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# A process-based model to forecast risk of potato late blight in Norway (The Nærstad model): model development, sensitivity analysis and Bayesian calibration

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ABSTRACT

Late blight caused by *Phytophthora infestans* is a serious, worldwide disease on potato (*Solanum tuberosum*). *Phytophthora infestans* normally reproduces in a clonal manner, but in some areas, as the Nordic Countries, sexual reproduction has become the major determinant of the population structure. To improve the late blight forecasting in Norway, the process-based Nærstad model was developed. The model includes the structure of the underlying processes in the disease development, including spore production, spore release, spore survival and infection of *P. infestans*. It needs hourly weather records of air temperature, precipitation, relative humidity, leaf wetness and global radiation. The model contained 19 uncertain parameters, and from a sensitivity analysis, 12 were detected as weakly sensitive to model outputs and fixed to a nominal value within their prior boundaries. The remaining seven parameters were detected as more sensitive to model outputs and were parameterized using maximum a'posteriori (MAP) estimates, calculated through Bayesian calibration. The model was developed based on literature combined with field data of daily observed number of lesions on trap plants of the Bintje cultivar (late blight susceptible) at Ås during the seasons 2006-2008 and 2010-2011. It was further tested on daily observed number of lesions on trap plants of the cultivars Bintje, Saturna (medium susceptible) and Peik (medium resistant) at Ås during the seasons 2012-2015. For all three cultivars, the Nærstad model improved with a higher model accuracy compared to the existing HOSPO-model and the Førsund rules that both have shown relatively good correlation with blight development in field evaluations in Norway. The best accuracy was found for Bintje (0.83) closely followed by Saturna (0.79), whereas a much lower accuracy was detected for Peik (0.66).

## 1. INTRODUCTION

Potato late blight caused by *Phytophthora infestans* Mont. (de Bary) has been and is still the most important disease on potatoes (*Solanum tuberosum*) in Norway, as in other potato producing countries (Fry et al., 2001). The pathogen is very destructive and can easily be spread by airborne sporangia produced under humid conditions (Harrison, 1992). Major pathogen population changes have occurred during the last decades from a mainly clonal propagating population to a sexual reproducing population in some areas, including the Nordic Countries (Brurberg et al., 2011).

Potato production is highly reliant on fungicides despite pressure from the governments, supermarkets and consumers to reduce the input of pesticides. In average, the potato area in Norway is sprayed 5.6 times each year (2000-2005) to protect against late blight (Sæthre et al., 2006). However, the number of treatments in Norway ranged from 3 to 8, depending on year and location (Cooke et al., 2011). Later, even more treatments were carried out in some seasons and locations (unpublished). To optimize the effects of protectant fungicides, it is important that they are applied shortly before the infection occurs.

It has long been recognised that potato late blight epidemics are highly dependent on weather conditions (Crosier, 1934) and that forecasting based on weather can be used to time fungicide treatments. Some forecasting models are included in Decision Support Systems (DSS) and are made available to farmers in Europe (Hansen et al., 2009; Cooke et al., 2011; Hansen et al., 2017) and in other parts of the world

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(Wharton et al., 2008; Fry, 2010). In Norway, potato late blight forecasting was initiated by the Førsund rules in 1957 (Førsund and Flaatten, 1959). The criterion was later adjusted according to results from validation trials (Hermansen and Amundsen, 2003).

Many late blight forecasting models, as the HOSPO-model (Hansen et al., 2006) require several hours with observed relative humidity above 90% and often combined with a minimum temperature threshold of 10 °C to alert risk of infection (Wallin and Hoyman, 1954; Smith, 1956; Bruhn and Fry, 1981; Winstel, 1993; Ullrich and Schrödter, 1966). The Førsund rules differ from most other late blight forecasting models in not requiring a long humid period. Still, fungicide treatments both according to the HOSPO-model and the Førsund rules has shown relatively good results regarding blight control in field evaluations in Norway (Hermansen and Nærstad, 2009).

To further improve the late blight forecasting in Norway, the Nærstad model was developed as a process-based model. The model describes the underlying processes in the disease development and it was developed based on accumulated knowledge from potato late blight research (reviewed by Schepers (1998) and Harrison (1992)) and from knowledge gained from field experiments. The model requires hourly inputs of five weather variables (air temperature, precipitation, relative humidity, global radiation and leaf wetness) and it contain 19 uncertain parameters.

Both the HOSPO-model and the Førsund rules are simpler models that follow an empirical approach by relying on correlative relationships together with a mechanistic understanding. Contrary, the process-based Nærstad model is more comprehensive and describes the mechanisms in the underlying system. Process-based models are increasingly used to simulate the interactions between vegetation and environment. In addition to forecast risk, such models can derive a better understanding of the underlying system and should work well in all situations through a proper parameterization.

Calibration is the process of finding the best estimates for the uncertain model parameters, using data from the underlying real-world system. The Bayesian calibration approach improves on more traditional calibration approaches, such as maximum likelihood, by automatically including uncertainty quantification. The method allows for prior information about the parameters and conclusions are made conditional on the data. Model complexity in combination with high dimensional parameter spaces makes the approach computationally demanding, and it is therefore still rarely used for such models (Hjelkrem et al., 2017; Gouache et al., 2013; Minunno et al., 2013; Thorsen and Höglind, 2010; van Oijen et al., 2005a, van Oijen et al., 2005b). A common strategy that increases the efficiency of model calibration, is to reduce the model complexity through a sensitivity analysis (Hjelkrem et al., 2017; Oomen et al., 2016). The parameters detected as weakly sensitive, can be fixed to a nominal value within their prior boundaries, without strongly affecting model output. Hence, only the remaining subset of strongly sensitive parameters can be selected for model calibration. From Hjelkrem et al. (2017), a higher error term may be achieved when fixing too many of the parameters. Also, such a simplification will cause underestimation of parameter uncertainty in model output, since the parameter values that are fixed to a nominal value are not known for certain (Hjelkrem et al., 2017).

This study gives a detailed presentation of the Nærstad model. The model complexity was reduced through a sensitivity analysis, and the remaining sensitive parameters were parameterized through Bayesian calibration. Finally, the model was tested on individual field data, and compared with the existing HOSPO-model and the Førsund rules.

## 2. MATERIAL AND METHODS

### 2.1. Field experiments

In 2006 to 2015 (except 2009), potato field plots (12 × 12 meter) were established in Ås in Norway, with alternating rows of three potato cultivars: the late blight susceptible cv. Astrix, the medium susceptible cv. Saturna and the medium resistant cv. Peik (Figure 1). The plot was inoculated in the beginning of July with a spore suspension. The spores were produced by spray inoculating with a spore suspension produced on detached potato leaves of cv. Bintje, grown in pots in the greenhouse. The potato leaves were incubated on a grid suspended over wet tissues in a tray covered with a plastic bag and put in a growth chamber with 16 hours light/ 8 hours dark at 15-16 °C for one week. Spores from sporulating leaflets were rinsed off with distilled water. A mixture of two to three *P. infestans* isolates, A1 mating type, collected in 2003 and characterized in Brurberg et al. (2011), Lehtinen et al. (2008) and Lehtinen et al. (2009) were used as inoculum. After that, the isolates were kept in liquid nitrogen at -196 °C and thawed every year before inoculation. Sporangia were rinsed from potato leaves (cv. Bintje grown in greenhouse) in distilled water and density determined using a haemocytometer. The potato field plot was inoculated with 500 sporangia/ml water and 20 ml spore suspension/plant in the evening and covered with thin fleece (Noragryl 17 g/m$^2$), that was removed the day after. A Burkard volumetric spore trap (600 L air/h) (Burkard Manufacturing Co Ltd, Rickmansworth, Hertfordshire, UK) and trap plants were placed in an open space of 3 × 3 meters in the centre of the potato field plot to catch *P. infestans* spores (Figure 1). The open space in the centre of the plot was framed with potato plants of a clone with very high level of late blight resistance (N-85-13-18) to avoid direct contact between the inoculated potato plants and the trap plants. Potato plants of cv. Bintje (late blight susceptible) grown in pots in the greenhouse were used as trap plants. The trap plants were grown at 15-18 °C and 16 hours light per day for 4-5 weeks from potting of seed tubers and trimmed down to three stems per pot. Seed tubers were produced in the greenhouse and potted each week so that all trap plants were approximately at the same age and size when exposed in the field. The first trap plants were placed in the field approximately 7 days after inoculation when the first late blight lesions were visible in the inoculated field plot.

A set of trap plants (four plants in 2006-2008 and two plants in 2010-2015) was put out every day at 3 pm and collected at 3 pm the following afternoon, which is normally the driest time of the day, and hence the time that interferes least with the infection process. The plants were then

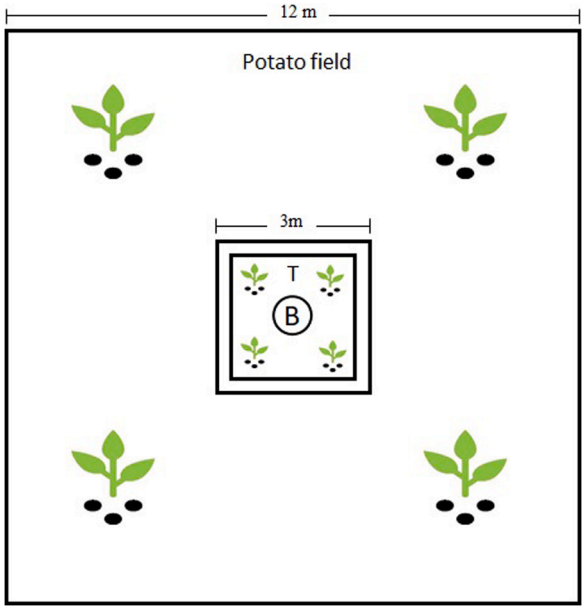


**Figure 1.** Field experiment with a Burkard spore trap (B) in the center of the field, trap plants (T) of potted potato plants (cv. Bintje) exchanged every day at 3 pm and with a frame of late blight resistant potato plants, all inside a potato field with alternating rows of three cultivars (cv. Astrix, cv. Saturna and cv. Peik).

incubated under dry conditions for one week in a growth chamber with 16 hours light (low light intensity)/ 8 hours dark at 15-18 °C. The last two days of the incubation the plants were sealed with plastic bags to promote lesion development and to prevent dispersal of spores. The plants were taken out of the incubation room before the plastic bags were removed. Late blight infection on the trap plants was recorded as number of lesions per plant 7 days after being removed from the field. The maximum number of lesions recorded per trap plant was limited to 50. Number of lesions was used to describe the blight risk during the 24 h period which the plants were exposed in the field.

The Burkard spore trap collect spores by sucking air through an orifice about 40 cm above ground. Spores and other particles in the airstream stuck to an adhesive tape (Melinex-tape coated with a layer of a mixture of white Vaseline (9 g), liquid paraffin (1 g) and toluene (100 ml)). The exposed area of the tape moves 2 millimetres per hour (one revolution per week), and the tape was replaced weekly. The exposed tape was stained with lactofuchsin, mounted on slides, and hourly spore counts were recorded.

### 2.2. Weather data

Weather data was provided by Agrometeorology Norway (2019). Hourly weather records of air temperature 2 m above ground (T; °C), precipitation (P; mm), short wave global radiation (GR; Wh/m$^2$) and leaf wetness on a sensor plate facing north with an inclination angle of 30 degree at 2 m (LW; min/hr) was measured at Ås weather station approximately 1 km from the field. Additionally, relative humidity 2 m above ground (RH; %) was measured at Åsbakken weather station, situated approximately 4 km from the field.

Vapour pressure deficit (vpd; Pa) is the difference between the amount of moisture in the air and the moisture the air can hold when saturated. Saturated vapour pressures were estimated from measured air temperature according to (Goff and Gratch, 1946), as recommended by the World Meteorological Organisation (2012). The actual vapour pressure was derived from the estimated saturated vapour pressure and the measured relative humidity (Perry and Green, 1997).

### 2.3. Model description

A dynamic process-based model was developed to predict the risk of late blight development. The model assumes that inoculum is present and describes how weather affects the different biological steps in the disease cycle. The model consists of sub-models, describing the steps in the disease cycle which are spore production, spore release, spore survival, spore infection and risk of blight development. The model consists of 19 uncertain parameters, a priori described by beta distributions with boundaries and modal value given in Table 1. Additionally, the model requires input of hourly weather data (air temperature, precipitation, relative humidity, global radiation and leaf wetness).

#### 2.3.1. Spore production

To produce spores, *P. infestans* needs a long humid period (Crosier, 1934, Schröter and Ullrich, 1967, Rotem et al., 1978, Harrison and Lowe, 1989). Free water is not required for sporangia to be produced, but the laminar layer needs to be saturated (Harrison and Lowe, 1989). Crosier (1934) observed sporangia formation in the temperature range from 3 to 26 °C. Accordingly, a spore producing hour (*SPH*) is here present if the temperature sum of humid hours (TSHH) exceeds a threshold value ($TSHH_{thres}$) (Equation 1).

$$\boldsymbol{SPH}(t) = \begin{cases} 1 & \textit{if } \boldsymbol{TSHH}(t) \geq \boldsymbol{TSHH}_{thres} \\ 0 & \textit{else} \end{cases} \quad (1)$$

Where $TSHH_{thres}$ is an uncertain parameter ($\theta_1$) and the variable *TSHH* defined in Equation 2.

**Table 1**
Prior parameter description for the Nærstad model. Beta distributions are used, with $\theta_i^{min}$ and $\theta_i^{max}$ representing the lower and upper boundaries and $\theta_i^{modal}$ represents the modal value of the parameter number i.

| Parmeter | Name | Unit | Equation | $\theta_i^{min}$ | $\theta_i^{max}$ | $\theta_i^{modal}$ |
|---|---|---|---|---|---|---|
| **Spore production** | | | | | | |
| $\theta_1$ | $TSHH_{thres}$ | °C | Equation 1 | 20 | 500 | 87 |
| $\theta_2$ | $vpd_1$ | Pa | Equation 2 | 100 | 500 | 220 |
| $\theta_3$ | $vpd_2$ | Pa | Equation 2 | 220 | 800 | *520* |
| $\theta_4$ | $r_1$ | - | Equation 2 | 0 | 1 | 0.75 |
| $\theta_5$ | $r_2$ | - | Equation 3 | 0.5 | 1 | 0.99 |
| $\theta_6$ | $vpd_3$ | Pa | Equation 3 | 100 | 500 | 220 |
| $\theta_7$ | $r_3$ | - | Equation 3 | 0 | 1 | 1 |
| $\theta_8$ | $r_4$ | - | Equation 3 | 0 | 1 | 0.05 |
| **Spore release** | | | | | | |
| $\theta_9$ | $\Delta GR$ | W/m$^2$ | Equation 4 | 0 | 300 | 7 |
| $\theta_{10}$ | $\Delta vpd$ | Pa | Equation 4 | 0 | 300 | 15 |
| $\theta_{11}$ | $r_5$ | - | Equation 5 | 0 | 1 | 0.6 |
| $\theta_{12}$ | $r_6$ | - | Equation 7 | 0 | 1 | 0.8 |
| $\theta_{13}$ | $r_7$ | - | Equation 7 | 0 | 1 | 0.1 |
| $\theta_{14}$ | $r_8$ | - | Equation 7 | 0 | 1 | 0.1 |
| **Infection** | | | | | | |
| $\theta_{15}$ | $vpd_4$ | Pa | Equation 8 | 100 | 500 | 180 |
| $\theta_{16}$ | $LW_1$ | min | Equation 8 | 0 | 180 | 150 |
| $\theta_{17}$ | $LW_2$ | min | Equation 8 | 0 | 60 | 42 |
| $\theta_{18}$ | $vpd_5$ | Pa | Equation 9 | 100 | 500 | 360 |
| $\theta_{19}$ | $TSWH_{thres}$ | °C | Equation 13 | 0 | 200 | 40 |

$$\boldsymbol{TSHH}(t) = \begin{cases} \boldsymbol{TSHH}(t-1) + \boldsymbol{T}(t) & \textit{if } \boldsymbol{vpd}(t) < \boldsymbol{vpd}_1 \textit{ or } \boldsymbol{P}(t) > 0 \\ \boldsymbol{r}_1 \cdot \boldsymbol{TSHH}(t-1) & \textit{if } \boldsymbol{vpd}_1 \leq \boldsymbol{vpd}(t) < \boldsymbol{vpd}_2 \\ 0 & \textit{else} \end{cases} \quad (2)$$

The model output, *TSHH*, at time *t* increases hourly with air temperature if the required vapour pressure deficit or precipitation is fulfilled. The threshold value to define a humid hour ($vpd_1$) was treated as an uncertain parameter ($\theta_2$). The calculated *TSHH* was set to zero and the temperature sum accumulation restarted when the air was dry, defined by a vapour pressure deficit higher than a threshold parameter $vpd_2$ ($\theta_3$). With moisture conditions between these two threshold values defining a dry and a wet hour, the *TSHH* was set back with a factor $r_1$ ($\theta_4$).

The amount of viable attached sporangia (*VAS*) is the sporangia produced the current hour and the proportion of *VAS* surviving from the previous hour. The total amount can be reduced by drought, and additional new spores can be added if the current hour is a spore producing hour. Part of the spores can be washed off during rain and some released into the air (Equation 3).

$$\boldsymbol{VAS}(t) = \frac{\boldsymbol{VAS}(t-1) \cdot \boldsymbol{r}_2 \cdot \left(1 - \frac{\boldsymbol{vpd}(t) - \boldsymbol{vpd}_3}{\boldsymbol{vpd}_{max}}\right) + \boldsymbol{SPH}(t)}{(1 + \boldsymbol{r}_3 \cdot \boldsymbol{P}(t-1)) \cdot (1 + \boldsymbol{r}_4 \cdot \boldsymbol{RTA}(t-1))} \quad (3)$$

The model output *VAS* at time *t* is the total amount of viable attached sporangia the previous hour (*t* - 1) reduced linearly by the ratio ($r_2$) giving natural survival of viable attached spores from last hour ($\theta_5$), and by dryer weather conditions than a threshold value $vpd_3$ ($\theta_6$). To define the relative amount of reduction, $vpd_{max}$ = 6000 Pa was used. Newly produced spores (*SPH*) was added for each hour. The total number of viable attached spores was additionally reduced linearly by the amount of precipitation the previous hour by a factor $r_3$ ($\theta_7$), and by the number of released sporangia to the air (*RTA*) the previous hour, by a factor $r_4$ ($\theta_8$).

#### 2.3.2. Spore release

After a night with high humidity and spore production, Hirst (1958) observed dispersal of sporangia during the following morning as the temperature was rising and relative humidity dropping. The drop in humidity within the laminar layer around the leaf was either caused by the sunlight heating the leaves or a reduction in the relative humidity of

the air. Accordingly, the release of sporangia to air (RTA) is defined by Equation 4

$$\boldsymbol{RTA}(t)=\begin{cases}2 & \textit{if } \boldsymbol{GR}(t)-\boldsymbol{GR}(t-1)>\Delta_{GR} \textit{ and } \boldsymbol{vpd}(t)-\boldsymbol{vpd}(t-1)\geq\Delta_{vpd}\\ 1 & \textit{if } \boldsymbol{GR}(t)-\boldsymbol{GR}(t-1)>\Delta_{GR} \textit{ or } \boldsymbol{vpd}(t)-\boldsymbol{vpd}(t-1)\geq\Delta_{vpd}\\ 0 & \textit{else}\end{cases} \tag{4}$$

Where $\Delta_{GR}$ ($\theta_9$) and $\Delta_{vpd}$ ($\theta_{10}$) was uncertain parameters.

The inhibition of sporangia release to air (IRTA) is defined by Equation 5.

$$\boldsymbol{IRTA}(t)=1-r_5\frac{\boldsymbol{LW}(t)}{60} \tag{5}$$

Where $r_5$ ($\theta_{11}$) is the rate of inhibition of sporangia release by leaf wetness.

The amount of viable released spores is strongly inhibited by solar radiation. After 1 hour of exposure on sunny days the viability of sporangia decreased by 95%, whereas on overcast days, survival was reduced only slightly (Mizubuti et al., 2000). The survival factor for released spores was set as a function of the short wave global radiation compared to the maximum short waved global radiation, which is about 850 W/m$^2$ in Norway. The survival factor of released spores (*SFRS*) is estimated from Equation 6.

$$\boldsymbol{SFRS}(t)=\boldsymbol{min}\left(0,1-\frac{\boldsymbol{GR}(t)^2}{850^2}\right) \tag{6}$$

The viable spore load was calculated as the number of spores released this hour in addition to the viable spores from the previous hour. A fraction of the viable attached spores the previous hour was considered to be unexposed to solar radiation, because they were shaded by the leaves above. The fraction exposed to solar radiation the previous hour was reduced by *SFRS*. Additionally, the newly released spores were calculated as the *VAS* multiplied by the factor of *RTA* and *IRTA*. This spore load that can give rise to new foliar infection is also reduced by precipitation and by germination (spores can only germinate once). The number of viable released spores (*VRS*) is defined by Equation 7.

$$\boldsymbol{VRS}(t)=\frac{r_6\cdot\boldsymbol{VRS}(t-1)\cdot\boldsymbol{SFRS}(t)+(1-r_6)\cdot\boldsymbol{VRS}(t-1)+\boldsymbol{VAS}(t)\cdot\boldsymbol{RTA}(t)\cdot\boldsymbol{IRTA}(t)}{(1+\boldsymbol{P}(t-1)\cdot r_7)\cdot(1+\boldsymbol{WHS}(t-1)\cdot r_8)} \tag{7}$$

Where $r_6$ is the fraction of viable released spores exposed to solar radiation ($\theta_{12}$). The total number of *VRS* was additionally reduced linearly by the amount of precipitation the previous hour, by a factor $r_7$ ($\theta_{13}$) and linearly when wet period has started (*WHS*) the previous hour, by a factor $r_8$ ($\theta_{14}$).

### 2.3.3. Infection

The *P. infestans* spores need free water from rain or dew to germinate (Crosier and Reddick, 1935), and longer periods of leaf wetness are required for germination as the temperature deviates from the optimum (Rotem et al., 1978). A short dry period initiated within the first three hours after infection substantially reduces the number of lesions that develops, but temporary surface dryness occurring later generally has less effect, presumably because infection is better established (Hartill et al., 1990). Here, the wet period is considered to start (*WHS*) if the vapour pressure deficit the previous and the current hour is low, if there is rain the current hour or if a sufficient duration of leaf wetness for the current and the next two hours has been fulfilled.

$$\boldsymbol{WHS}(t)=\begin{cases}1 & \textit{if } \boldsymbol{vpd}(t-1)+\boldsymbol{vpd}(t)<\boldsymbol{vpd_4} \textit{ or } \boldsymbol{P}(t)>0\\ & \textit{or } \boldsymbol{LW}(t)+\boldsymbol{LW}(t+1)+\boldsymbol{LW}(t+2)>\boldsymbol{LW}_1\\ & \textit{or } \boldsymbol{LW}(t)>\boldsymbol{LW}_2\\ 0 & \textit{else}\end{cases} \tag{8}$$

Where $vpd_4$ ($\theta_{15}$), $LW_1$ ($\theta_{16}$) and $LW_2$ ($\theta_{17}$) were uncertain parameters.

The wetness will continue if the vapour pressure deficit remains low or if there is rain. Wetness continuation (*WHC*) was calculated as follows

$$\boldsymbol{WHC}(t)=\begin{cases}1 & \textit{if } \boldsymbol{vpd}(t)<\boldsymbol{vpd_5} \textit{ or } \boldsymbol{P}(t)>0\\ 0 & \textit{else}\end{cases} \tag{9}$$

With the threshold parameter $vpd_5$ ($\theta_{18}$).

From this we can estimate the wetness duration (*WD*) in the crop, accumulating the *WHS* as long as the wetness continues.

$$\boldsymbol{WD}(t)=\boldsymbol{WHC}(t)\cdot(\boldsymbol{WD}(t-1)+\boldsymbol{WHS}(t)) \tag{10}$$

Further, wet hours (WH) are defined according to Equation 11.

$$\boldsymbol{WH}(t)=\begin{cases}1 & \boldsymbol{WD}(t)>0\\ 0 & \textit{else}\end{cases} \tag{11}$$

The temperature sum of wet hours (*TSWH*) was calculated as follows

$$\begin{aligned}\boldsymbol{TSWH}(t)=\Big\{&(WH(t)\cdot(T(t)+WH(t+1)\cdot(T(t+1)+WH(t+2)\cdot(T(t+2)\\&+WH(t+3)\cdot(T(t+3)+WH(t+4)\cdot(T(t+4))\\&+WH(t+5)\cdot(T(t+5)))))))\textit{if } \boldsymbol{WHS}(t)\\&=10\textit{else}\end{aligned} \tag{12}$$

For the spores to be able to infect, the wet period (*TSWH*) must be above a threshold value ($TSWH_{thres}$), and infection risk (*IR*) is defined by Equation 13.

$$\boldsymbol{IR}(t)=\begin{cases}1 & \textit{if } \boldsymbol{TSWH}(t)\geq\boldsymbol{TSWH}_{thres}\\ 0 & \textit{else}\end{cases} \tag{13}$$

With the threshold parameter $TSWH_{thres}$ ($\theta_{19}$).

### 2.3.4. The blight risk

The risk of blight development is a function of the amount of viable released spores and the duration of the leaf wetness when there is an infection risk.

The estimated hourly risk of late blight infection (*RISK*) is then calculated as:

$$\boldsymbol{RISK}(t)=\frac{\boldsymbol{TSWH}(t)}{\boldsymbol{TSWH}_{thres}}\cdot\boldsymbol{VRS}(t)\cdot\boldsymbol{IR}(t) \tag{14}$$

## 2.4. Sensitivity Analysis

Model outputs will generally be more sensitive to changes in some parameters than others. Sensitivity analysis is the study of how the variation in model output can be appointed to different sources of variation in the parameters (Saltelli et al., 2004). It is a suitable tool for model simplification as the parameters that are detected to have minor impact on model output can be fixed to a nominal value.

The sensitivity method introduced by Morris (Morris, 1991) is a screening method that is suitable for complex models where the number of parameters or the computational cost limits the possibility of numerical calculation. Here, the parameter space is defined by a *p*-level grid within the parameter boundaries, and the parameter $\theta_i$, where $i$=1, …,$k$, is mapped to [0, 1] ($\theta_i^*$) and assumed to vary across the $p$ selected levels. Elementary effects ($EE_i$) of the model output are calculated from two consecutive model runs according to Equation 15.

$$EE_i(\boldsymbol{\theta}^*)=\left(\frac{y(\theta_1^*,\ldots,\theta_{i-1}^*,\theta_i^*+\Delta,\theta_{i+1}^*,\ldots,\theta_k^*)-y(\boldsymbol{\theta}^*)}{\Delta}\right) \tag{15}$$

Here, $\Delta$ is in the range of [1/($p$-1), 1-1/($p$-1)], $p$ is the number of levels, $\boldsymbol{\theta}^*$ is any selected parameter mapped to the [0, 1] space and $\boldsymbol{\theta}$ is the selected parameter vector in the parameter space. The transformed point $\boldsymbol{\theta}$ from ($\boldsymbol{\theta}^*$+$\mathbf{e}_i\Delta$) remains within the parameter space for each index $i$=1,2,…,$k$ and $\mathbf{e}_i$ is a vector of zeros with a unit corresponding to its $i$'th component.

The finite distribution of elementary effects, denoted $EE_i(\boldsymbol{\theta}) \sim F_i$, is constructed by $r$ elementary effects that are sampled using an efficient design that constructs $r$ trajectories of $(k+1)$ points in the parameter space. Two sensitivity measures can then be calculated from $\boldsymbol{EE}$: (1) $\boldsymbol{\mu}$ (the mean value), which evaluates the overall influence of the parameters on model output, and (2) $\boldsymbol{\sigma}$ (the standard deviation), which is used to detect parameters involved in interaction with other parameters or whose effect is nonlinear. To avoid the problem of effects of opposite signs which occur when the model is non-monotonic, we will in this study use $\boldsymbol{\mu}^*$ (the mean of the absolute value of $\boldsymbol{EE}$) that was introduced by Campolongo et al. (2007).

As the Nærstad model simulates hourly risk of blight infection, the sensitivity of model parameters may change depending on the timing of the risk considered. It would be most appropriate to consider the hourly outputs over the whole season (Lamboni et al., 2009), but the large number of responses that need to be evaluated makes this approach impossible. Therefore, the summed risk of late blight infection over the whole season was selected as the response in this study.

The screening method of Morris was applied using weather data from Ås in Norway, during the seasons 2006-2008 and 2010-2011. The analysis was performed using weather data from one year at a time. The ranking order of the parameters with respect to sensitivity was determined by considering the results for all years together, as means and standard deviations over the years.

### 2.5. Bayesian calibration

The Bayesian framework is based on Bayes theorem (Berger, 1985) and is given in Equation 16.

$$\pi(\boldsymbol{\theta}|\boldsymbol{D}) = \frac{\pi(\boldsymbol{\theta}) \cdot f(\boldsymbol{D}|\boldsymbol{\theta})}{f(\boldsymbol{D})} \propto \pi(\boldsymbol{\theta}) \cdot f(\boldsymbol{D}|\boldsymbol{\theta}) \tag{16}$$

Here, $\boldsymbol{\theta}$ is the vector of the model parameters and $\boldsymbol{D}$ is the observed data. The resulting posterior parameter distribution ($\pi(\boldsymbol{\theta}|\boldsymbol{D})$) is the probability distribution for the parameters conditional on the data, determined as a combination of our prior knowledge of the parameters before new data are included ($\pi(\boldsymbol{\theta})$, the prior parameter distribution) and the distribution of the new data conditional on model parameterization ($f(\boldsymbol{D}|\boldsymbol{\theta})$, likelihood function). The integrated likelihood ($f(\boldsymbol{D})$) is the marginal probability of the data, which is a constant. With only few experimental data, the prior parameter distribution will highly affect the posterior probability distribution, but more data added to the calibration will reduce the impact of the prior parameter distribution.

Integration problems make exact calculations impossible when the parameter space is highly dimensional. In this study, calculations were done using the Markov chain Monte Carlo (MCMC) algorithm Random walk Metropolis (Liu, 2001). The prior probability distributions were described by beta distributions with minimum, maximum and nominal value given in Table 1. Prior independence was assumed, and the joint distribution was thus determined as the product of the marginal parameter distributions. The likelihood function was determined by the distribution of measurement error (see Equation S2 in the eXtra), following van Oijen et al. (2005b). As specific information about the precision of the measurements was not available, the standard deviation of each measurement was set to 5% of its observed value.

The model was calibrated using field data of number of lesions on trap plants at Ås in Norway during the seasons 2006-2008 and 2010-2011. Only the parameters regarded as strongly sensitive in the sensitivity analysis was calibrated, whereas the remaining parameters were fixed to its modal value (Table 1).

### 2.6. Model fit and validation

The collected field data on daily number of lesions per trap plant was divided into three categories: (1) no blight infections (no lesions on trap plants), (2) low blight infection (up to 1.5 lesions per trap plant) and (3) high blight infection (more than 1.5 lesions per trap plant). Daily model outputs of blight risk were found as the maximum estimated hourly blight risk for that day. By calculating the receiver operating characteristic (ROC) curves (Hastie et al. 2009) on the training data (Ås, 2006-2008 and 2010-2011), the ability of the system to binary classify the results with the discrimination thresholds were adjusted. Threshold values to group the predicted blight risk into: (1) low blight risk, (2) moderate blight risk and (3) high blight risk were calculated as the value for which sensitivity equals specificity from the ROC curves. Two ROC curves were created to distinguish between no blight risk and moderate blight risk, and between moderate and high blight risk. The accuracy of the classifiers (AUC) was estimated by the area under the ROC curve. AUC estimates the accuracy of the model into the classes: excellent (0.9-1), good (0.8-0.9), fair (0.7-0.8), poor (0.6-0.7) and fail (0.5-0.6).

Following Agresti (2002), 3 times 3 and 2 times 2 confusion matrixes (Table 2) were created and summary statistics of sensitivity (Equation 17, represents the ratio of infected trap plants being correctly identified with moderate to high blight risk), specificity (Equation 18, the ratio of non-infected trap plants being correctly identified with no blight risk), false positive (ratio of non-infected trap plants being incorrectly identified with moderate or high blight risk) and false negatives (the ratio of infected trap plants being incorrectly identified with no blight risk) estimated. At last, the accuracy rate was calculated as the ratio of correctly classified observations (Equation 19).

$$Sensitivity = (A+B+D+E)/(A+B+D+E+G+H) \tag{17}$$

$$Specificity = (I)/(C+F+I) \tag{18}$$

$$Accuracy = (A+B+D+E+I)/(A+B+C+D+E+F+G+H+I) \tag{19}$$

### 2.7. Model comparison

The HOSPO90 model and the Førsund rules have been tested in several fungicide field trials in Norway. They performed on the same level measured as control of blight infection in the field, except that they did not always predict blight risk on the same days (Hermansen et al. 2007). The idea behind making the new late blight model was to improve the late blight forecasting in Norway. To evaluate if the new model could better predict blight risk than the Førsund rules or the HOSPO90 model, the predictions from the three models were compared to field observations of daily number of lesions per trap plant.

#### 2.7.1. The Førsund rules

The Førsund rules were developed in 1957 (Førsund and Flaatten, 1959) and later adjusted according to results from validation trials (Hermansen and Amundsen, 2003). The current Førsund rules consist of the following four daily criteria: 1) maximum air temperature between 16 °C (15 °C) and 24 °C, 2) minimum temperature above 8 °C, 3) relative humidity of at least 75% at noon, and 4) rainfall of at least 0.1 mm. The model predicts risk of blight at days when all four criteria are fulfilled.

#### 2.7.2. The HOSPO model

The HOSPO90-model is given by a simple equation, and it predicts risk of blight at days when a minimum of 10 hours of relative humidity above 90% combined with a temperature of at least 10 °C occurs

**Table 2**
Example of a 3 times 3 confusion matrix, describing the performance of a classification.

| | *High blight risk* | *Moderate blight risk* | *Low blight risk* |
|---|---|---|---|
| *High blight infection* | A | B | C |
| *Low blight infection* | D | E | F |
| *No blight infection* | G | H | I |

between 16:00 yesterday and 15:00 today (Hansen et al. 2006).

### 2.8. Implementations

All calculations were performed using MATLAB (R2019a).

## 3. RESULTS

The training data (2006-2008 and 2010-2011) included a total of 147 days with trap plants of cv. Bintje (susceptible to blight infection) and 62 (only 2010-2011) days with trap plants of cv. Saturna (medium susceptible to blight infection) and cv. Peik (medium resistant to blight infection). This resulted in 39, 12 and 22 days with no blight infections, 19, 2 and 6 days with low blight infection (up to 1.5 lesions per trap plant) and 89, 48 and 34 days with high blight infection (more than 1.5 blight lesions per trap plant). The validation data (2012-2015) included 145 days with trap plants of each of the cultivars Bintje, Saturna and Peik. This resulted in 34, 44 and 72 days with no blight infections on the trap plants, 20, 28 and 22 days with low blight infections and 91, 73 and 51 days with high infection for cv. Bintje, cv. Saturna and cv. Peik, respectively.

### 3.1. Sensitivity Analysis

The Morris method was used with 200.000 trajectories and six levels ($p$). Five years of weather data from Ås (2006-2008 and 2010-2011) was used for cv. Bintje and two years (2010-2011) for cv. Saturna and cv. Peik, and the total summarized risk of late blight for all years used as model output. This resulted in unstable results. Therefore, the sensitivity analysis was rerun using one year of weather data at a time and with yearly summarized risk of late blight as model output. Results of the mean ($\mu^*$) and the standard deviation ($\sigma$) of the absolute value of the elementary effects were estimated for each year and normalized. The sensitivity of each parameter to model output varied highly between years (Figure S1 and S2 in the eXtra). Still, some parameters clearly stood out as weakly sensitive independent of year of weather data used. Figure 2 gives the results for cv. Bintje as a mean over the five years considered. Seven parameters stood out as more sensitive according to $\mu^*$ and $\sigma$. These parameters are $\theta_{19}$ ($TSWH_{thres}$, threshold value defining a wet period for spores to be able to infect), $\theta_1$ ($TSHH_{thres}$, threshold value defining a humid period for spore production), $\theta_8$ ($r_4$, factor controlling the reduction of viable attached sporangia caused by the number of released sporangia to air), $\theta_5$ ($r_2$, fraction of natural surviving viable attached spores from last hour), $\theta_6$ ($vpd_3$, threshold value controlling the reduction in survival attached spores caused by dry conditions), $\theta_7$ ($r_3$, fraction controlling the reduction of viable attached sporangia caused by precipitation) and $\theta_{14}$ ($r_8$, fraction controlling the reduction of viable released spores caused by WHS (wet period considered to start infection)). The remaining 12 parameters were considered as less sensitive to model output.

For Saturna and Peik, only two years of data were considered in the sensitivity analysis. Roughly, the same parameters were considered as more sensitive, but the order of importance were not consistent (Figure 2). All seven parameters considered as more sensitive according to Bintje, were among the eight parameters considered as more sensitive according to Peik. For saturna, $\theta_{19}$ ($TSWH_{thres}$, threshold value defining a wet period for spores to be able to infect) was not considered to be sensitive, whereas $\theta_2$ ($vpd_1$, lower threshold value defining a humid hour for spore production) was considered sensitive to model outputs.

### 3.2. Bayesian calibration

The seven highly sensitive parameters from the sensitivity analysis of Bintje was parameterized by Bayesian calibration. Two Markov chains were run in parallel for 160.000 iterations and burn-in was detected within the first 100.000 iterations. Maximum a'posteriori estimates (MAP) were calculated from the Markov chains of the posterior probability distributions. All these seven sensitive parameters were found to have been overestimated in their priors, given the lower MAP estimates for all parameters compared to their modal values. The most sensitive parameter was the threshold value defining a wet period for spores to be able to infect ($\theta_{19} = 33$) and the second most sensitive parameter which was the threshold value defining a humid period for spore production ($\theta_1 = 72$) were both reduced by 17% compared to their modal values. For the fraction of natural surviving viable attached spores from last hour ($\theta_5 = 0.74$) and the threshold value controlling the reduction in survival of attached spores caused by dry conditions ($\theta_6 = 164$), a reduction of 25% compared to their modal values was found. A higher

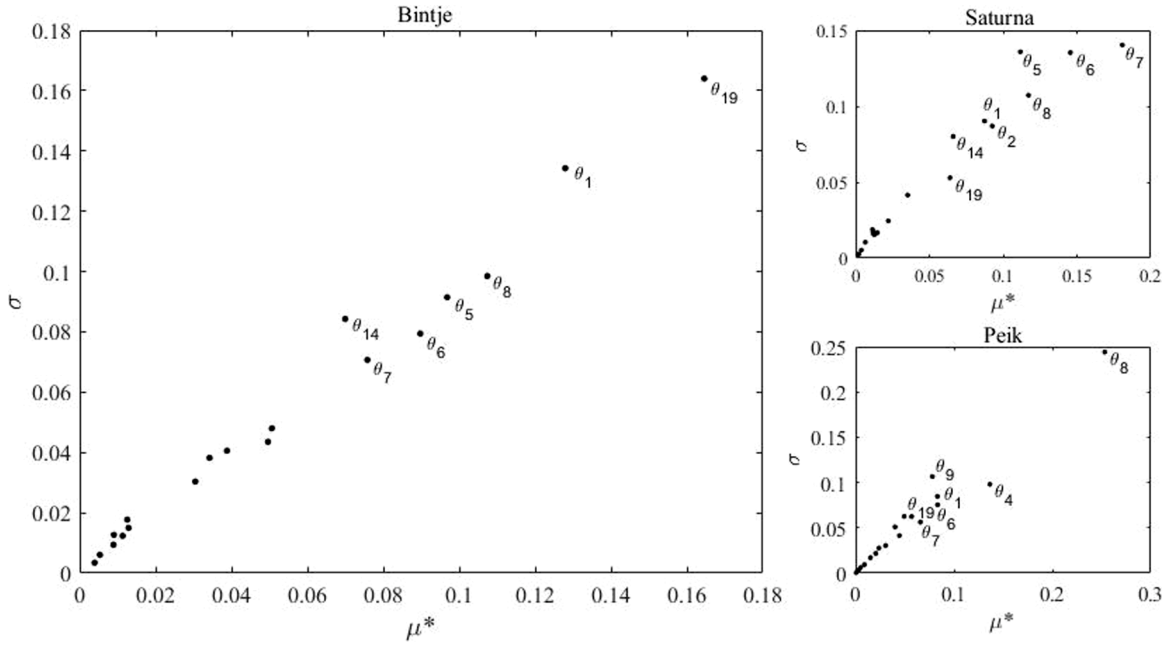


**Figure 2.** Results from sensitivity analysis of the Nærstad model, using the Morris method. Only the seven or eight most important parameters according to the sensitivity analysis are named for the varieties Bintje, Saturna and Peik separately.

reduction of 46% was found for the fraction controlling the reduction of viable released spores caused by WHS (wet period considered to start infection) ($\theta_{14}$ = 0.05) compared to its modal value. The absolute highest reduction of 79%, was found for the factor controlling the reduction of viable attached sporangia caused by the number of released sporangia to air ($\theta_8$ = 0.01) followed by the fraction controlling the reduction of viable attached sporangia caused by precipitation ($\theta_7$ = 0.35).

### 3.3. Model fit and risk categorization

Two ROC-curves were created from the training data to separate between low and moderate blight risk and between moderate and high blight risk, respectively, using the MAP parameter estimates (eXtra, Figure S3a, b). To distinguish between low and moderate blight risk, a low AUC of 0.57, corresponding to fail was detected, while a high AUC of 0.87, corresponding to good fit, was detected when distinguishing between high and moderate blight risk. From the ROC curve, a threshold value based on Pythagoras (minimizing the sum of squares of 1-sensitivity and 1-specificity) were found at 0.91 when distinguishing between low and moderate blight risk and at 2.63 when distinguishing between moderate and high blight risk.

### 3.4. Model validation

Performance of the Nærstad model was evaluated through independent test data. From the model, blight risk was calculated using both the original modal parameter values and the estimated MAP parameter values for the seven most sensitive parameters detected for Bintje through sensitivity analysis. Mean square error between observed (daily number of lesions per trap plant) and estimated (daily risk, defined as maximum hourly risk for that day) value were calculated and decomposed into bias, variance error and the phase shift component (Figure 3). The total MSE was reduced by 11% when using the MAP parameter estimates compared to the original modal values. From the decomposition, phase shift totally dominated MSE, and totaled in 99% of the error term using the modal parameter values and 67% using the MAP estimates. When the MAP estimates were used, the bias accounted for 12% and the variance error for 21% of the total MSE

The observed daily number of lesions per trap plant for cv. Bintje is given in Figure 4, with high difference between days and years. Also, the hourly number of spores recorded in the spore traps within the field is plotted for the same time interval, with high hourly, daily and yearly variations. The figure did not show any clear correlations between the number of lesions and the number of spores.

Finally, the estimated risk category detected as low, moderate and high is showed with colored dots in green, orange and red, respectively, with a good match to the observed number of lesions. A confusion matrix was developed for all test years combined (Table 3). The accuracy of the model was 0.83, with a sensitivity of 0.89 and specificity of 0.62. Consequently, a false positive rate of 0.38 and a false negative rate of 0.11 was found (Table 4).

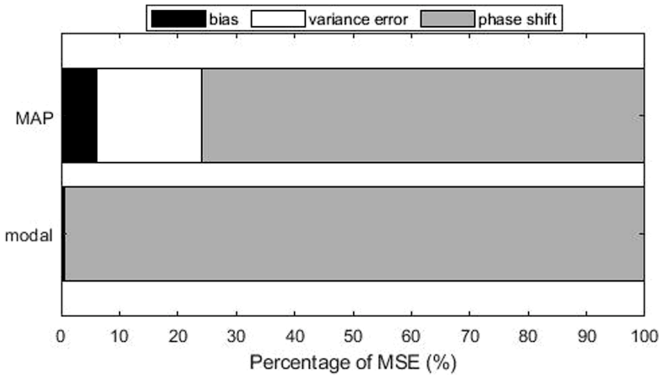


**Figure 3.** The percentage decomposition of mean square error (MSE) into bias, variance error and phase shift using the individual test data, using both the original modal parameter values and their maximum a'posteriori (MAP) parameter estimates.

For cv. Saturna and cv. Peik, the model was tested using both the Bintje threshold values and the cultivar specific threshold values (Table 4). For the cultivars Saturna and Peik, the model accuracy decreased to 0.79 and 0.66, respectively when the Bintje threshold was used. For Saturna, the use of a cultivar specific threshold increased the accuracy to 0.81, with a corresponding increase in sensitivity from 0.90 to 0.94. Use of the cultivar specific threshold for Peik reduced the accuracy from 0.66 to 0.63, and the sensitivity decreased from 0.93 to 0.58. For both Saturna and Peik, the specificity was lower (0.52 and 0.39, respectively) compared to the specificity for Bintje. The cultivar specific thresholds gave a slightly reduced specificity for Saturna (0.50) and increased for Peik (0.69).

## 4. Model comparison

The two late blight forecasting models, HOSPO90 and the Førsund rules were tested on the validation data. Both models require daily weather inputs, but since the trap plants were exposed from 3 pm one day to 3 pm the following day, daily inputs from the same time period were generated from the hourly recorded weather data.

The accuracy of the Nærstad model was higher compared to both the Førsund rules and the HOSPO90 model. The sensitivity of the Nærstad model was much higher compared to the two other models, while the specificity was lower.

## 5. DISCUSSION

Potato late blight epidemics highly depend on weather conditions (Crosier, 1934), but the weather affects differently in the different parts of the epidemic cycle. Temperature affects the physiology of both the pathogen and the host and it has an increasing influence in most stages of the disease development, with possible exception of spore dispersal (Harrison, 1992). Other weather variables have a more compound effect, as sunlight for example that promotes spore release (Hirst, 1958) while it inhibits spore survival (Mizubuti et al., 2000) or leaf wetness that is known to inhibit spore release while it promotes spore germination and infection (Rotem et al., 1978). To better understand and to be able to more precisely simulate the effect of inter-related weather conditions on blight development, these processes were described mathematically into a process-based simulation model, the Nærstad model. With an hourly time-step, the dynamic model describes the structure of the underlying processes in the disease development, including spore production, spore release, spore survival and infection of *P. infestans*. Realistic relationships between these processes are then given through the mathematical descriptions, and blight will for example not develop despite good weather conditions for infection when no spores are produced or if the produced spores are not viable. Only process-based models provide this flexibility to realistically predict the impact of the different weather conditions through the simulation period. The drawback is the complexity in respect to high computational cost, generally with a high number of input variables and uncertain parameters.

While model complexity with an increased number of parameters improves the model fit to a particular dataset, it may lead to over-fitting and poor predictive performance when the model is applied to new situations. Parameter-rich models with high dimensional parameter spaces are also related to a high computational cost, leading to calibration challenges. Satisfactory simplifications of process-based models by fixing the weakly sensitive parameters detected through a sensitivity analysis have been shown (Hjelkrem et al., 2017; Oomen et al., 2016; Raj et al., 2016). From Hjelkrem et al. (2017), a higher error term may

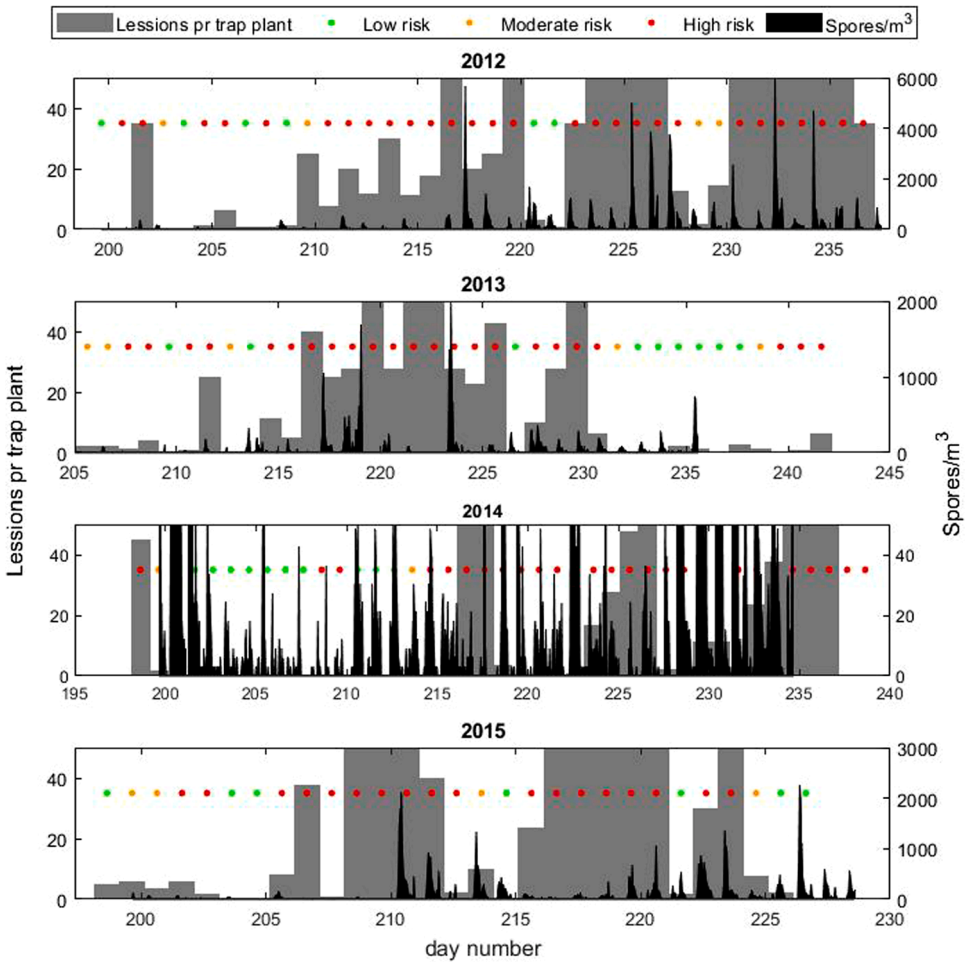


**Figure 4.** For the test data of cv. Bintje (Ås, 2012 to 2015), subplots are given with observed number of lesions per trap plant, estimated risk level (low, moderate or high) and the observed number of spores per $m^3$.

**Table 3**
Number of days in the different categories of infection risk on trap plants exposed from 3 pm to 3 pm the following day versus predicted risk with the new late blight model in trap plant trials 2012-2015.

| | *High blight risk* | *Moderate blight risk* | *Low blight risk* | *Total* |
|---|---|---|---|---|
| *High blight infection* | 76 | 10 | 5 | 91 |
| *Low blight infection* | 9 | 4 | 7 | 20 |
| *No blight infection* | 11 | 2 | 21 | 34 |
| *Total* | 96 | 16 | 33 | 145 |

**Table 4**
Model accuracy, sensitivity and specificity calculated when testing the Nærstad model, the Førsund rules and the HOSPO90 model on trap data on the potato cultivars Bintje, Saturna and Peik collected between 2012 and 2015 at Ås.

| | *Accuracy* | *Sensitivity* | *Specificity* |
|---|---|---|---|
| | *Bintje* | | |
| *Nærstad model** | 0.83 | 0.89 | 0.62 |
| *Førsund rules* | 0.61 | 0.57 | 0.76 |
| *HOSPO90* | 0.57 | 0.46 | 0.91 |
| | *Saturna* | | |
| *Nærstad model** | 0.79 | 0.90 | 0.52 |
| *Nærstad model*** | 0.81 | 0.94 | 0.50 |
| *Førsund rules* | 0.64 | 0.59 | 0.75 |
| *HOSPO90* | 0.61 | 0.49 | 0.89 |
| | *Peik* | | |
| *Nærstad model** | 0.66 | 0.93 | 0.39 |
| *Nærstad model*** | 0.63 | 0.58 | 0.69 |
| *Førsund rules* | 0.59 | 0.58 | 0.60 |
| *HOSPO90* | 0.61 | 0.48 | 0.74 |

* Bintje threshold
** Cultivar specific threshold

be achieved when fixing too many of the parameters and model testing on independent data is thus important to justify. A sensitivity analysis in form of the Morris method was carried out for the Nærstad model to assess the importance of the 19 uncertain parameters. The sensitivity analysis was performed using weather data from five years separately. In line with previous studies (Hjelkrem et al., 2017; Confalonieri et al., 2010), the range of parameter importance was not homogenous across years. Still, the same group of parameters stood out as weakly sensitive independent of the year of weather data used. The most sensitive parameter overall was $\theta_{19}$, which is the threshold value defining a wet period for spores to be able to infect ($TSWH_{thres}$), being part of the infection sub-model. Spore production sub-model turned out to be very important for blight development, with as many as five out of totally eight parameters detected as highly sensitive. Additionally, one parameter from the spore release sub-model was detected as important for disease development across the different sets of weather data used.

The sensitivity analysis was additionally carried out using data of cv. Saturna and cv. Peik (2010 and 2011). This showed the same group of sensitive parameters, whereas the order differed. This indicates that it is the same factors in disease development that trigger or inhibit disease development for the different cultivars.

Bayesian calibration was performed to parameterize the seven most important parameters, that was detected through the sensitivity analysis

of cv. Bintje. In the calibration, the parameter providing the best simulation of blight risk (reflected by observed number of lesions per trap plant) was detected. Maximum a'posteriori estimates was calculated for these parameters within their prior boundaries. All parameters were identified with lower parameter values compared to their modal value.

The Nærstad model was developed to improve the potato late blight forecasts in Norway. The model was developed as a process-based model based on literature and field data of the potato cultivar Bintje (susceptible to blight infection). Test results on this cultivar showed that the error term between risk of late blight and the observed number of lesions per trap plant was characterized by timing (phase shift). Still, a high accuracy (83%) with few exceptions improperly classified as low risk (11%) were detected. Reduced accuracy was detected for the cultivars Saturna (medium susceptible) and Peik (medium resistant), with respectively accuracy of 79 and 66%. For these cultivars, the percentage improperly classified as low risk decreased to 10 and 7%. The percentage improperly classified as high risk was higher all over and increased from 38% for Bintje to 48% and 61% respectively for Saturna and Peik. Cultivar specific thresholds to distinguish between low, moderate and high infection was additionally calculated and tested for Saturna and Peik, with no clear effect (slightly improved accuracy for Saturna and slighty reduced for Peik). Partial resistance of potato cultivars to *P. infestans* consists of four components, which are infection efficiency, lesion growth rate, generation time and sporulation capacity (Colon et al., 1995). This shows that the model should be parameterized specifically for the cultivar in order to achieve better accuracy.

The model is based on infections on trap plants from five different seasons, but from only one location. Even though the model gives a good prediction of the infections on the trap plants, the model only takes into account the factors that were limiting to blight development during these five years. The trap plant tests should also be carried out at different locations to explore how robust the model is in predicting late blight infections under varying climatic conditions.

The improved potato late blight forecasting model is based on hourly weather data and predicts the risk of spore production, with subsequent spore release, spore survival and infection, when there is inoculum in the field. The model is programmed on VIPS (www.vips-landbruk.no) a Norwegian web site with forecasting models for prediction of diseases and pests in crop plants.

## 6. CONCLUSIONS

The Nærstad model was developed to improve the potato late blight forecasts in Norway. The model was developed as a process-based model based on literature and field data of observed number of lesions per trap plant of the potato cultivar Bintje (susceptible to blight infection). The structure of the underlying processes in the disease development is described, including spore production, spore release, spore survival and infection of *P. infestans*. It is a dynamic model with an hourly time step, based on air temperature, precipitation, relative humidity, global radiation and leaf wetness.

For all three cultivars tested (Bintje, Saturna and Peik), the Nærstad model improved with a higher model accuracy compared to the existing HOSPO-model and the Førsund rules that both have shown relatively good correlation with blight development in previous field evaluations in Norway. Still, the results of Saturna and Peik were not as good, and cultivar specific models would be preferred. Also, further testing at other sites should be preferred, to approve use of the model in other parts of the country.

## CRediT authorship contribution statement

**Anne-Grete Roer Hjelkrem:** Formal analysis, Software, Methodology, Validation, Visualization, Writing - original draft. **Håvard Eikemo:** Writing - review & editing. **Vinh Hong Le:** Data curation, Investigation, Writing - review & editing. **Arne Hermansen:** Conceptualization, Methodology, Funding acquisition, Project administration, Writing - review & editing. **Ragnhild Nærstad:** Conceptualization, Methodology, Funding acquisition, Validation, Visualization, Project administration, Writing - review & editing.

## Declaration of Competing Interest

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

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2021.109565.

## REFERENCES

Agrometeorology Norway, 2019, Weather observations in Norway. https://lmt.nibio.no. (accessed 5 October 2019).
Agresti, A., 2002. Categorical Data Analysis, Second Edition. John Wiley & Sons, Inc., New York.
Berger, O. J., 1985. Statistical Decision Theory and Bayesian Analysis, New York.
Bruhn, J.A., Fry, W.E., 1981. Analysis of potato late blight epidemiology by simulation modeling. Phytopathology 71, 612–616.
Brurberg, M.B., Elameen, A, Le, V.H., Nærstad, R, Hermansen, A, Lehtinen, A, Hannukkala, A, Nielsen, B.J., Hansen, J.G., Andersson, B., Yuen, J., 2011. Genetic analysis of Phytophthora infestans populations in the Nordic European countries reveals high genetic variability. Fungal Biology 115, 335–342.
Colon, L.T., Turkensteen, L.J., Prummel, W., Budding, D.J., Hoogendoorn, J., 1995. Durable resistance to late blight (Phytophtora infestans) in old potato cultivars. European Jounral of Plant Pathology 101, 387–397.
Campolongo, F., Cariboni, J., Saltelli, A., 2007. An effective screening design for sensitivity analysis of large models. Environmental Modelling & Software 22, 1509–1518.
Confalonieri, R., Bellocchi, G., Tarantola, S., Acutis, M., Donatelli, M., Genovese, G., 2010. Sensitivity analysis of the rice model WARM in Europe: Exploring the effects of different locations, climate and methods of analysis on model sensitivity to crop parameters. Environmental Modelling & Software 25, 479–488.
Cooke, L.R., Schepers, H.T.A.M., Hermansen, A., Bain, R.A., Bradshaw, N.J., Shaw, D.S., Evenhuis, A., Kessel, G.J.T., Wander, J.G.N., Andersson, B., Hansen, J.G., Hannukkala, A., Nærstad, R., Nielsen, B.J., 2011. Epidemiology and integrated control of potato late blight in Europe (Review). Potato Research. 54, 183–222.
Crosier, W., 1934. Studies in the biology of Phytophthora infestans (Mont.) de Bary, 155. Cornell University Agricultural Experiment Station Memoir., pp. 1–40
Crosier, W., Reddick, D., 1935. Some ecological relations of the potato and its chief fungus parasite Phytophthora infestans. American Potato Journal 12, 205–219.
Fry, W. E., Thurston, H. D., Stevenson, W. R., 2001. Late Blight in: Compendium of Potato Diseases, Second Edition. Eds: Stevenson WR, Loria R, Franc GD, Weingartner DP. APS Press. 28-30.
Fry, W., 2010. Guide to the late blight decision support system (DSS) for potatoes and tomatoes. www.plantpath.cornell.edu/Fry/lateblightDSS2010.pdf (accessed 12 June 2012).
Førsund, E., Flaatten, H.K., 1959. The interrelationship between climate and outbreak of late blight epiphytotics. Meldinger fra Norges Landbrukshøgskole 38 (6), 1–61.
Goff, J.A., Gratch, S., 1946. Low-pressure properties of water from -160 to 212 F. In. Transactions of the American society of heating and ventilating engineers. American Society of Heating and Ventilating Engineers, New York.
Gouache, D., Bensadoun, A., Brun, F., Pagé, C., Makowski, D., Wallach, D., 2013. Modelling climate change impact on Septoria tricici blotch (STB) in France: accounting for climate model and disease model uncertainty. Agricultural and Forest Meteorology 170, 242–252.
2005 Hansen, J.G., Nielsen, B.J., Bødker, L., Andersson, B., Yuen, J., Wiik, L., Hermansen, A., Nærstad, R., Le, V.H., Brurberg, M.B., Hannukkala, A., Lehtinen, A., 2006. Blight management in the Nordic countries. In: Westerdijk, C.E., Schepers. PPO356, H.T.A.M. (Eds.), Blight management in the Nordic countries. Proceedings

of the Ninth Workshop on European network for development of an integrated control strategy of potato late blight 11, 39–52, 2005Special Report.
2008 Hansen, J.G., Andersson, B., Bain, R., Schmiedl, J., Soellinger, J., Ritchie, F., Bucena, L., Cakir, E., Cooke, L., Dubois, L., Filippov, F., Hannukkala, A., Hausladen, H., Hausvater, E., Heldak, J., Hermansen, A., Kapsa, J., Pliakhnevich, M., Koppel, M., Lees, A., Musa, T., Ronis, A., Schepers, H., Vogelaar, K., Vanhaverbeke, P., 2009. The development and control of Late blight (Phytophthora infestans) in Europe 2007 and 2008. In: Schepers, H.T.A.M (Ed.), The development and control of Late blight (Phytophthora infestans) in Europe 2007 and 2008. Proceedings of the Eleventh EuroBlight Workshop, 2008PPO 384, Special Report No 13.
Hansen, J.G., Lassen, P., Hjelkrem, A.G.R., Eikemo, H., Cucak, M., Lees, A., Gaucjer, D., Chatpt, C., Kessel, G., 2017. Integration of pathogen and host resistance information in exisiting DSSs – introducing the IPMBlight2.0 approach. Proceeding of the sixteen EuroBlight Workshop 18, 147–158.
Harrison, J.G., 1992. Effects of the aerial environment on late blight of potato foliage- a review. Plant Pathology 41, 384–416.
Harrison, J.G., Lowe, R., 1989. Effects of humidity and wind speed on sporulation of Phytophthora infestans on potato leaves. Plant Pathology 38, 585–591.
Hartill, W.F.T., Young, K., Allan, D.J., Henshall, W.R., 1990. Effects of temperature and leaf wetness on the potato late blight. New Zealand Journal of Crop and Horticultural Science 18, 181–184.
Hastie, T., Tibshirani, R., Friedman, J.H., 2009. The elements of statistical learning: data mining, inference, and prediction (2nd ed.).
Hermansen, A., Amundsen, T., 2003. Evaluation of old potato late blight forecasting rules during 1994-1999 in fields with the new Phytophthora infestans population in Norway. Acta Agriculturae Scandinavica, Section B, Soil and Plant Science 53, 118–128.
Hermansen, A., Nærstad, R., Le, V.H., 2007. Potettørråte - forsøksresultater og erfaringer fra 2006 sesongen. Bioforsk FOKUS 2 (1), 136–137.
Hermansen, A., Nærstad, R., 2009. Forecasting potato late blight in Norway. In: Schepers, H.T.A.M. (Ed.), Forecasting potato late blight in Norway. Proceedings of the Eleventh EuroBlight Workshop 13, 301–306, 28-31 October 2008. PPO-Special Report.
Hirst, J.M., 1958. New methods for studying plant disease epidemics. Outlooks on Agriculture 2, 16–26.
Hjelkrem, A.G.R., Höglind, M., van Oijen, M., Schelberg, J., Gaiser, T., Ewert, F., 2017. Sensitivity analysis and Bayesian calibration for testing robustness of the BASGRA model in different environments. Ecological Modelling 359, 80–91.
Lamboni, M., Makowski, D., Lehuger, S., Gabrielle, B., Monod, H., 2009. Multivariate global sensitivity analysis for dynamic crop models. Field Crops Res 113, 312–320.
Lehtinen, A., Hannukkala, A., Andersson, B., Hermansen, A., Le, V.H., Nærstad, R., Brurberg, M.B., Nielsen, B.J., Hansen, J.G., Yuen, J., 2008. Phenotypic variation in Nordic populations of Phytophthora infestans in 2003. Plant Pathology 57, 227–234.
Lehtinen, A., Andersson, B., Le, V.H., Nærstad, R., Rastas, M., Ketoja, E., Hannukkala, A. O., Hermansen, A., Nielsen, B.J., Hansen, J.G., Yuen, J., 2009. Aggressiveness of Phytopthora infestans on detached potato leaflets in four Nordic countries. Plant Pathology 58, 690–702.
Liu, J. S. 2001., Monte Carlo Strategies in Scientific Computation, New York.
Minunno, F., van Oijen, M., Cameron, D.R., Pereira, J.S., 2013. Selecting parameters for bayesian calibration of process-based model: a methodology based on canonical correlation analysis. SIAM/ASA J. Uncertainty Quantification. 1, 370–385.
Mizubuti, E.S.G., Aylor, D.E., Fry, W.E., 2000. Survival of Phytophthora infestans sporangia exposed to solar radiation. Phytopathology 90, 78–84.
Morris, M.D., 1991. Factorial sampling plans for preliminary comutational experiments. Technometrics 33, 1–14.
Oomen, R.J., Ewert, F., Snyman, H.A., 2016. Modelling rangeland productivity in response to degredation in a semi-arid-climate. Ecological Modelling 322, 54–70.
Perry, R.H., Green, D.W., 1997. Perry's chemical Engineers' handbook. McGraw-Hill, New York.
Raj, R., Hamm, N.A.S., van der Tol, C., Stein, A., 2016. Bayesian integration of flux tower data into process-based siumulator for quantifying uncertainty in simulated output. Geoscientific Model Development 11, 83–101.
Rotem, J., Cohen, Y., Bashi, E., 1978. Host and environmental influence on sporulation in vivo. Annual Review of Phytopathology 16, 83–101.
Saltelli, A., Taranola, S., Campolongo, F., Ratto, M., 2004. Sensitivity Analysis in Practice, New York.
Schröter, H., Ullrich, J., 1967. Eine matematischstatistische Lösung des Problems der Prognose von Epidemien mit Hilfe meteorologischer Parameter, dargestellt am Beispiel der Kartoffelkrautfäule (Phytophthora infestans). Agricultural Meterology 4, 119–135.
1997 Schepers, H.T.A.M., 1998. Epidemiological parameters in decision support systems for Phytophthora infestans. In: Schepers, H.T.A.M., Bouma, E. (Eds.), Epidemiological parameters in decision support systems for Phytophthora infestans. Proceedings of the Workshop on European network for development of an integrated control strategy of potato late blight 3, 30–36, 1997PAV-Special Report.
Smith, L.P., 1956. Potato blight forecasting by 90 percent humidity criteria. Plant Pathology 5, 83–87.
Sæthre, M.G., Hermansen, A., Nærstad, R., 2006. Economic and Environmental impacts of the introduction of Western flower thrips (Frankliniella occidentalis) and Potato late blight (Phytophthora infestans) to Norway. Bioforsk Report 1 (64), 1–35.
Thorsen, S.M., Höglind, M., 2010. Assessing winter survival of forage grasses in Norway under furture climate scenarios by simulating potential frost tolerance in combination with simple agroclimatic indices. Agricultural Forest Meteorology 150, 1272–1282.
Ullrich, J., Schrödter, H., 1966. Das problem der vorhersage des aufretens der kartoffelkrautfaule (Phytophthora infestans) und die moglichkeit seiner losung durchen eine negativprognose. Nachrichtenblatt Dt. Pflanzenschutzdienst (Braunscweig). 18, 33–40.
Wallin, J.R., Hoyman, W.G., 1954. Forecasting potato late blight in Dakota. North Dakota Agricultural Experiment Station Bimonthly Bulletin 16, 226–231.
Wharton, P.S., Kirk, W.W., Baker, K.M., Duynslager, L., 2008. A web-based interactive system for risk management of potato late blight in Michigan. Computer and Electronics in Agriculture 61 (2), 136–148.
Winstel, K., 1993. Kraut- und knollenfaule der kartoffel eine eeue prognosemoglichkeit- sowie bekampfungsstrategien. Med. Fac. Landbouww. Univ. Gent, 58/3b.
World Meteorological Organisation, 2012. General Meteorological Standards and Recommended Practices. WMO, Gineva, p. 49.
van Oijen, M., Höglind, M., Hanslin, H.M., Cadwell, N., 2005a. Process-based modeling of timothy regrowth. Agronomy Journal 97, 1295–1303.
van Oijen, M., Rougier, J., Smith, R., 2005b. Bayesian calibration of process-based forest models: bridging the gap between models and data. Three Physiology 25, 915–927.