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Evaluation of foliar late blight resistance of potato cultivars in northern Baltic conditions

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Abstract

The aim of this study was to evaluate foliar late blight resistance and yield of selected foreign and Estonian potato cultivars, to determine the most promising cultivars for the northern Baltic region. We hypothesized that local cultivars have higher potato late blight (*Phytophthora infestans*) resistance and yield due to higher blight resistance. Potato late blight observation field trials were carried out in 2012 and 2013 in Einola Farm, Tartu County, Estonia. In both growing seasons, twelve potato cultivars were compared: nine from the Dutch breeding company "Agrico" and three from the Estonian Crop Research Institute (ECRI). They comprised four early cultivars 'Ranomi', 'Esmee', 'Romie' and 'Maret', four medium early cultivars 'Toluca', 'Mariska', 'Madeleine' and 'Teele', and four medium late / late cultivars 'Excellency', 'Bellefleur', 'Manitou' and 'Anti'. Of these, only two, 'Anti' and 'Toluca', qualified as highly foliar late blight resistant. This research clearly indicates that, despite unfavourable conditions for the pathogen, late blight is able to destroy potato foliage in most of these cultivars before the end of the growing season in northern Baltic conditions. This reflects local genetic heterogeneity of populations of *P. infestans*, probably associated with the presence of strains adapted to a wide range of humidity conditions. In 2012 that had late blight favourable weather, the cultivar 'Toluca' showed high foliar blight resistance, as it reached the maximum yield compared to other cultivars, which were susceptible or very susceptible to late blight and had drastically reduced yield. However, although the late blight infection was not recorded in the growing season 2013, the cultivar 'Toluca' did not tolerate the dry weather well and its tuber yield remained significantly lower than that in all other cultivars. Additionally, in 2013, a potato early blight (*Alternaria solani*) outbreak was recorded with the two most susceptible cultivars being the local cultivar 'Teele' and the Dutch cultivar 'Excellency'.

Key words: cultivar, disease assessment, foliar resistance, potato late blight, tuber yield.

Introduction

Potato late blight, caused by the oomycete pathogen *Phytophthora infestans* is a re-emerging potato disease (Fry et al., 2015), being for more than 160 years one of the most destructive potato diseases worldwide. Its management is a challenge for both organic and conventional production systems. Late blight causes losses for potato production of more than 6 billion $ and its management costs annually 1 billion (Haverkort et al., 2009). Furthermore, changes in *P. infestans* populations due to the presence of sexual reproduction have changed its epidemiology and increased its adaptability, and this in turn has changed the way the disease could be controlled (Cooke et al., 2011; Lehsten et al., 2017). Recent studies of *P. infestans* in Estonia have indicated that the pathogen is indeed reproducing sexually in northern climates, resulting in higher population diversity and production of oospores that contribute to better survival through the cold winters. Altogether, the *P. infestans* population in Estonia is characterised by great virulence diversity as well as by very high genetic diversity (Runno-Paurson et al., 2016). Genetically diverse populations of *P. infestans* occur also in other north, north-east and east European populations (Brurberg et al., 2011; Chmielarz et al., 2014).

Late blight infection was recorded in Estonia earlier than ever before in 2014, when already by mid-June, several conventional potato production fields in southern regions were infected (monitored by E. Runno-Paurson). This is in agreement with the evidence that in the Nordic region, there are clear indications of earlier outbreaks of late blight, requiring more frequent fungicide treatments to control the disease, probably partly because of oospore-derived infections (Hannukkala et al., 2007). Consequently, late blight control is becoming even harder and more

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costly (Haverkort et al., 2009; Runno-Paurson et al., 2013). In Estonia, conventional farmers apply fungicides on average 4–7 times per season and in some seasons up to 11 times (Runno-Paurson et al., 2016). Elsewhere in some European countries, up to 25 sprays are applied per season in severe blight years (Hansen etal., 2009), and several active ingredients have to be used because the strains have become increasingly insensitive to common fungicides (Nielsen, 2014). However, in the Baltic countries, there is a large percentage of small conventional farms, in Latvia and Lithuania approximately 90%, where fungicides are not used or are used irregularly for the control of late blight (Aav et al., 2015; Runno-Paurson et al., 2015 a). Thus potato foliage of a substantial production area is not protected. Control of the late blight is complicated as quite a large proportion of this area is still traditionally managed (Runno-Paurson et al., 2015 a). This is a direct risk for conventional seed and large production fields because an initial infection source comes from these unprotected fields, increasing late blight pressure in large commercial production fields especially in rainy seasons when it is more difficult to treat the foliage against late blight infection and when the spread of the disease is favoured.

Thus, when late blight infection starts earlier in the season (Lehsten et al., 2017) and conventional growers are forced to spray leaves with fungicides even more frequently than every five days to control the disease (communication with Jens G. Hansen; personal observations in 2016), cultivars resistance to late blight might become a more promising way to control late blight disease. Potato cultivars with partial resistance to late blight do exist, such as 'Bionica', 'Carolus', 'Connect', 'Sarpo Mira' and 'Vitabella' (Forbes, 2012; Lammerts van Bueren et al., 2014), but they have not been exploited sufficiently by conventional producers. In Europe, the resistant cultivars are not grown on a large scale because other commercially important characteristics such as quality, yield and earliness are not usually present in the cultivars with late blight resistance (Cooke et al., 2011).

This research work on foliar late blight resistance was initiated by Estonian seed potato producers that have identified the vulnerability to late blight as one of the essential problems in seed production. The majority of conventional potato growers prefer cultivars bred by the several breeding companies from The Netherlands and Germany. However, local seed potato producers' experience has shown so far that, in northern Baltic conditions, information about the late blight resistance of cultivars poorly reflects their description from breeding companies. Seed producers need cultivar resistance information pertinent to local conditions to sell the seed material of newer cultivars to local potato growers. This is particularly essential for small-scale conventional and organic growers with heightened interest in potato cultivars with higher late blight resistance with feedback about insufficient resistance level. Organic growers buy seed material also from conventional seed producers because organic seed material is not available and cultivar choice thus depends on the availability of cultivars offered by potato seed producers. Although local potato cultivars bred by the Estonian Crop Research Institute (ECRI) may be partially, moderately or highly late blight resistant, their availability and distribution are hampered by low multiplication rate. Cultivars from the Dutch breeding company "Agrico" have been selected for foliar late blight testing and Einola Farm located in Uhti village at Tartu County, Estonia has had the experience of conducting demonstration field trials since 2002 in order to introduce promising potato cultivars to the Estonian potato market. Over the years, the popularity of several "Agrico" cultivars, such as 'Arielle', 'Fontane' and 'Impala', has increased and they have been widely grown (Runno-Paurson et al., 2013).

The aim of this study was to evaluate foliar late blight resistance and yield of potato cultivars from the "Agrico" and to assess their suitability for cultivation in the northern Baltic region in large fields. These relatively new Dutch cultivars for the Estonian market were compared with local standard cultivars of each maturity group from the ECRI. We hypothesize that local ECRI cultivars have higher late blight resistance and yield due to their higher blight resistance. Cultivar 'Toluca' from the "Agrico" was included in the evaluation trial due to its high resistance level to monitor its foliar late blight resistance stability / instability in northern Baltic field conditions, where the *P. infestans* populations are genetically highly diverse (Runno-Paurson et al., 2016) compared with Dutch and other western European populations, which consist of clonal less diverse genotypes.

Materials and methods

Field trials. Potato late blight observation field trials were carried out on Einola Farm, Uhti village (58°17′ N, 26°43′ E) distribution, Tartu County, Estonia. In both 2012 and 2013, twelve potato cultivars were compared: nine from the Dutch breeding company "Agrico" and three from the Estonian Crop Research Institute (ECRI). The cultivars differed in maturity; four were early: 'Ranomi', 'Esmee', 'Romie' ("Agrico") and 'Maret' (ECRI); four were medium early: 'Toluca', 'Mariska', 'Madeleine' ("Agrico") and 'Teele' (ECRI); four were medium late: 'Excellency', 'Bellefleur', 'Manitou' ("Agrico") and one 'Anti' (ECRI) was a late cultivar. In both years, the preceding crop in the trial area was field pea. In 2012, seed potato tubers were planted on 8 May, and in 2013, on 9 May. Trials were laid out in a randomized block design with four replications. Plot size was two rows (7.0 × 0.8 m). The soil was *Stagnic Luvisol* (*LV-st*) by WRB (2014) classification with a sandy loam texture and a humus layer of 20–30 cm. No irrigation was used. Mineral fertilizers were applied in both years before tuber cultivation in mid-April 500 kg ha^{-1} ($N_{12}P_8K_{16}$ + Mg_3 + microelements) and 5 May 660 kg ha^{-1} ($N_{11}P_{11}K_{21}$ + $Mg_{1.5}$ + microelements). The trial was hilled three times and harrowed once. No fungicides or herbicides were used. Potatoes were harvested on 10 September in 2012 and on 9 September in 2013. Tuber yield was determined by weighing directly after harvest of both rows.

Weather conditions. In 2012, temperature records (Tõravere Weather Station of the Estonian Weather Service) in May and June were similar to the long-term (20 years) average, although June and August were slightly cooler than the long-term average (Table 1). Rainfall in 2012 was similar to the long-term average in June and July, but more rainfall was recorded in May (+17.8 mm) and in August (+25.8 mm) than the 20-year average. In 2013, July and August, temperature records were similar to the 20-year average, but May was warmer by 3.5°C and June – by 2.8°C. In 2013, there was slightly more rainfall in May, but in August it was similar to the long-term average. June was very dry and with only 35.0 mm rainfall (long-term average – 81.4 mm) and July rainfall was also lower than the long-term average.

Potato late blight assessment. Foliar disease was evaluated as a percentage of total foliage twice each week, every three or four days. Disease assessments were made after infection from 13 July to 31 August in 2012 (15 observations), and from 22 July to 2 September in 2013 (13 observations). Late blight infection was assessed according to the 0–100% scale (EPPO Bulletin, 1989).

Table 1. Average monthly temperature and rainfall in Tõravere[1] during the vegetation periods of 2012 and 2013 together with long-term average

Month	Ten-day period	Temperature °C			Rainfall mm		
		average of 2012	average of 2013	average of 1990–2013	sum of 2012	sum of 2013	average sum of 1990–2013
May	I	10.5	12.6	10.3	1.0	1.3	11.7
	II	12.3	16.4	11.3	52.7	51.3	24.0
	III	13.0	15.6	12.5	22.6	20.6	22.8
June	I	11.6	19.4	14.9	21.1	6.4	18.0
	II	15.5	15.4	15.2	33.6	13.8	33.4
	III	14.4	19.9	16.0	33.9	14.8	30.0
July	I	19.8	18.5	17.7	7.0	17.3	17.9
	II	15.4	17.6	18.1	50.7	15.9	24.7
	III	19.7	17.8	18.4	11.6	26.0	27.7
August	I	16.8	20.1	17.9	37.3	5.8	22.9
	II	15.4	16.5	16.6	14.4	63.0	25.1
	III	13.8	15.2	15.3	51.6	9.9	29.5
September	I	12.6	13.4	13.2	28.6	2.7	18.6
May–September	I–III	14.7	16.8	15.2	366.1	248.8	306.2

[1] – according to Tõravere Weather Station of the Estonian Weather Service

Estimation of disease scale (1–9) values from relative area under disease progression curve (RAUDPC). The area under the disease progression curve (AUDPC) was calculated from the date of first occurrence of late blight until the last observation of the disease in the trial according to Shaner and Finney (1977):

$$\text{AUDPC} = \sum_{i=1}^{n-1} \left(\frac{y_i + y_{i+1}}{2}\right)(t_{i+1} - t_i),$$

where n is the number of assessments, y – the percentage of affected foliage at each assessment, t – the time in days of each reading; AUDPC was standardized to RAUDPC values according to Fry (1978).

Estimation of 1–9 scale values from RAUDPC values were calculated according to Hansen et al. (2005); for this the linear regression model:

$y = a + bx$,

where y is observed values, a – intercept, b – slope; x = (√RAUDPC for cultivar / √RAUDPC for cultivar ‘Toluca’) × 100.

A smaller value of the index indicates higher resistance in a potato cultivar. Estimated scale values for cultivars tested in both years were compared with scale values for the same cultivars from the European Cultivated Potato Database, “Agrico” website and breeder information from ECRI, where the scale for resistance against foliar blight is defined as: 1 – very low, 2 – very low to low, 3 – low, 4 – low to medium, 5 – medium, 6 – medium to high, 7 – high, 8 – high to very high and 9 – very high.

Statistical analysis was performed with the software package *R*. Differences in the severity percentage of late blight and potato yield between maturity types or cultivars were tested with one-way analysis of variance (*ANOVA*) and Tukey HSD post-hoc tests ($p = 0.05$). Differences in the severity of late blight disease depending on date and maturity type or cultivar were tested by two-way *ANOVA*. All factors such as “year”, “cultivar” and “maturity type” were treated as categorical variables. “Cultivar” was nested within “maturity type”. Tukey HSD post-hoc tests ($p = 0.05$) were applied to find specific differences between years and cultivars. For each replicate, the apparent infection rate (AIR), which represents the rate of disease increase during the epidemic part of disease development, was calculated as the slope of the linear regression line of logistic transformed severity data. From the estimated regression equation the number of days until 1% disease from the first observation in the trial was evaluated.

Results

In 2012, early maturity cultivars emerged by 28–29 May, medium early cultivars by 30 May and medium late and late cultivars by 3 June. In 2013, sprouts of tubers emerged irregularly and there were differences between cultivars of the different maturity groups. Emergence was first recorded during 28–31 May in the early cultivar ‘Maret’ and surprisingly in the late ‘Anti’. During 1–2 June, early cultivars ‘Ranomi’ and ‘Romie’, medium ‘Madeleine’, ‘Mariska’, ‘Teele’ and medium late ‘Bellefleur’ emerged. The last to emerge, during 4–6 June were early cultivar ‘Esmee’, medium ‘Toluca’, medium late ‘Excellency’ and ‘Manitou’ (huge variation from 31 May to 6 June).

Development of foliar blight. Late blight infected cultivars in both years enabled evaluation of foliar blight. Overall, 2012 was very favourable for late blight development and spread onto potato fields. The weather in June was cool with sufficient rainfall and hence the first late blight early outbreaks in the neighbourhood were already recorded at the end of June. At the beginning of July, late blight had already spread to allotments and small fields of susceptible early potato cultivars in southern Estonia. However, at the beginning of July the rainfall was low (Table 1), but the rainfall on 11 and 12 July favoured the pathogen, with further late blight infection in the observation trial on 13 July and afterwards (Fig. 1A). On 13 July, late blight infection was recorded on most cultivars, except ‘Toluca’ and ‘Anti’. However, the infection rate was very low at approximately 0.1–0.5% of total foliage surface in trial plots. A week later, on 20 July, the first late blight spots were noticed on foliage of the late cultivar ‘Anti’, but the disease developed very slowly, still progressing three weeks later, on 13 August.

On early cultivars ‘Ranomi’, ‘Esmee’ and ‘Romie’ late blight developed very intensively from 20 July and continued due to favourable weather conditions with most foliage destroyed by the end of July (Fig. 1A). This rapid blight development was favoured also by frequent foggy nights in July with dense dew, leaf surface remaining moist for hours. The local early cultivar ‘Maret’ from ECRI had significantly slower late blight development after 30 July ($F_{3,8} = 10.43$, $p < 0.005$; Tukey HSD test) compared to the Dutch cultivars, and disease infection reached 100% more than 10 days later (Fig. 1A). Therefore, ‘Maret’ had the longest growing period (81 days) compared to the other early potato cultivars. In medium early cultivars ‘Mariska’ and ‘Teele’ late blight infection was found on 13 July, in the ‘Madeline’ three

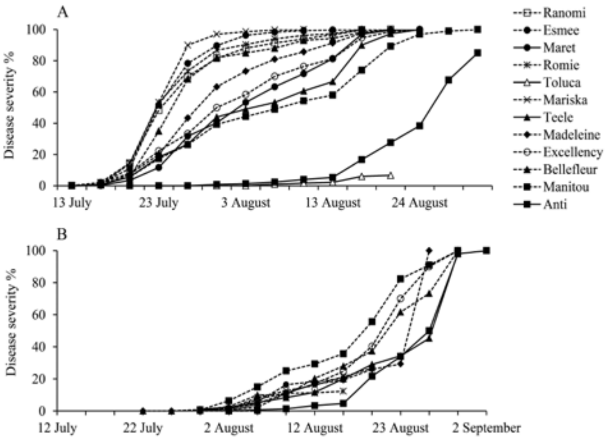


Figure 1. Development of foliar late blight disease in the tested potato cultivars in 2012 (A) and 2013 (B)

days later on 16 July. The most susceptible medium early cultivar to late blight was 'Mariska', where late blight developed very intensely after 20 July and most of the foliage (90%) was destroyed within seven days by 27 July (Fig. 1A). Thus, the growing period of 61 days remained very short, even shorter than that of the early maturity cultivars. In cultivars 'Teele' and 'Madeleine', late blight development progressed after 23 July. Disease pressure was more moderate in the Estonian medium early cultivar 'Teele' at the pathogen epidemiological phase ($F_{3.8}$ = 275.6, p < 0.001, Tukey HSD test). Most foliage was destroyed in the cultivar 'Madeleine' by 13 August and in the 'Teele' by 17 August leaving only 82 growing days, which was barely sufficient for yield development. Late blight development in the 'Toluca' differed completely from the disease development in all other cultivars with disease outbreak a few weeks later and with remarkably slower late blight development (Fig. 1A). The first late blight infection of just a few spots in the 'Toluca' was noted 17 days later on 30 July and subsequent progression of disease was significantly slower than in other medium early cultivars ($F_{3.8}$ = 50.74, p < 0.001, Tukey HSD test). Cultivar 'Toluca' was able to maintain the majority of its foliage until the end of its growing period of 86 days. By the end of its vegetation period, late blight infection was observed only for 6.7% of the foliage area.

Late blight development in medium late and late cultivars was similar to that in medium early cultivars at the beginning of development and later during the pathogen epidemiological phase. Significant differences in late blight development between medium late cultivars were found ($F_{3.161}$ = 14.33, p < 0.001, Tukey HSD test). The most susceptible medium late cultivar 'Bellefleur' had its foliage destroyed already by 10 August. Therefore, the growing period remained rather short at 69 days. Late medium cultivars were infected at the same time on 13 July as early and medium early, except for the late cultivar 'Anti', in which the infection was found a few weeks later on 30 July. The 'Anti' had significantly slower disease progression after 20 July ($F_{3.8}$ = 8.35, p < 0.001, Tukey HSD test) compared to medium late cultivars. However, after 13 August late blight progressed intensively and by 24 August 38% of potato foliage was infected. After the heavy rainfall on 24 and 27 August, late blight spread very intensively and by 31 August 85% of the foliage was dead (Fig. 1A).

Overall, the growing season 2013 was drier compared to the long term average, especially in June and also during a twenty-day period in July (Table 1). June and August temperatures were warmer than the long term averages. These conditions were suitable for a potato early blight (*Alternaria* spp.) outbreak. In our trial, early blight was first noticed on 12 July on the lowest leaves of the early cultivar 'Ranomi'. A week later on 19 July, the early 'Romie', medium early 'Madeleine', 'Mariska' and 'Teele' and medium late 'Excellency' were infected. Other cultivars were infected on 22 and 29 July, although the infection rate remained at a very low level. The most susceptible cultivars to potato early blight were the local medium early 'Teele' and Dutch medium late 'Excellency', in which approximately 20–21% of foliage was infected by 19 August. However, the weather conditions improved for late blight by increased rainfall in the last ten-day period of July. The development of early blight succumbed to late blight while it destroyed the foliage of most cultivars rapidly.

The first late blight infection was recorded in this trial on 22 July in the medium early 'Madeleine' and medium late 'Bellefleur' (Fig. 1B). On 29 July, the first late blight infection was observed in the early 'Esmee', medium early 'Mariska', 'Teele', medium late 'Excellency' and 'Manitou', and on 2 August in early 'Ranomi', 'Romie', 'Maret' and late 'Anti'. Hereafter, late blight development continued at moderate rate and more intensive progression started after 16 August. In the early 'Ranomi' the growing period lasted 68 days until 9 August. In other early 'Romie', 'Esmee' and 'Maret' the growing period was more or less of sufficient duration (Table 2), and plants dried off before late blight could kill the foliage (Fig. 1B). In the medium early 'Toluca' late blight infection was not noticed; however, the growing period remained very short 63 days (Table 2).

Significant differences in late blight development between medium late cultivars were found ($F_{3.161}$ = 14.33, p < 0.001, Tukey HSD test). In the 'Mariska' by the end of the growing period on 19 August late blight infection rate was 27%, and in the 'Madeleine' on 23 August the late blight infection was 29%. The local cultivar 'Teele' had the longest vegetation period of 91 days and foliage was finally destroyed by late blight by 31 August. In medium late and late cultivars the late blight development was similar to that in medium early cultivars at the beginning of infection; however, after 6 August disease developed more intensively in 'Excellency', 'Bellefleur' and 'Manitou' compared to medium early cultivars (Fig. 1B). By contrast, in the late 'Anti' late blight infection started 10 days later and disease developed more slowly after 9 August compared to the other three cultivars (Fig. 1B) and had the longest growing period of 96 days (Table 2). The weather conditions became more favourable for late blight from the end of July and in August, thus the disease damaged most the late medium and late cultivars by the end of August (Fig 1B).

Evaluation of RAUDPC and estimated scale values. The growing year 2012 was very favourable for late blight foliar resistance evaluation (Table 2). However, by contrast, the 2013 growing season was less favourable for late blight. Analysis of RAUDPC data suggested that the estimated scale values should be not used to make further considerable conclusions. The foliar resistance of different cultivars varied between 3.0 and 9.0 points (Table 2). Potato cultivars with foliar resistance of 1.0–3.0 points qualify as very susceptible to late blight, 3.1–5.0 points as susceptible to late blight, 5.1–7.0 points as relatively late blight resistant and 7.1–9.0 as resistant to late blight, according to Hansen et al. (2005). Eight potato cultivars from the "Agrico" and two from the ECRI scored as susceptible to late blight (3.0–4.6 points). Most resistant were the medium 'Toluca' from the "Agrico" in 2012 and 2013 and the late 'Anti' from the ECRI in 2012 (Table 2).

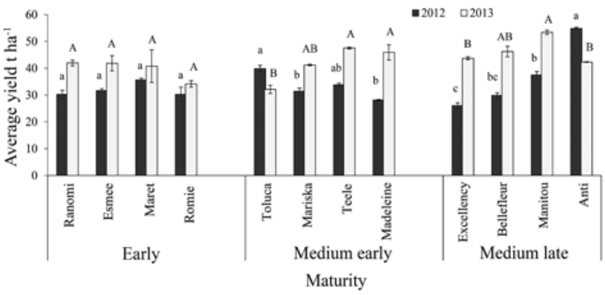
The pre-existing scale values were similar to estimated mean scale values with a little fluctuation,

Table 2. Growing period, mean relative area under disease progression curve (RAUDPC), estimated scale values and pre-existing scale values of potato cultivars evaluated for foliar resistance to late blight pathogen in field conditions in Estonia in 2012 and 2013

Cultivar	Maturity	Growing period		RAUDPC		Estimated scale values			Pre-existing scale values
		2012	2013	2012	2013	2012	2013	mean ± SD	
Ranomi	early	77	68	0.74	0.62	3.3	3.1	3.22 ± 0.12	3
Esmee	early	70	72	0.77	0.42	3.2	3.8	3.51 ± 0.35	3
Romie	early	70	77	0.76	0.40	3.2	3.9	3.59 ± 0.36	3
Maret	early	81	74	0.58	0.62	4.4	3.1	3.75 ± 0.64	4
Toluca	medium early	82	63	0.19	0.00	7.7	9.0	8.35 ± 0.65	9
Mariska	medium early	61	80	0.79	0.36	3.0	4.1	3.59 ± 0.55	4
Madeleine	medium early	82	84	0.66	0.30	3.9	4.4	4.15 ± 0.28	4
Teele	medium early	82	91	0.55	0.25	4.6	4.7	4.63 ± 0.05	5
Excellency	medium late	77	86	0.61	0.26	4.2	4.6	4.41 ± 0.23	5
Bellefleur	medium late	69	91	0.72	0.32	3.5	4.3	3.89 ± 0.41	4
Manitou	medium late	81	86	0.51	0.40	4.9	3.9	4.41 ± 0.47	4
Anti	late	88	96	0.15	0.21	8.2	4.9	6.54 ± 1.67	7

except for the cultivar ‘Anti’ with 1.7 in 2013. However, in 2012 with high late blight pressure ‘Anti’ showed very high resistance to late blight (Table 2). Accordingly, the ECRI cultivar ‘Anti’ is highly resistant or immune to foliar late blight and little susceptible to tuber blight. RAUDPC is a standardized relative area under the disease progression curve. In 2013, cultivar ‘Toluca’ was totally immune to foliar late blight and, in 2012, showed high foliar resistance. RAUDPC values were on average higher in 2012 and lower in 2013 (Table 2). The results are strongly influenced by the different weather conditions. The results of foliar resistance with RAUDPC and estimated scale values are not comparable between years because of the differences of seasonal weather conditions.

Late blight effects on tuber yield. In 2012, the overall crop yield was on average 34.1 t ha^{-1}. The highest yield was recorded for the late ‘Anti’ and the medium early ‘Toluca’ (Fig. 2), being as good as most late blight resistant cultivars in this trial. The local ‘Maret’ had the highest yield (35.6 t ha^{-1}) in the early cultivar maturity group. This was explained by its longest growing period of 81 days due to higher late blight resistance. However, statistically significant differences in yield between early cultivars were not found ($F_{3.8}$ = 0.84, p = 0.508). The average yield of medium early cultivars ranged from 28.2 to 39.9 t ha^{-1}. Significant differences were found in yield between medium early cultivars ($F_{3.8}$ = 10.86, p < 0.001). The highest yield of 40 t ha^{-1} was recorded in the cultivar ‘Toluca’, which also had the longest growing period of 82 days. Cultivars ‘Teele’ and ‘Madeline’ had the same duration of growing period, but their yields remained 3–4 t ha^{-1} lower. Even though ‘Mariska’ had the shortest growing period of 61 days, its yield was similar to that in other medium early cultivars, except for the ‘Toluca’.



Note. Different letters above the maturity columns indicate statistically significant differences (*ANOVA*, Tukey HSD test at p < 0.05).

Figure 2. Average tuber yield of potato cultivars from breeding company “Agrico” and Estonian Crop Research Institute (ECRI) in 2012 and 2013

The crop yield in medium late cultivars differed considerably ($F_{3.8}$ = 54.51, p < 0.001). Late cultivar ‘Anti’ produced the highest tuber yield of 55 t ha^{-1}, which was 29 t ha^{-1} higher than that of ‘Excellency’ and 24 t ha^{-1} higher than ‘Bellefleur’.

In 2013, late blight infection started in the field trial in ‘Madeleine’ and ‘Bellefleur’ 9 days later and in the rest of the cultivars 16 days later than in 2012 and the overall disease pressure was lower (Fig. 1B). Thus, the overall crop yield in 2013 (on average 42.6 t ha^{-1}) turned out higher with 8.5 t ha^{-1} compared to the previous year ($F_{1.70}$ = 20.50, p < 0.0001). The highest tuber yields were obtained in medium late ‘Manitou’ (53.4 t ha^{-1}), ‘Bellefleur’ (46.2 t ha^{-1}) and in medium ‘Teele’ (47.5 t ha^{-1}) and ‘Madeleine’ (45.9 t ha^{-1}) (Fig. 2). The lowest yield was produced by early ‘Romie’ (34.1 t ha^{-1}) and the medium early ‘Toluca’ (32.1 t ha^{-1}). No significant differences in tuber yield of early potato cultivars were found ($F_{11.24}$ = 2.03, p = 0.071). For early cultivars the growing period was on average 73 days, which is barely sufficient for the early maturity group, 70–85 days. There were differences in the yield among medium early cultivars ($F_{3.8}$ = 5.97, p = 0.019), where the highest yield was produced by local ‘Teele’. Sufficient yield was also obtained in the Dutch cultivars ‘Madeline’ and ‘Mariska’. The lowest yield was in the Dutch cultivar ‘Toluca’ with 32.1 t ha^{-1}, i.e. 32% lower than in ‘Teele’. The growing period of cultivars ‘Mariska’, ‘Madeleine’ and ‘Teele’ was on average 85 days, barely enough to achieve good tuber yield. On medium late and late cultivars, ‘Manitou’ gave the highest yield with 53.4 t ha^{-1}. Other cultivars produced tuber yields of over 40 t ha^{-1}. The average growing period in medium late and late cultivars was 90 days that is approximately 2–3.5 weeks shorter than needed, although they produced on average 9.4 t ha^{-1} more than last year.

Discussion

Development of foliar late blight differed considerably in the twelve potato cultivars tested in the field trial. The two growing seasons were contrasting. Overall, 2012 was the more favourable for late blight development with the first infection starting nine days, and, in most cultivars, 16 days earlier than in 2013. Disease development was also faster in 2012; the majority of the foliage of susceptible cultivars was destroyed within 12–15 days. Only two cultivars, ‘Anti’ and ‘Toluca’, were classified as highly resistant to foliar blight, ‘Teele’ and ‘Manitou’ were moderately foliar resistant whereas all other cultivars were susceptible. However, foliar late blight resistance of the studied cultivars was not comparable among the two trial years. Despite the unfavourable weather conditions for

P. infestans in 2013 in June, July and in the first ten days of August, late blight was still able to severely damage the foliage and destroy it prematurely in most cultivars. This study clearly indicates that in spite of unfavourable conditions for the pathogen, late blight is able to destroy potato foliage in most cultivars before the end of the growing season in northern Baltic conditions. This is a result of the local heterogeneous populations of *P. infestans* (Runno-Paurson et al., 2016), probably with strains adapted to a wider range of humidity conditions (Lehsten et al., 2017). Consequently, late blight control has become more challenging requiring even more intensive chemical input as in other European countries, such as in The Netherlands and Belgium, where 14 sprays and in the UK where 10 sprays per season on average are applied (Cooke et al., 2011; Hansen et al., 2015). However, using cultivar resistance as part of the control strategy for late blight has not lost its relevance. Although several blight resistant potato cultivars are available, they have not been accepted by potato producers due to some unwanted traits and therefore are not widely cultivated (Forbes, 2012). Thus, it is a continuous challenge to find late blight resistant cultivars with persistent field resistance and with the traits desired by potato growers.

Estonian potato cultivars were included in this research to compare their resistance to late blight and yield and to liken them to the Dutch cultivars. These local cultivars have been bred specifically for cultivation in northern Baltic region conditions and are moderately resistant or resistant to potato late blight. This two-year trial partly confirmed our hypothesis. Under high late blight pressure in 2012, the late 'Anti' scored as highly late blight resistant based on estimated scale value of foliar resistance and had the highest yield of all tested cultivars. The 'Anti' has been available since 1997, has not lost its high blight resistance and shows the same stability of high field resistance to foliar late blight as it did ten years ago (Hansen et al., 2005). The high blight resistance of 'Anti' originates from a multiple cross with *Solanum demissum* and *S. infundibuliforme*. However, although 'Anti' has several valuable traits, its late maturity is not a desired trait for growers (Tähtjärv, 2016). Likewise, local cultivars 'Maret' and 'Teele' had the highest foliar resistance scores of their maturity groups, being classified as moderately resistant. The 'Teele' contains in its pedigree four wild *Solanum* species *S. andigenum*, *S. demisissum*, *S. chilense* and *S. vernei* giving it moderate field resistance to potato late blight, which persisted even under heavy late blight pressure as observed in 2012 (Tähtjärv, 2016). Also, 'Maret' and 'Teele' achieved the highest tuber yield of their maturity groups, 'Maret' in 2012 and 'Teele' in 2013, although differences were not significant. Thus, overall local ECRI cultivars did not exceed imported Dutch cultivars and remained quite at the same level concerning tuber yield and foliar late blight resistance of different maturity groups with some exceptions. Cultivars with late blight pathogen race-specific resistance do not work anymore as the pathogen has overcome existing resistance genes. Therefore, more attention has been paid towards breeding cultivars with non-race-specific resistance like horizontal, partial, quantitative or field resistance (Cooke et al., 2011). Nowadays, the Estonian potato breeding program is aimed at breeding new cultivars with durable late blight field resistance (Tähtjärv, 2016).

In this study, potato early blight (*Alternaria* spp.) infection was recorded in 2013. The growing season 2013 was overall drier and warmer than 2012 as well as the long-term average. These conditions favoured development and spread of early blight before the late blight outbreak. June and the first twenty days of July were especially dry. However, based on results of this trial, most cultivars from the "Agrico" were quite resistant to early blight. Two cultivars out of twelve, 'Teele' from the ECRI and 'Excellency' from the "Agrico", were found to be susceptible to early blight. Recently, the increasing importance of early blight disease in European potato fields, including the northern region has become apparent (Leiminger et al., 2015; Runno-Paurson et al., 2015 b; Odilbekov et al., 2016). Thus, it is important to select more carefully cultivars that are not susceptible to early blight. Recent studies in the northern Baltic region have confirmed that, besides the susceptibility to potato late blight, early blight can cause severe infection and defoliation, and thus susceptible cultivars must be avoided in sustainable cultivation in conventional and organic farming systems. When early blight pressure is high, three or four occasional sprays with slightly effective fungicides do not give sufficient control and therefore, an efficient and carefully planned early blight control strategy is needed (Runno-Paurson et al., 2015 b). Furthermore, the predicted increase in the number of warmer and drier summers could increase problems due to *Alternaria* spp. pathogen damage and early blight control in northern regions (Pulatov et al., 2015).

Considerable differences in crop yield were found between the two growing seasons. A direct connection between cultivar late blight resistance and yield reduction was found in 2012. In 2012, average tuber yield remained low due to the early late blight outbreak when disease pressure was heavy and the foliage of early cultivars from the "Agrico" was destroyed already within 10 days. Only the two late blight resistant cultivars 'Toluca' and 'Anti' differed from the others and produced higher yields. In contrast in 2013, late blight infection did not have a great influence on potato yield in early, medium early or medium late cultivars. Potato late blight infection in the field trial started more than two weeks later and disease pressure was lower compared to the previous season, and therefore the overall crop yield in 2013 was on average 20% higher than in the previous year. Although the length of growing period in medium early and medium late cultivars was longer in 2013 than in 2012, it was still on average 2–4 weeks shorter than needed. Tuber yields were significantly lower of 'Toluca' and 'Anti' compared to the previous year. In 2013, 'Toluca' had the lowest tuber yield of all tested cultivars. This is apparently explained by the short growing period, being 17–28 days shorter than for other medium early cultivars. The short growing period of 'Toluca' was apparently caused by high sensitivity and stress due to excessive dryness. These results confirm previous outcome of late blight observation trials, where plants of the 'Toluca' suffered severely and more in growing seasons with dry weather conditions than other potato cultivars in the northern Baltic region (Runno-Paurson et al., 2013).

The 'Toluca' was included in the trial to monitor its foliar late blight resistance in northern Baltic conditions to test the suitability of this medium early cultivar as part of sustainable late blight control strategy. In 2012, the 'Toluca' entirely fulfilled these hopes having high foliar blight resistance; the blight favourable weather conditions did not lower upper yield compared to most other cultivars, which were susceptible to late blight. Thus, based on the results of 2012 growing season 'Toluca' could be recommended for growing without any fungicide input. The 'Toluca' is described as totally immune to foliar late blight, containing the *Bulbo* gene *Rpi-blb2* from *S. bulbocastanum*, which is vertical and single, but also the horizontal resistance level of other wild *Solanum* species, which has not been measured (Runno-Paurson et al., 2013). This cultivar has shown excellent high resistance values in several trial sites across Europe, but also some ambivalent and unstable results in some seasons as reported in 2009 in Poland, Scotland and in 2010 in Estonia. In Estonia, 'Toluca' has been tested in trials since 2009, showing quite a high late blight resistance level, but not immunity to the pathogen (Runno-Paurson et al., 2013).

However in 2013, when late blight infection was not recorded in 'Toluca', the cultivar tolerated the dry weather conditions poorly and its tuber yield remained significantly lower than that in all other cultivars. The local potato agrotechnology in the dry weather conditions seems a weak point of this valuable Dutch cultivar, and unfortunately 'Toluca' could not offer an advantage of late blight resistance and yield remained low. Indications about plants stress of 'Toluca', believed to be caused by drought, have been previously reported (Runno-Paurson et al., 2013). In larger areas, 'Toluca' has been noted to have average or lower yields and to be unstable in different growing seasons compared to cultivars selected for seed multiplication and grown in larger areas (A. Einola observations). Although, the 'Toluca' has two desirable traits, medium early maturity and high foliar late blight resistance, because of its above mentioned weak points, it is not selected for wider cultivation and is no longer imported for the Estonian market (personal communication with "Agrico's" Estonian representative, 2016).

This work also points out the need for modification of existing agrotechnologies with irrigation systems to be used when there is a lack of precipitation in certain growing seasons. To date, use of irrigation systems is not common practice in the northern Baltics and this is the main reason why higher yields remain at 40–50 t ha^{-1} (Tartlan, 2014). Dry weather occurred in 2013, but was also observed in several recent seasons 2010 and 2011 (Runno-Paurson et al., 2013). In dry and hot periods plants are under stress and considerable part of yield is not achieved (Bita, Gerats, 2013). Hence, more investment in irrigation technologies for Estonian potato production is needed in dry years. Furthermore, the frequency of hot summers has increased in northern Europe (Kocmánkova et al., 2010; Pulatov et al., 2015), implying that the need for irrigation is expected to increase in the future.

In conclusion, our findings confirmed that the 'Toluca' was highly late blight resistant in the season with heavy pressure of the pathogen, but the productivity of this cultivar is compromised in warm summers in northern Baltic region conditions. Despite this, this late blight resistant cultivar should be exploited more widely using optimized agrotechnologies in organic farming in Baltic region.

Conclusions

1. The results of our study indicated that despite unfavourable conditions for pathogenesis, late blight destroyed potato foliage in most cultivars before the end of the growing season in northern Baltic conditions. Late blight in early cultivars was responsible for yield losses up to 5 t ha^{-1}, in medium early – up to 10 t ha^{-1} and in medium late – up to 20 t ha^{-1}.

2. Only two cultivars: 'Anti' from the Estonian Crop Research Institute (ECRI) and 'Toluca' from the Dutch breeding company "Agrico", had high foliar late blight resistance. Late blight in these cultivars appeared very late, and estimated yield losses were only 2 t ha^{-1}.

3. Although late blight infection was not recorded in 2013, the 'Toluca' tolerated the dry weather conditions poorly and therefore its tuber yield remained significantly lower than that in all other cultivars.

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Įvairių veislių bulvių atsparumo marui įvertinimas Šiaurės Baltijos šalių sąlygomis

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Santrauka

Tyrimo metu siekta įvertinti pasirinktų estiškų ir užsieninių veislių bulvių atsparumą marui, nustatyti jų derlingumo potencialą ir perspektyviausias veisles, tinkančias auginti Šiaurės Baltijos regione. Buvo iškelta hipotezė, kad vietinių veislių bulvės yra atsparesnės marui (*Phytophthora infestans*) ir duoda didesnį derlių dėl didesnio atsparumo šiam patogenui. Bulvių maro lauko eksperimentas vykdytas 2012 ir 2013 metais Einola ūkyje, Tartu apskrityje, Estijoje. Eksperimentų vykdymo laikotarpiu buvo ištirta ir palyginta dvylikos veislių bulvės: devynios iš Olandijos selekcinės kompanijos “Agrico” ir trys iš Estijos žemės ūkio augalų tyrimų instituto (ECRI). Buvo tirtos keturios ankstyvos bulvių veislės: ‘Ranomi’, ‘Esmee’, ‘Romie’ bei ‘Maret’, keturios vidutinio ankstyvumo: ‘Toluca’, ‘Mariska’, ‘Madeleine’ bei ‘Teele’, ir keturios vidutinio vėlyvumo / vėlyvos: ‘Excellency’, ‘Bellefleur’, ‘Manitou’ bei ‘Anti’. Iš jų tik veislių ‘Anti’ ir ‘Toluca’ bulvės yra labai atsparios marui.
Tyrimo duomenimis, nepaisant patogenui nepalankių sąlygų, Šiaurės Baltijos šalių sąlygomis bulvių maras daugumos tirtų veislių bulvienojus gali sunaikinti dar nepasibaigus vegetacijos laikotarpiui. Tai atskleidžia *P. infestans* vietinių populiacijų genetinis heterogeniškumas, kuris galbūt yra susijęs su padermėmis, prisitaikiusiomis augti esant didelei drėgmei. 2012 metais, kai oro sąlygos buvo palankios marui plisti, veislės ‘Toluca’ bulvės buvo jam atspariausios, nes gautas didžiausias gumbų derlius, lyginant su kitų veislių bulvėmis, kurios buvo jautrios arba labai jautrios marui, smarkiai sumažinusiam jų derlių. 2013 metais bulvių maras dėl meteorologinių sąlygų (buvo sausa) neplito, ir veislės ‘Toluca’ bulvių gumbų derlius buvo mažesnis nei kitų tirtų veislių. Be to, 2013 metais buvo užregistruotas bulvių sausligės (*Alternaria solani*) protrūkis, kuriam jautriausios buvo dviejų veislių bulvės: vietinės ‘Teele’ ir olandiškos ‘Excellency’.

Reikšminiai žodžiai: atsparumas, gumbų derlius, ligų vertinimas, maras, veislė.