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Enhancing crop shelf life with pollination

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Abstract

Background: Globally, high amounts of food are wasted due to insufficient quality and decay. Although pollination has been shown to increase crop quality, a possible impact on shelf life has not been quantitatively studied.

Results: We tested how shelf life, represented by fruit decay, firmness and weight, changes as a function of pollination limitation in two European, commercially important strawberry varieties. Pollination limitation resulted in lower amounts of deformed fruits. Whereas 65% of wind-pollinated fruits were deformed, open pollination resulted in only 20% deformed fruits. During storage, the proportion of decayed fruits increased in relation to the degree of deformation. In the variety Yamaska, 80% of the fruits with high degrees of deformation decayed after four days, whereas in the variety Sonata, all highly deformed fruits had already decayed after three days. Fruit weight decreased independent from the degree of deformation. However, strongest deformations resulted in a generally lower fruit weight in Sonata, whereas in Yamaska, also medium deformed fruits had a lower weight than highly deformed fruits. Effects of deformation on firmness declines were mostly variety dependent. Whereas firmness declined similarly for all degrees of deformation for Yamaska, highly deformed fruits lost firmness fastest in Sonata.

Conclusions: Our results suggest that crop pollination has the potential to reduce food loss and waste in pollinated crops and thus to contribute to global food security. However, this relationship between pollination and food waste has so far been almost completely ignored. Future pollination research should therefore focus not only on yield effects but also on crop quality. A more comprehensive understanding of how pollination can benefit global food security should lead to a more efficient crop production to help meeting future food demands.

Keywords: Decay, Deformation, Food loss, Food waste, Fruit quality, Pollination limitation

Background

The global population is predicted to increase to up to 9 billion people by the year 2050 [1]. The main consequence will be a rising demand for food, which highlights the importance of global food security [2]. Fruits and vegetables form a substantial proportion of human food with a global consumption of more than 1.5 million tons in 2011 [3]. They contribute to a healthy human diet by providing essential nutrients such as vitamins, antioxidants and fibre [4]. Many people are lacking a sufficient nutrient supply even today [1]. Nevertheless, large portions of fruits and vegetables are being lost due to degradation during handling, transport and storage directly after harvest or are wasted at retail and consumer levels [5]. Thus, nutrient

supply is not only a matter of production quantities, but further depends on the quality of agricultural products, which has become a major problem with increasing attention in policy and scientific research [6].

An important factor determining the quality of fruits and vegetables is their shelf life [7,8]. In particular, fruits have a relatively short shelf life leading to declining quality during storage due to degradation of the fruit through softening, weight loss and decay [8]. Several studies have focused on the potential extension of fruit shelf life [8] by using postharvest treatments like modified storage procedures with specific coatings [9] or heat treatments [10]. In addition, quality manipulations in transgenic plants have been considered [11]. There is evidence from a few recent studies that insect pollination may not only benefit crop yield but also influence the shelf life of agricultural products. Greater firmness of insect-pollinated tomato [12], oriental melon [13], cucumber [14] and strawberry [15] only indirectly indicates possible effects of insect

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pollination on shelf life. Pollinator-enhanced shelf life could be an important solution to reduce postharvest losses, but data proving a direct relationship between insect pollination and shelf life are still lacking. Furthermore, firmness has been used as a proxy for shelf life, whereas it has not yet been tested whether increased firmness results in pollinator-enhanced shelf life under storage conditions.

The aim of this study was to test the direct relationship between insect pollination and crop shelf life, using strawberry as a model crop. The economic importance of strawberry is increasing globally [3], and insect pollination can improve yield as well as quality. Strawberries have a short shelf life because of fast quality loss during storage, which is due to high metabolic activity and sensitivity to fungal decay [16]. Almost 90% of fruits are lost after only four days in storage [16]. Thus, shelf life is an important determinant of postharvest quality in strawberries [17]. We analysed the impact of pollination on the shelf life of strawberries based on the degree of fruit deformation, which is another important reason for quality loss in strawberries. Deformations are caused by pollination limitation, which leads to achenes, the true nut-fruits of the strawberry, being unfertilized and thereby unable to build tissue [17]. Firmness, fruit weight and decay were used as fruit quality parameters determining shelf life [16]. We expected fruit quality to decline during storage due to decreasing firmness and fruit weight and increasing decay of the fruits. The degradation was expected to vary in relation to the degree of deformation, which is directly related to pollination limitation [17-19].

Methods

The study was conducted on a conventionally managed strawberry field near the city of Göttingen in 2012, focusing on the simultaneously yielding varieties Yamaska and Sonata. For the variety Sonata, 15 pairs of adjacent strawberry plants were randomly selected to assess whether fruit deformations were a result of pollination limitation. From each pair, one plant was covered with

gauze to prevent insect pollination (wind pollination treatment), whereas the other plant was left open and thus accessible for insect pollinators. Three flowers from each plant were selected for analysis before pollination. For those flowers, fruit set was recorded and the fruits were harvested at maturity, when the entire fruit showed an intense red colour.

To assess the relationship between pollination limitation and shelf life, we focused on fruits showing different degrees of deformation, when these were obviously caused by pollination limitation. As development of all achenes depends on pollination and deformations are the result of missing achenes, pollination limitation is visible by aggregations of small unfertilized achenes at the deformation. Fruits from both varieties, Sonata and Yamaska, were harvested at maturity and then grouped in three categories based on their degree of deformation (Figure 1) following the official trade guidelines [20]. Fruits without deformations were assigned to the group 'None', fruits with slight to medium deformations were assigned to the group 'Medium' and heavily deformed as well as overall misshapen fruits were assigned to the group 'High'. All selected fruits did not show any physical damage or fungal infection. Strawberries flower in consecutive flowering periods [21]; only data collected from the second flowering period were analysed because of low numbers of fruits from other flowering periods.

The fruits were stored at 20°C for four days to simulate retail conditions [16,22]. To prevent fruits from infecting each other with fungi or being mechanically damaged during storage, fruits were carefully laid in egg boxes, eliminating direct contact. On each consecutive day, a random set of 7 to 13 fruits was selected from each group of deformation ('None', 'Medium', 'High'), and shelf life was assessed by analysing firmness, fruit weight and the proportion of decayed fruits. First, each fruit was visually inspected for surface damage and fungal decay and then weighed (BA2001 S, Sartorius). Firmness was then analysed using a texture analyser (TA-XT2 Texture Analyzer, Stable Micro Systems) following Sanz et al. [22]. The

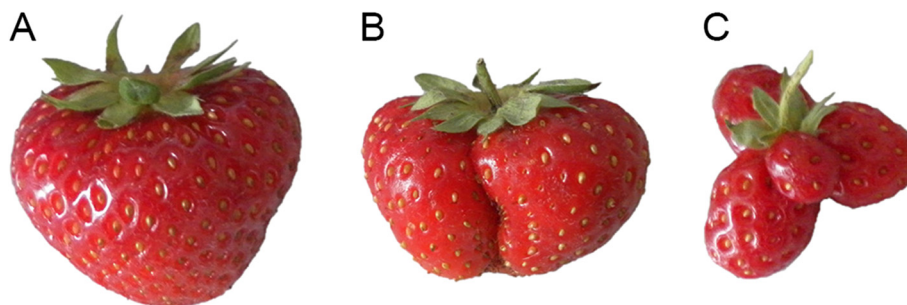


Figure 1 Strawberry fruits with different degrees of deformation. (A) Fruit without deformations (*None*). (B) Fruits with slight up to medium deformations (*Medium*). (C) Fruits with high deformations (*High*).

peduncle and calyx were removed and fruits were bisected. Firmness was measured at the centre of each half. The texture analyser was fitted with a 5-mm-diameter probe and a 25-kg compression cell with the following adjustments: pre-test speed 6.00 mm/s; test speed 1.0 mm/s; post-test speed 8.0 mm/s; penetration distance 4 mm; trigger force 1.0 N. The maximum force in Newtons reached during tissue breakage was recorded as a measure of firmness [22], and mean values of both halves for each fruit were used for statistical analysis.

We used generalized linear models 'glm'-function in package 'stats'; [23] in R 3.1.1 [24], to test whether the amount of deformed fruits differed between open and wind-pollinated plants, using quasi-poisson distribution to account for overdispersion. The influence of fruit deformation on shelf life was analysed using generalized linear mixed effects models 'glmer' function in package 'lme4'; [25] by testing whether degrees of deformation in interaction with storage time had an effect on decay, firmness and fruit weight. According to our study design, degrees of deformation and storage time were also used as random effects. First, the model of each shelf life parameter was simplified until reaching the best fit by stepwise deleting interactions and fixed effects, using second order Akaike's Information Criterion 'AICc'-function in package 'MuMIn' [26]. In all models, the interaction between storage time and degrees of deformation had to be deleted, whilst storage time and degrees of deformation stayed. Second, we tested whether the different degrees of deformation equally contributed to explain changes in the response variable by comparing a model with degrees of deformation kept separately (full model), models with successively pooled degrees of deformation and a model without fixed effects (see Additional file 1) [27]. Again, AICc was used for model comparisons and the results were listed in Table 1. The lowest AICc for models with pooled levels indicated that these levels did not differ, whereas the lowest AICc for the full model indicated that degrees of deformation generally differed. If there was no difference between any

degree of deformation, the model with just time as a fixed effect had the lowest AICc value. Decay was modelled using binomial distribution, firmness and fruit weight assuming normal distribution. Residuals were inspected to meet model assumptions of variance homogeneity and specific distributions and data were transformed where necessary. There were several obvious measurement failures from the last day in storage for highly deformed fruits from the variety Sonata. Few mistakes have happened during harvest due to possibly harvesting the wrong variety, in the identification of the degree of deformation or during measurements, but could not be post-experimentally evaluated and thus these values were excluded from analysis.

Results

The amount of deformed fruits differed significantly between open- and wind-pollinated plants ($F_{1,24} = 11.088$; $P = 0.003$; Figure 2). On average, less than 20% of the open-pollinated fruits showed deformations, whilst almost 65% of the wind-pollinated fruits were deformed. The shelf life of strawberries in both varieties was strongly determined by fruit deformation and thus pollination limitation. In Yamaska, decay differed according to all degrees of deformation, indicated by the lowest AICc for the model with unpooled fixed effects (Figure 3A; Table 1). Medium and highly deformed fruits decayed faster compared with the non-deformed fruits. After four days in storage, almost 80% of the fruits with medium and high degrees of deformation were decayed, but only 30% of the fruits without deformations were decayed. In Sonata, decay was similar for non- and medium deformed fruits, indicated by the lowest AICc for the model where these effects were pooled (Figure 3B; Table 1). However, highly deformed fruits decayed fastest. Almost 60% of non- and medium deformed fruits were decayed after four days in storage, whilst 100% of the highly deformed fruits were already decayed after the third day in storage.

Table 1 Delta AICc values resulting from model comparisons

Variety	Fruit parameter	Pooled levels				
		None	None and medium	Medium and high	None and high	Sans
Sonata	Decay (<i>n</i> = 123)	2.026	<i>0</i>	9.755	10.193	8.671
	Firmness (<i>n</i> = 123)	5.349	<i>0</i>	4.808	4.651	3.052
	Fruit weight (<i>n</i> = 123)	0.974	<i>0</i>	2.433	2.952	3.480
Yamaska	Decay (<i>n</i> = 157)	<i>0</i>	2.613	0.706	5.677	3.572
	Firmness (<i>n</i> = 154)	3.311	1.738	0.036	2.448	<i>0</i>
	Fruit weight (<i>n</i> = 157)	<i>0</i>	3.448	3.005	4.625	7.611

AICc = 0 indicates the model with the highest explanatory power. Lower delta AICc indicates better explanatory power of a model. The most explanatory models are highlighted in *italics*. Sample sizes are given in *brackets* behind fruit parameters. None = all treatment levels kept separately; Sans = model without treatment as fixed effect.

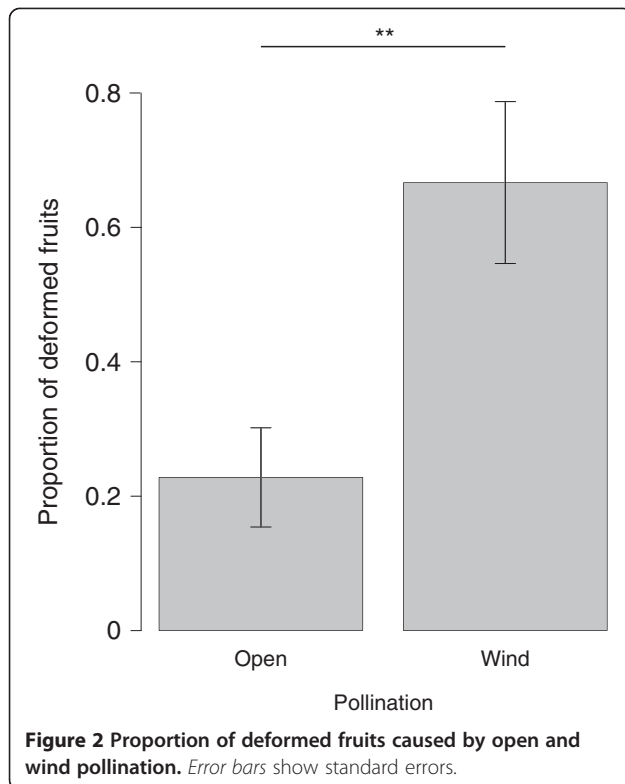


Figure 2 Proportion of deformed fruits caused by open and wind pollination. Error bars show standard errors.

The declines in firmness and fruit weight were also related to the degree of deformation, except for the variety Yamaska. Here, firmness similarly declined in all degrees of deformation (Figure 3C; Table 1). In Sonata, firmness decreased equally in non- and medium deformed fruits, but much faster in highly deformed fruits (Figure 3D; Table 1). In both varieties, fruit weight decreased to a similar extent in all degrees of deformation (Figure 3E,F; Table 1). However, fruit weight generally differed between all degrees of deformation in the variety Yamaska, with a highest weight in non-deformed fruits and lowest weight in highly deformed fruits. In Sonata, non- and medium deformed fruits had similar weight, whilst highly deformed fruits were much lighter.

In both varieties, fruit decay was negatively correlated to firmness (Sonata: *Spearman's correlation* = -0.91; $P < 0.001$; Yamaska: *Spearman's correlation* = -0.91; $P < 0.001$) and fruit weight (Sonata: *Spearman's correlation* = -0.70; $P = 0.005$; Yamaska: *Spearman's correlation* = -0.79; $P < 0.001$), whilst firmness and fruit weight were less strong, but positively correlated (Sonata: *Spearman's correlation* = 0.65; $P = 0.015$; Yamaska: *Spearman's correlation* = 0.63; $P = 0.015$).

Discussion

Our results verify the relationship between pollination limitation and shelf life, with experimental data. The decay

of strawberry fruits was strongly dependent on the degree of deformation, which was caused by pollination limitation.

Pollination limitation and fruit deformation

Open pollination produced almost solely non-deformed fruits, whilst wind pollination resulted in high amounts of deformed fruits. Deformations in strawberry fruits are a result of pollination limitation, mainly due to the absence of insect pollinators [28]. The mechanism is based on the amount of fertilized achenes [17], the true 'nut'-fruits of strawberry being an aggregated fruit [18]. Unfertilized achenes are a result of pollination limitation [28] and have no physiological functionality [29]. Aggregations of unfertilized achenes usually lead to deformations in strawberry fruits [17,30] and thus deformations can be directly linked to insufficient pollination.

Shelf life as a function of fruit deformation due to pollination limitation

We used deformations resulting from pollination limitation to test the relationship between pollination and shelf life. In both varieties, highly deformed and thus strongly pollination-limited fruits had a shorter shelf life, due to faster decay as well as lower firmness and fruit weight during the entire storage time. However, differences between medium and undeformed fruits were not the same across varieties. Fertilized achenes produce hormonal growth regulators which enhance cell progeny and size and thereby increase fruit weight [31]. Also, the firmness of strawberry fruits is functionally based on fertilized achenes. During fruit ripening, the fruit produces cell wall-degrading proteins [32], which lead to decreasing firmness. The expression of several of these proteins is limited by the growth regulators [33], which thereby decelerate fruit softening and lead to higher firmness. Cell wall-degrading proteins lead to the loss of water and fruits become softer and lighter [16] and thereby also more sensitive to mechanical damage as well as fungal decay [16]. This explains the strong correlation of the loss of firmness and weight with the decay of strawberry fruits. However, although decay and fruit weight of Yamaska was more strongly affected by both, medium and non-deformed fruits, there was no difference between undeformed and medium deformed fruits in Sonata. Thus, effects of fruit deformation and therefore pollination seem to change with variety. Although strawberries are generally dependent on insect pollination, this varies between varieties due to differences in the dependence on insect pollination. This has been shown for fruit weight and the amount of deformations caused by pollinator exclusion [19] and also for various quality aspects [15]. Reasons could be morphological differences, e.g. when anthers are located above the receptacle allowing for better self pollination [34] or differences in

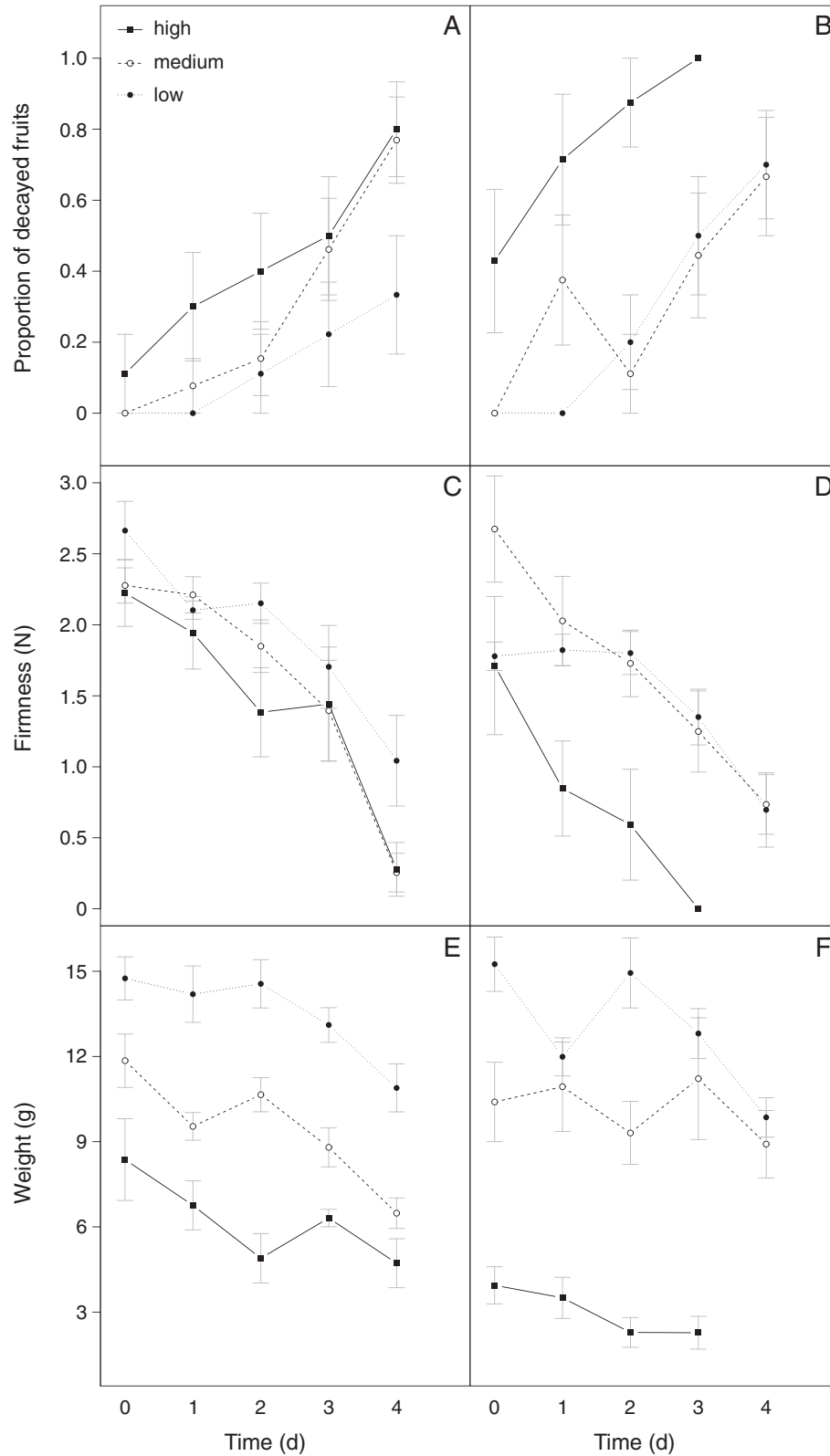


Figure 3 The dependence of fruit degradation during storage on the degree of deformation. Proportion of decayed fruits: (A) Yamaska, (B) Sonata. Firmness: (C) Yamaska, (D) Sonata. Fruit weight: (E) Yamaska, (F) Sonata. Standard errors are displayed in grey for better visualization.

attraction of pollinators by varieties varying in the amount of floral volatiles emitted [35].

General significance: application to other crops

In general, plant hormones play a key role for developmental processes and also determine fruit development [36]. Deformation and decreased weight are common problems triggered by pollination limitation in fruit crops such as strawberries [18]. For a few crop species, an influence of pollination limitation on fruit firmness has also been demonstrated [18]. Hence, it is likely that pollination limitation generally results in reduced shelf life in fruits and vegetables by impeding the production of plant hormones [36]. However, those effects so far have only been shown for strawberry and more research is required to confirm more general effects for other pollinated crops.

Although most pollinated crops do not belong to the major food crops, their products are of essential importance for a healthy human diet because they contain large amounts of essential nutrients [4]. Even today, nutrient supply is limited for large parts of the human population. In the following decades, an increasing world population will lead to further rising demands for food [1], especially given that the importance of pollination-dependent crops is largely increasing [2]. Our findings suggest that declining pollination services in agricultural landscapes [37] will likely increase the economic loss and waste of products from pollinated crops in the food chain as a consequence of decreasing shelf life. Thus, these products could become scarcer in the near future, leading to a general depletion in the supply of essential nutrients and further limiting availability to people in the developing world due to increasing prices. Already today, shelf life for which deformations and decay are important values appears to be of tremendous importance due to the increasing loss and waste of food [5]. Deformed fruits and vegetables have a lower market value [38] but can still be found at retail and consumer levels.

Conclusions

In conclusion, pollination is a key driver for both the appearance and the shelf life of strawberries. Similar effects of pollination limitation on pollinated crops suggest this pattern could be generally applicable, but empirical evidence for such effects is largely missing. Nevertheless, our results highlight the need to stabilize pollination services, as the importance of pollination-dependent crops is rapidly increasing [2], whilst pollination services are in danger of various anthropogenic threats [37]. Our study provides a new perspective on the relationship between food shelf life and pollination, emphasizing the need to protect and enhance pollination

services through international policies and conservation strategies.

Availability of supporting data

Supporting data will be made available in a publicly-accessible data repository (e.g. 3TU Datacenter: <http://data.3tu.nl/repository>).

Additional file

Additional file 1: Example for statistical analysis, comparing models with separate fixed effect levels, pooled fixed effect levels and without fixed effect.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

BKK evolved the design of the study, performed statistical analysis and interpretations of results and wrote the manuscript. FK performed lab analysis and participated in drafting the manuscript. CW and TT contributed to the design of the study, gave intellectual input to data interpretation and helped to draught the manuscript. All authors have read and approved the final version of the manuscript.

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