some environments, the low level of late blight infections does not allow observers to score fruit infections. In the present experiment, selection for field resistance against fruit infections (significant in all three crosses) has been more efficient than selection for field resistance against leaf infections (significant in two crosses). Nevertheless, if the scoring of fruit infections is not possible, selection for leaf resistance will also result in a selection gain due to the high correlation of fruit and leaf infections. At early stages of leaf infections, it is not always possible to distinguish between leaf spots caused by late blight or early blight (*Alternaria solani*). This situation provides an explanation for reduced selection efficiency for leaf infections, and may explain the phenomenon observed in cross 1 Rote Murmel × Zuckertraube (Table 4): F_1 and F_2 suffered less from leaf infections than the resistant parent, Rote Murmel.

In screenings, a high level of field resistance is easier to find in genotypes with smaller fruits. However, a significant correlation between fruit weight and fruit infection was only observed in one of the three crosses.

Other traits, including yield, fruit weight, days to maturity, harvest period, and plant height, were not considered in selection. The indirect effects of a selection for resistance on these traits depended on the cross. However, it was evident that selection for suitable traits combined with field resistance is promising, even in wide crosses. Harvest period was mainly influenced by earliness and field resistance. Both traits were successfully incorporated from wild tomatoes. Harvest period and yield were not always correlated. Both traits are particularly important for the fresh tomato supply. As shown earlier (Horneburg and Becker 2008), selection at suitable locations with frequent exchange of breeding lines might be the best strategy to combine a long harvest period with high yield.

The least desirable attribute of wild tomatoes is the formation of shoots on leaves and in inflorescences, as their removal is necessary and labor intensive. The fact that no correlation between field resistance and shoot formation was observed allows for the selection of genotypes with both improved field resistance and yield, but without morphological disadvantages.

A major advantage of selection in field trials versus selection under more controlled conditions in the laboratory or greenhouse is their relatedness to the target environment in practical horticulture. Field resistance is directly assessed, including interactions with pedoclimatic conditions, cultivation practices, pests, and other diseases. In most indoor experiments with artificial infection, only one or a few *Phytophthora* strains have been applied on tomatoes (Michalska and Pazio 2005; Drenth et al. 1995) and potatoes (Zimnoch-Guowska et al. 2003; Vleeshouwers et al. 1999; Swiezynski et al. 1997). According to the recent review by Foolad et al. (2008), no particular method for the artificial infection of tomato fruits has been published to date. Serious drawbacks in field tests occur when climatic conditions are unfavorable for *Phytophthora* infections. For example, during the unusually hot and dry summer of 2003, late blight did not appear in approximately 50% of our field experiments.

Selection for field resistance between adult plants in the field limits the population size, because training tomatoes is laborious. However, the advantage is that all other important agronomic and morphological traits can be selected simultaneously. F_2 selection depends on scoring individual plants, and the experimental error is expected to be high. F_3 selection would reduce experimental error, because progenies can be assessed. However, this approach would delay selection for one year. The present study has demonstrated that F_2 selection is a successful approach. These results will help to improve the efficiency of outdoor tomato breeding for *Phytophthora* resistance.

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