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The effect of relative humidity and the use of algae-based biostimulants on fruit set, yield and fruit size of arctic bramble (*Rubus arcticus*)

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Arctic bramble is a niche berry crop with highly variable yield and fruit quality, often limited by low fruit set and incomplete fruit development. In this study, we investigated the effects of relative humidity (RH) and algae-based biostimulants on fruit set, yield, fruit weight and the number of drupelets per fruit. In Experiment 1, arctic bramble cvs. 'Alli' and 'Mesma' were grown in a greenhouse in 40, 60 or 80% RH and pollinated by bumblebees. In Experiments 2 and 3, commercial biostimulant products Kelpak, Cremalga, Kriss and Alginamin were tested on cv. 'Alli' in a greenhouse, and an open high tunnel. Fruit set and yield were strongly affected by RH, being highest in either 40% RH for cv. 'Mesma' or 60% RH for cv. 'Alli', reduced by nearly 50% in 80% RH. Kriss and Alginamin increased fruit weight by as much as 18% but there was no effect on total yield. We conclude that control of relative humidity in greenhouse cultivation, especially to avoid very high RH conditions, can be highly beneficial for arctic bramble, and that algae-based biostimulants show potential to improve fruit weight.

Key words: fruit crops, cropping systems, fruiting potential, pollination

Introduction

Arctic bramble (*Rubus arcticus* L.) is a niche *Rubus* fruit harvested from the wild and cultivated on a small scale, mainly in Finland. It is highly valued for its exquisite aroma, while efficient production methods are still under development and the cost of production remains high. The yields fluctuate strongly between years both in the wild (Mavi 2012) and in traditional field cultivation (Ryynänen 1973, Kokko et al. 1993). We believe that if a modernized cultivation system allowed reliable production of high quality fruit, arctic bramble could have a substantially wider market as a high value luxury berry crop.

The arctic bramble is a perennial rhizomatous plant, with annual aboveground shoots of typically 10–30 cm in length that originate during the previous year from either root buds or basal axillary buds (Ryynänen 1972, 1973). The shoot apices undergo floral initiation at an early growth stage, while still underground, and remain dormant over winter (Zeller 1964). After the initial growth flush and flowering in the spring, there is often a second flowering associated with the growth of axillary shoots (Ryynänen 1973, Palonen et al. 2012). The arctic bramble is self-sterile and requires insect cross-pollination for fruiting (Tammisola and Ryynänen 1970, Tammisola 1988). The main challenges of arctic bramble field cultivation in Finland include weak competitiveness of the plant against weeds (Ryynänen 1973, Hellqvist 2000, Kokko et al. 2012) and the emergence of fungal diseases during the 1990s, particularly 'dryberry' disease (Lindqvist et al. 1998, Kokko et al. 1999, Koponen et al. 2000). Harvest is complicated by the relatively long ripening season, low fruit weight of typically ca. 1 g (Ryynänen 1972, Kostamo et al. 2013), and the often prostrate habit of the plant, which also exposes the ripening fruits to soil contamination and mold infections. Many of these problems can be solved with, container cultivation in a protected environment (greenhouse or plastic tunnel), as has become common in e.g. strawberry cultivation, protecting the fruits from weather and elevating the plants to a more convenient picking height. Tommila et al. (2022a, 2022b) evaluated different organic substrate materials in arctic bramble protected container cultivation, and found *Sphagnum* moss to be a highly promising renewable alternative for traditional peat-based substrates.

The reasons for arctic bramble yield fluctuations remain poorly understood, although the likely main factors are weather conditions affecting flower bud development, pollination and fruit development (Kostamo et al. 2018). The arctic bramble plants usually flower abundantly, but fruit set is often poor (Ryynänen 1973, Kostamo et al. 2015) and many of the fruits that are set may dry up or otherwise spoil during development (Kokko et al. 2012, Kostamo et al. 2015). Poor fruit set in arctic bramble is associated with lower fruit quality due to the development of fewer drupelets per aggregate fruit, resulting in smaller and often misshapen or otherwise aesthetically less appealing fruits. Likewise, in other *Rubus* species such as red raspberry (*Rubus idaeus* L.), fruit weight, fruit shape

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and the number of drupelets are considered relevant morphological criteria for fruit quality (Titirică et al. 2023). Hiirsalmi (1975), observing that elevating the relative humidity (RH) by misting in protected cultivation increased arctic bramble fruit yield in dry summer conditions, concluded that arctic bramble pollination may benefit from a moderately high RH during flowering season. On the other hand, flowering often continues concurrently with fruit development and ripening, where high RH or associated rain and dew could increase the risk of fruit spoilage due to mold infections. Kostamo et al. (2018) note that rainy weather during harvest season often causes spoilage in the ripening fruits.

Biostimulants have been recently adopted in agriculture as a diverse group of beneficial substances applied to crops, outside the conventional categories of fertilizers, soil improvers and pesticides. du Jardin (2015) defines plant biostimulants as "any substance or microorganism applied to plants with the aim to enhance nutrition efficiency, abiotic stress tolerance, and/or crop quality traits, regardless of its nutrients content". EU Fertilizer Regulation (EC) No 2019/1009 defines plant biostimulants for EU regulatory purposes as products that are meant to "stimulate plant nutrition processes independently of the product's nutrient content", to improve either nutrient use efficiency, tolerance to abiotic stress, quality traits or nutrient availability. According to du Jardin (2015), biostimulant preparations can include seaweed and plant extracts, humic and fulvic acids, protein hydrolysates and other N-containing compounds, biopolymers such as chitosan, salts containing certain chemical elements and beneficial fungi and bacteria.

In particular, biostimulant preparations based on brown algae such as *Ascophyllum nodosum* have been extensively used and studied for their effects in horticulture (reviewed by Parađiković et al. 2019, Shukla et al. 2019). According to Craigie (2011) and Khan et al. (2009), seaweed extracts contain a large variety of growth-promoting substances, including the plant hormones cytokinins, auxins, abscisic acid and gibberellins, as well as sterols, polyamines, certain polysaccharides, N-containing compounds and micro- and macronutrients. Wally et al. (2013a, b) found evidence that the hormonal effects of algal extracts may be based on down- and upregulation of hormone biosynthesis pathways in the plants themselves, rather than the hormones present in the extracts themselves.

In berry crops, biostimulants can be used to improve various crop quality traits, including fruit set and the amount of yield (for example Grajkowski and Ochmian 2007, Krok and Wieniarska 2008, Ochmian et al. 2008, Loyola and Muñoz 2009, Szot et al. 2014). In arctic bramble, elicitors i.e. plant immunity-enhancing compounds have been assessed as a method to control downy mildew (*Peronospora sparsa*) (Kostamo et al. 2015), but there has been no research on the improvement of arctic bramble yield or fruit quality using biostimulants.

The aim of this study was to test the following hypotheses: (1) RH conditions during flowering affect arctic bramble fruit set, yield, fruit weight or the number of drupelets in a fruit, (2) RH conditions during fruit development affect the rate of fruit spoilage before harvest, (3) the use of algae-based biostimulant preparations during shoot growth increases the number or flowers produced, and (4) the use of algae-based biostimulant preparations during flowering and fruit development increases fruit set, fruit weight or the number or weight of individual drupelets in a fruit. Hypotheses 1 and 2 were tested in a greenhouse cultivation experiment using two arctic bramble cultivars (Experiment 1, [Exp 1.]), while hypotheses 3 and 4 were tested in both greenhouse (Experiment 2, [Exp 2.]) and high tunnel (Experiment 3, [Exp 3.]) environment on only one cultivar.

Material and methods

Cultivation environment

The three cultivation experiments took place at University of Helsinki Viikki campus (60°14'N 25°1'E) using container-grown arctic bramble plants that had been propagated at the start of the previous growth season by dividing parental root systems into small units. These divisions were planted in 10 cm containers filled with unlimed peat (Luonnonturve, von Post 2–4, Kekkilä, Vantaa, Finland) as substrate, cultivated outdoors until freezing in November and subsequently cold-stored at –1 °C. For the experiments, the plants were replanted in larger containers and cultivated in a protected environment for 14–16 weeks (Exp. 1 and Exp. 2) or for one full natural growth season (Exp. 3). Cross-pollination was provided by placing plants of at least one additional arctic bramble cultivar in close proximity to the plants used in the experiments. Bumblebee (*Bombus terrestris*) hives (Minipol, Koppert Biological Systems, Romulus, MI, USA) were used as the sole pollinator in greenhouse (Exp. 1 and Exp. 2), and to assist natural pollinators during early flowering in plastic high tunnel (Exp. 3). Predatory mites *Neoseiulus cucumeris* and *Phytoseiulus perisimilis* (Biotus Oy, Forssa, Finland) were used to control thrips and spider mites. In Exp. 2 and Exp. 3, foliar spray of 5% ethanol was used to control powdery mildew after visible symptoms began to appear on the leaves.

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Relative humidity treatments in a greenhouse

Exp. 1 was conducted from January to May 2014 in three 50 m^2 greenhouse compartments where RH was controlled at 40%, 60% or 80% (thereafter referred to as RH40, RH60 and RH80) using automated misting and ventilation. Each treatment setup included 30 single container replicates of cv. 'Alli' and 30 of cv. 'Mesma', laid out together in a nested block design. There were five blocks in each treatment, each block consisting of six replicates of each cultivar. The subpopulation sample included one randomly selected container per block per cultivar, in total five replicates. Spacing of plants was 30 cm × 30 cm in four rows. Each treatment setup was surrounded by a single row of cv. 'Mesma' and cv. 'Pima' plants serving as a buffer and pollinizer. The plants were taken from cold storage on 15 January and kept all in RH60 during early shoot growth. During this period, the temperature was 15 °C. On 23 January, the plants were replanted in 2-liter containers filled with unlimed peat. On 31 January, the RH40 and RH80 groups were separated, and on 7 February, temperature was raised to 18 °C. Artificial lighting was given 18 hours a day with high pressure sodium lamps, and intensity adjusted in all treatments to ca. 130 µmol s^{-1} m^{2-1} (measured with LI-189 Light Meter and LI-190 Qantum Sensor, LI-COR Biosciences, Lincoln, NE, USA). The plants were watered manually, using individual trays to collect drainage. Fertilization included 5 g per plant of Puutarhan Syksy (Kemira GrowHow, Finland, N-P-K 0-5-20) mixed in the substrate during planting and 6 g per plant of Taimi-Superex (Kekkilä, Finland, N-P-K 19-4.4-20) divided into 12 weekly fertigation doses.

Flowering started on 10 February, but the first stage of flowering did not peak until the end of February. The second stage of flowering started in March and continued well into April. Bumblebee hives were installed in each greenhouse compartment on 25 February, and flowers that had opened prior to this were removed, since they had not had a chance to be pollinated. By the end of March, the hives were deemed to have become nearly inactive, and flowers that opened after 31 March were also removed. The observations on flowering and yield formation were thus based on flowers that opened between 25 February and 31 March, which we refer to as pollination period. Fruits were picked in four batches on 6 April, 16 April, 24 April and 2 May. More than half of the total harvested yield accumulated from the second batch, which corresponded to the peak of first flowering phase.

Biostimulant preparations

In Exp. 2 and 3 we focused on using commercial biostimulant preparations based on brown algae extracts, selecting products that are widely used in fruit cultivation. The four preparations selected for this study (Cremalga, Biolchim, Medicina, Italy; Kelpak, Kelp Products (Pty) Ltd, Simon's town, South Africa; Kriss, Biolchim, Medicina, Italy and Alginamin Campag, Munster, Germany) had largely similar active ingredients: exclusively or most prominently the bioactive compounds present in brown algae (*Ecklonia*, *Ascophyllum*, *Macrocystis*, *Sargassum*; Table 1).

Table 1. List of the biostimulant products used in Experiments 2 and 3, their ingredients according to the manufacturers and, for different treatments, application concentrations, numbers of applications, application schedules and targeted growth stages

Preparation	Ingredients	Exp.	Concentration (%)	Number of applications	Interval (days)	Starting day	Target stage
Cremalga	*Ecklonia*, *Ascophyllum*, VAAs	2	0.10	7	7	21	flowering, fruit development
Kelpak	*Ecklonia*	2	0.25	3	14	28	flowering, fruit development
		2	0.50	3	14	28	
		3	0.25	5	14	10	shoot growth, flowering
		3	0.25	3	28	10	
Kriss	*Trigonella*, *Ascophyllum*, CGE, VAAs, tryptophan, arginine, UBs	2	0.25	3	7	35	early fruit development
		3	0.25	9	7	24	flowering, fruit development
		3	0.25	5	14	24	
Alginamin	*Ascophyllum*, *Macrocystis*, *Sargassum*, peptides, VALMWs	3	0.05	9	7	10	shoot growth, flowering

VAA = vegetal amino acid; CGE = corn germ extract; UB = uptake bioenhancer; VALMW = vegetal amino acid of low molecular weight

All preparations are claimed to have broad beneficial effects on plant growth and metabolism, with specific references to improved yield (Kelpak,), fruit set (Cremalga (Biolchim, Medicina, Italy), fruit size and quality (Kelpak, Kriss,

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Alginamin) and extended flowering/harvest season (Kelpak). The preparations were applied as a foliar spray diluted with tap water, following the user instructions as closely as applicable. Diluted concentrations and targeted growth stages (Table 1) were selected based on the instructions.

Biostimulant treatments in a greenhouse

Exp. 2 was conducted from February to May 2015 in a 50 m^2 greenhouse compartment. The setup included four biostimulant treatments plus control with 16 single container replicates of cv. 'Alli' for each, laid out in four rows as a randomized complete block design. Each row constituted a block with four replicates per treatment. Spacing was 60 cm between the rows and 21 cm between the plants in a row. The plants were surrounded by a single row of cv. 'Mesma' and cv. 'Pima' containers serving as a buffer and pollinizer. The plants were taken from cold storage on 4 February and replanted in 2-liter containers filled with horticultural peat (OPM 420 W, von Post 1–3, Kekkilä, Vantaa, Finland). The temperature was 16 °C and artificial lighting was given for 20 hours a day at 150 µmol s^{-1} m^{2-1} with high pressure sodium lamps. The plants were watered manually, using individual trays to collect drainage. Fertilization included 5 g per plant of Puutarhan Syksy (Kemira GrowHow, Finland, N-P-K 0-5-20) mixed in the substrate during planting and 6 g per plant of Taimi-Superex (Kekkilä, Finland, N-P-K 19-4.4-20) divided into 12 weekly fertigation doses.

Flowering started on 25 February, at which time a bumblebee hive was installed in the greenhouse and the treatments (Table 1) were started. The preparations used included Cremalga, Kelpak and Kriss. The plants were treated seven times with weekly foliar sprays until 8 April, using always either the preparation or tap water as a control. The first flowering phase peaked during the first half of March and the second phase started shortly after that, continuing into April. On 31 March, the bumblebee hive and subsequent flowers were removed, limiting the pollination period to five weeks. Fruit harvest took place weekly from 9 April to 14 May. The accumulation of yield peaked on 16 April and 7 May, corresponding to the peaks of the two flowering phases. The development of fruits from first flowering took place mostly concurrently with the biostimulant treatments. The fruits from second flowering were set during the treatments, but their development took place largely after the treatment regime had ended.

Biostimulant treatments in a high tunnel

Exp. 3 was conducted from May to September 2015 in a high polyethylene tunnel (length 35 m, width 8 m, maximum height 3.8 m) under natural light conditions, partially shaded by red raspberry (*Rubus idaeus* L.) plants. The setup included six biostimulant treatments plus control with 16 single container replicates of cv. 'Alli' for each, laid out in four rows as a completely randomized design. The subpopulation sample included four replicates per treatment. Spacing was 120 cm between the rows and 60 cm between the plants in a row. Every third place in a row was substituted with a cv. 'Mesma' or alternately cv. 'Pima' container serving as a pollinizer. At the end of each row, there were in total six containers of cv. 'Mesma' and cv. 'Pima' serving as a buffer. The plants were taken from cold storage on 10 May and replanted in 3.5-liter containers filled with horticultural peat. Fertigation was automatic with 1.0 mS cm^{-1} (0.6 g l^{-1}) Ferticare (Yara, Oslo, Norway, N-P-K 7-3.9-27)

Flowering started on 25 May, but only became abundant in mid-June, with no clear lag between the first and second flowering phases, and effectively ended by 31 July. The preparations used in included Kelpak, Kriss and Alginamin (Table 1) The plants were treated eleven times with weekly foliar sprays from 20 May to 29 July, using always either the preparation or tap water as a control. Fruit harvest took place weekly from 29 July to 1 September.

Observations and statistical analyses

In all experiments, observations included the total number of flowers and fruits produced, and the fruit set percentage based on these. Fruits of marketable quality were counted and weighted separately as harvested yield, for which mean fruit weight was calculated. Fruits that spoiled before ripening due to mold infection or drying were counted separately from the yield, and fruit spoilage rate was calculated as percentage of the total number of set fruits.

In statistical analysis, single containers were treated as experimental units. In Exp. 1 and Exp. 3, a smaller number of containers was randomly selected from the whole population to form a subpopulation sample, in which all fruits harvested as yield were dissected to count the number of drupelets within a fruit. Based on the number of drupelets, and the fruit weight within the subpopulation, the mean weight of individual drupelets was calculated.

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All data (harvested yield, number of flowers, fruit set, fruit spoilage, number of harvested fruits and fruit weight in the whole population; fruit weight, number of drupelets and drupelet weight in the subpopulation sample) were subjected to analysis of variance (ANOVA) using ANOVA procedure (Exp. 1 and Exp. 2) or GLM procedure (Exp. 3) of SAS (SAS 241 Institute 2003). Means were separated using Tukey's Studentized Range (HSD) test. Pearson's correlation coefficients were calculated using CORR procedure between the six variables from the whole population and between the three variables from the subpopulation sample.

Results

In Exp. 1, the total number of flowers produced during the pollination period was affected by RH in cv. 'Mesma', being highest in RH60 (Table 2). The fruit set was lowest in RH80 in both cultivars, although the effect of RH was more pronounced in cv. 'Mesma'. The rate of fruit spoilage was affected by RH in cv. 'Mesma', being highest in RH60. In cv. 'Alli', the rate of fruit spoilage was overall much lower, with no difference between the treatments. The yield and the number of harvested fruits were distinctly highest in RH60 in cv. 'Alli' and in RH40 in cv. 'Mesma'. The fruit weight was affected in cv. 'Alli', being lowest in RH80. Positive correlations were observed in both cultivars between fruit set, the number of harvested fruits and yield (Table 3). Positive correlations with a relatively low coefficient (< 0.5) were also observed between fruit set and fruit weight, and between fruit weight and yield in both cultivars.

Table 2. Fruit yield and total number of flowers per container, fruit set, fruit spoilage, number of harvested fruits per container and fruit weight of two arctic bramble cultivars grown in three different RH treatments in a greenhouse. Values are means of 30 single container replicates, followed by ± standard error.

Cultivar	Treatment	Yield, g	Nr of flowers	Fruit set, %	Spoilage, %	Nr of fruits	Fruit weight, g
cv. 'Alli'	RH40	19 ± 1 b	36.6. ± 2.0 a	52 ± 2 a	6 ± 1	17.9 ± 1.3 b	1.09 ± 0.03 a
	RH60	28 ± 2 a	48.6 ± 3.3 a	57 ± 2 a	10 ± 2	24.7 ± 1.9 a	1.15 ± 0.03 a
	RH80	16 ± 1 b	41.4 ± 1.6 a	42 ± 2 b	9 ± 2	15.8 ± 1.1 b	0.97 ± 0.04 b
	p	< 0.001	n.s.	< 0.001	n.s.	< 0.001	< 0.001
cv. 'Mesma'	RH40	21 ± 1 a	90.7 ± 3.3 b	43 ± 2 a	33 ± 4 b	26.4 ± 1.2 a	0.79 ± 0.03 a
	RH60	12 ± 1 b	107.2 ± 3.0 a	30 ± 2 b	45 ± 2 a	17.6 ±1.4 b	0.70 ± 0.03 a
	RH80	10 ± 1 b	95.5 ± 3.5 b	23 ± 1 c	34 ± 3 b	14.5 ± 1.5 b	0.69 ± 0.03 a
	p	< 0.001	0.002	< 0.001	0.001	< 0.001	0.039

Different letters indicate statistically significant differences between the means for each cultivar separately by Tukey's test at $p< 0.05$. n.s. = not significant

Table 3. Pearson's correlation coefficient between the variables observed from the whole population (N = 90), combining three different RH treatments. A = cv. 'Alli'. M = cv. 'Mesma'.

Variable	Nr of flowers	Fruit set	Spoilage	Nr of fruits	Yield	Fruit weight
Nr of flowers		A n.s.	A n.s.	A 0.816***	A 0.760***	A n.s.
Fruit set	M n.s.		A n.s.	A 0.561***	A 0.566***	A 0.293**
Spoilage	M n.s.	M n.s.		A n.s.	A n.s.	A n.s.
Nr of fruits	M 0.283**	M 0.767***	M -0.545***		A 0.946***	A n.s.
Yield	M n.s.	M 0.823***	M -0.456***	M 0.912***		A 0.445***
Fruit weight	M -370***	M 0.371***	M n.s.	M n.s.	M n.s.	

Double asterisks indicate statistical significance at $p< 0.01$ and triple asterisks at $p< 0.001$. n.s. = not significant.

Within the subpopulation sample, no difference in fruit weight was observed, but the number of drupelets per fruit and the drupelet weight were affected by RH in both cultivars (Table 4). The number of drupelets was about twice as high in RH40 compared to RH80, while the drupelet weight was substantially lower. There was also a statistically non-significant trend towards higher fruit weight in lower RH. A positive correlation was observed in both cultivars between the fruit weight and the number of drupelets, and a negative correlation between the number

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of drupelets and the drupelet weight (Table 5). In cv. Alli, a negative correlation was also observed between fruit weight and drupelet weight.

Table 4. Fruit weight, number of drupelets per fruit and drupelet weight in a subpopulation sample of two arctic bramble cultivars grown in three different RH treatments in a greenhouse. Values are means of five single container replicates, followed by ± standard error.

Cultivar	Treatment	Fruit weight, g	Nr of drupelets	Drupelet weight, mg
cv. ‘Alli’	RH40	1.16 ± 0.04	25.5 ± 1.0 a	45 ± 1 b
	RH60	1.20 ± 0.09	22.3 ± 2.3 a	55 ± 2 b
	RH80	0.93 ± 0.10	11.7 ± 1.9 b	83 ± 5 a
	p	n.s.	< 0.001	< 0.001
cv. ‘Mesma’	RH40	0.85 ± 0.05	12.0 ± 1.0 a	72 ± 4 c
	RH60	0.78 ± 0.04	8.9 ± 0.5 ab	88 ± 3 b
	RH80	0.72 ± 0.10	6.6 ± 0.9 b	109 ± 5 a
	p	n.s.	0.002	< 0.001

Different lower case letters indicate statistically significant differences between the means for each cultivar separately by Tukey’s test at $p < 0.05$. n.s. = not significant

Table 5. Pearson’s correlation coefficient between the variables observed from the subpopulation sample (n = 15), combining three different RH treatments. A = cv. ‘Alli’. M = cv. ‘Mesma’.

Variable	Fruit weight	Nr of drupelets	Drupelet weight
Fruit weight		A 0.855 ***	A -0.680 ***
Nr of drupelets	M 0.731**		A -0.936***
Drupelet weight	M n.s.	M -0.823 ***	

Double asterisks indicate statistical significance at $p < 0.01$ and triple asterisks at $p < 0.001$. n.s. = not significant

In Exp. 2, the biostimulant treatments had no effect on the total number of flowers produced during the pollination period (Table 6). No effects on the fruit set, fruit spoilage, yield or the number of harvested fruits were observed either, although there were statistically non-significant trends towards higher yield and number of harvested fruits in several biostimulant treatments compared to the control, most prominently in plants treated with Kelpak. The fruit weight was affected by Kriss, being 12% higher compared to the control treatment (Table 3). Positive correlations were observed between the number of flowers, the number of harvested fruits and yield (Table 7). Positive correlations with a relatively low coefficient (< 0.3) were also observed between fruit set and the number of harvested fruits, and between fruit set and yield.

Table 6. Fruit yield and total number of flowers per container, fruit set, fruit spoilage, number of harvested fruits per container and fruit weight of arctic bramble cv. ‘Alli’ grown in a greenhouse with four different biostimulant treatments plus control. Treatment name consists of the name of the product followed by the concentration (%) and the number of applications. Values are means of 16 single container replicates, followed by ± standard error.

Treatment	Yield, g	Nr of flowers	Fruit set, %	Spoilage, %	Nr of fruits	Fruit weight, g
Cremalga (0.10) (7)	36 ± 3 ab	31.4 ± 2.9 a	85 ± 2	4 ± 1	25.3 ± 2.1	1.42 ± 0.05 ab
Kelpak (0.25) (3)	41 ± 3 a	34.9 ± 2.7 a	89 ± 1	4 ± 1	29.8 ± 2.1	1.39 ± 0.03 b
Kelpak (0.5) (3)	37 ± 3 ab	32.1 ± 2.6 a	85 ± 2	4 ± 1	26.3 ± 2.3	1.40 ± 0.04 ab
Kriss (0.25) (3)	38 ± 4 ab	31.1 ± 2.6 a	82 ± 3	1 ± 1	25.6 ± 2.4	1.52 ± 0.05 a
Control	29 ± 3 b	26.4 ± 3.3 a	85 ± 2	3 ± 1	21.6 ± 2.7	1.35 ± 0.03 b
p	n.s.	n.s.	n.s.	n.s.	n.s.	0.007

Different letters indicate statistically significant differences between the means within each treatment by Tukey’s test at $p<0.05$. n.s. = not significant

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Table 7. Pearson's correlation coefficient between the variables observed from the whole population (n = 80), combining five different biostimulant treatments.

Variable	Fruit set	Spoilage	Nr of fruits	Yield	Fruit weight
Nr of flowers	n.s.	n.s.	0.959***	0.859***	n.s.
Fruit set		n.s.	0.272*	0.275*	n.s.
Spoilage			n.s.	n.s.	n.s.
Nr of fruits				0.939***	n.s.
Yield					n.s.

Single asterisks indicate statistical significance at *p*< 0.05 and triple asterisks at *p*< 0.001. n.s. = not significant

In Exp. 3, the total number of flowers produced during the experiment was affected by the biostimulant treatments, being 27% lower with nine applications of Kriss (0.25%) and Alginamin (0.05%) compared to the control treatment (Table 8). No effects on the fruit set, fruit spoilage, fruit yield or the number of harvested fruits were observed, but the fruit weight was affected by nine applications of Kriss (0.25%) and Alginamin (0.05%), being 13 to 18% higher compared to the control treatment. Positive correlations were observed between the number of flowers, the number of harvested fruits and fruit yield (Table 9). Positive correlations with a relatively low coefficient (< 0.4) were also observed between fruit set and the number of harvested fruits, and between fruit set and fruit yield. In addition, the number of fruits and the fruit yield correlated negatively with fruit spoilage.

Table 8. Fruit yield and total number of flowers per container, fruit set, fruit spoilage, number of harvested fruits per container and fruit weight of arctic bramble cv. 'Alli' grown in a high tunnel with six different biostimulant treatments plus control. Treatment name consists of the name of the product followed by the concentration (%) and the number of applications. Values are means of 16 single container replicates, followed by ± standard error.

Treatment	Yield, g	Nr of flowers	Fruit set, %	Spoilage, %	Nr of fruits	Fruit weight, g
Kelpak (0.25) (5)	94 ± 10	116.7 ± 7.5 a	79 ± 2	33 ± 3	64.2 ± 7.3	1.50 ± 0.05 c
Kelpak (0.25) (3)	81 ± 10	108.8 ± 7.9 ab	79 ± 1	36 ± 3	55.9 ± 6.2	1.45 ± 0.05 c
Kriss (0.25) (9)	78 ± 10	83 ± 5.9 c	84 ± 1	39 ± 4	44.1 ± 5.8	1.78 ± 0.04 a
Kriss (0.25) (5)	87 ± 7	100.3 ± 5.8 abc	82 ± 1	34 ± 3	53.7 ± 3.9	1.62 ± 0.03 abc
Alginamin (0.05) (9)	83 ± 7	83.6 ± 5.2 bc	81 ± 1	30 ± 3	48.3 ± 4.5	1.71 ± 0.05 a
Alginamin 0.05) (5)	84 ± 7	95.7 ± 4.7 abc	81 ± 1	37 ± 3	49.3 ± 4.2	1.70 ± 0.05 ab
Control	82 ± 7	113.9 ± 4.1 a	80 ± 2	42 ± 3	53.9 ± 4.3	1.51 ± 0.04 bc
p	n.s	< 0.001	n.s.	n.s.	n.s.	< 0.001

Different lower case letters indicate statistically significant differences between the means by Tukey's test at *p*<0.05. n.s. = not significant

Table 9. Pearson's correlation coefficient between the variables observed from the whole population (n = 112), combining seven different biostimulant treatments.

Variable	Fruit set	Spoilage	Nr of fruits	Yield	Fruit weight
Nr of flowers	n.s.	n.s.	0.804***	0.730***	-0.236*
Fruit set		n.s.	0.257**	0.310***	n.s.
Spoilage			-0.683***	-0.672***	n.s.
Nr of fruits				0.946***	n.s.
Yield					n.s.

Single asterisks indicate statistical significance at *p*< 0.05, double asterisks at *p*< 0.01 and triple asterisks at *p*< 0.001. n.s. = not significant

Within the subpopulation sample, no difference in fruit weight, number of drupelets or drupelet weight compared to the control was observed, but the nine-dose treatments with Kriss (0.25%) and Alginamin (0.05%) produced a higher fruit weight than the three-dose treatment with Kelpak (0.25%) (Table 10). Nine applications of Kriss (0.25%) also produced a higher drupelet weight than either of the Kelpak treatments. A positive correlation was observed between fruit weight and the number of drupelets (0.62, *p*< 0.001), and between fruit weight and the drupelet weight (0.51, *p*= 0.005).

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Table 10. Fruit weight, number of drupelets per fruit and drupelet weight in a subpopulation sample of arctic bramble cv. 'Alli' containers in a high tunnel with six different biostimulant treatments plus control. Treatment name consists of the name of the product followed by the concentration (%) and the number of applications. Values are means of four single container replicates, followed by ± standard error.

Treatment	Fruit weight, g	Nr of drupelets	Drupelet weight, mg
Kelpak (0.25) (5)	1.44 ± 0.03 ab	35.2 ± 1.5	41 ± 3 c
Kelpak (0.25) (3)	1.19 ± 0.10 b	28.5 ± 3.3	42 ± 3 bc
Kriss (0.25) (9)	1.76 ± 0.05 a	32.5 ± 0.8	54 ± 1 a
Kris (0.25) (5)	1.54 ± 0.03 ab	30.8 ± 2.1	51 ± 3 abc
Alginamin (0.05) (9)	1.71 ± 0.12 a	35.1 ± 2.7	49 ± 3 abc
Alginamin (0.05) (5)	1.60 ± 0.15 ab	30.4 ± 2.3	52 ± 2 ab
Control	1.54 ± 0.07 ab	34.6 ± 2.0	45 ± 3 abc
p	0.009	n.s.	0.003

Different letters indicate statistically significant differences between the means by Tukey's test at $p < 0.05$. n.s. = not significant

Discussion

The effect of relative humidity on arctic bramble yield formation

In Experiment 1, we observed a strong effect of relative humidity in both cultivars. Hypothesis 1 was confirmed with regard to fruit set, yield and in cv. 'Alli' also with regard to fruit weight. Highest yields were achieved in low to mid (40 to 60%) RH range. There was a marked difference between the two cultivars in this regard, i.e. cv. 'Mesma' yielded best in RH40 and cv. 'Alli' in RH60. In RH80, the yields were reduced almost by half. The yield reductions in higher than optimal RH conditions were mainly associated with the strongly reduced fruit set in these treatments, although the fruit weight of cv. 'Alli' was also 16% lower in RH80 compared to RH60. Of the two cultivars, cv. 'Mesma' seemed to be especially sensitive to the effect of high RH on fruit set. Meanwhile, although higher fruit spoilage rate was associated with lower yield in cv. 'Mesma', there was no strong relationship between RH and fruit spoilage. In cv. 'Mesma', there was an unexpected 18% increase in the total number of flowers in RH60 compared to RH40, but this was not sufficient to counteract the reduction in fruit set.

Hypothesis 1 was also confirmed with regard to the number of drupelets per fruit. The reduced yield in high RH conditions was associated with substantially reduced drupelet count, which reduced fruit weight in cv. 'Alli'. Although lower number of drupelets was largely compensated by higher weight of individual drupelets, the correlation between the number of drupelets and total fruit weight was positive. The effect on number of drupelets, as well as fruit set, suggests poor pollination success in high RH conditions. Overall, the observed fruit weights and drupelet counts were lower than expected, while similar to those we have previously observed (Tommila et al. 2022a) in cv. 'Alli' in a similar greenhouse environment. In Exp. 2 and 3 of this study, the fruit weight of cv. 'Alli' was substantially higher than in any of the treatments in Exp. 1. According to Kostamo et al. (2013), the fruit weight of field-grown cvs. 'Alli' and 'Mesma' is typically in the 1 g range. In Exp. 3, the number of drupelets per fruit was also higher than in Exp. 1, suggesting better pollination success. In our previous experience, a higher drupelet count is easier to achieve in a high tunnel open to natural pollinators, while drupelet weight tends to be higher in a greenhouse environment (Tommila et al. 2022a, 2022b). The total fruit weight likely depends in large part on plant water status and general vigor, which affect the size of individual drupelets, while pollination success affects the number of drupelets.

This study did not explore the details of pollination process, from insect activity and pollen dehiscence to pollen tube growth. The effect of RH on bumblebee activity is relatively little studied, compared to the effects of temperature (Maebe et al. 2021, Karbassioon et al. 2023). However, Peat and Goulson (2005) and Karbassioon et al. (2023) observed that the ability of honeybees and bumblebees to harvest pollen was limited in high RH conditions. *Bombus terrestris* starts to decrease pollen harvesting in 57% RH, but its nectar foraging activity was not negatively affected by high RH (Peat and Goulson 2005, Karbassioon et al. 2023). While bees generally avoid flying in rainy weather, bumblebees have been found to be more tolerant of wet conditions than honeybees (Peat and Goulson 2005, Tuell and Isaacs 2010). However, as maintaining RH80 in this study often required heavy misting, occasionally resulting in visible water on plant leaves and tables, this may have negatively influenced pollination activity.

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The overall effect of weather on arctic bramble fruit development after fruit set is not clear. In Exp. 1 of this study, Hypothesis 2 was confirmed on the part of fruit spoilage in cv. 'Mesma'. The fruit spoilage rate, as a percentage of set fruits, was surprisingly high in this cultivar (33 to 45% in different treatments) compared to cv. 'Alli' (6 to 10%). Additionally, the higher fruit spoilage rate observed in cv. Mesma in RH60, compared to other treatments, has no clear explanation. One possibility could be that the fruits of cv. 'Mesma' are more vulnerable than fruits of cv. 'Alli' to drying in low RH conditions, to fungal infections in high RH conditions, and potentially to both in intermediate conditions. Kostamo et al. (2015) found cv. 'Mesma' to be more susceptible than cv. 'Alli' to one specific strain of *Peronospora sparsa*, but there is no comprehensive research on the disease resistance of these two cultivars. As is relevant for fruit aesthetic quality, Kostamo et al. (2013) note that the fruits of cv. 'Alli' have an outstandingly uniform red color compared to cv. 'Mesma' or other common arctic bramble cultivars. Saastamoinen (1930) reported that wild arctic bramble fruits may dry up in hot weather conditions. However, the recent problems with dryberry disease in Finnish arctic bramble cultivation have been attributed to downy mildew (*Peronospora sparsa*) infection and associated with rainy summers (Lindqvist et al. 1998, Kokko et al. 1999). According to Kostamo et al. (2015), dryberry disease is characterized with the hardening and desiccation of already swollen drupelets, while various pathogens other than *P. sparsa* may cause moldy, desiccated and misshapen fruits in arctic bramble. An attempt was made in this experiment to visually classify spoiled fruits into "dry" and "moldy" categories, but this was found unfeasible, in part because many of the spoiled fruits were only collected at the end of the experiment, long after they had become desiccated regardless of the original pathology. Only few if any fruits had symptoms consistent with dryberry disease, whereas many of the spoiled fruits desiccated during early development, and others were clearly infected by fungi during or shortly before ripening. Overall, the results on two cultivars suggest that RH in a greenhouse environment has no major effect on arctic bramble fruit spoilage rate, but instead there are major differences between cultivars in susceptibility to spoilage.

The reduced yield of cv. 'Alli' in RH40 compared to RH60 has no clear explanation. It was mainly associated with a lower number of flowers, although this was not statistically significant in itself, and may have been random variation. Overall, the optimal RH range in this experiment was lower than expected, particularly for cv. 'Mesma', as the fruit set was found to be surprisingly sensitive to high RH. Due to technical constraints, RH levels lower than 40% were not included in the experiment. The effects of very low RH and high temperatures during flowering warrant further investigation, as these conditions are common in protected cultivation, and arctic bramble pollination and fruit set may be sensitive to them.

The effects of algae-based biostimulants on arctic bramble yield formation

In Exp. 2 and 3, Hypothesis 3 on increased number of flowers was not confirmed. As for Hypothesis 4, an increase in arctic bramble fruit weight was observed when the plants were treated with Kriss in a greenhouse, and with the series of nine repeated treatments of both Kriss and Alginamin in a high tunnel. No increase in fruit yield was observed, as the increase in fruit weight with Kriss and Alginamin in Exp. 3 was entirely counteracted by the unexpected reduction in the number of flowers. The effect on fruit weight was associated with a statistically non-significant trend towards higher drupelet weight, but no such trend was observed in the number of drupelets. The positive correlation observed between fruit weight and drupelet weight suggests that these biostimulants have a potential to improve fruit weight via increased drupelet weight, rather than via fruit set and the number of drupelets in a fruit. This is contrary to Exp. 1, where cv. 'Alli' showed a negative correlation between fruit weight and drupelet weight, presumably because a higher number of drupelets tends to reduce the weight of individual drupelets.

Previous research on algae-based biostimulants in raspberry has shown improvements mainly in fruit size and fruit chemical composition (Ochmian et al. 2008, Krok and Wieniarska 2008). However, Ochmian et al. (2008) also achieved a 15 % increase in the yield of cv. 'Polka' primocane raspberry using the algae-based product Acadian Seaplants. In the study by Krok and Wieniarska (2008), the alga-based biostimulant Goëmar BM 86 increased raspberry fruit set in the primocane cvs. 'Polesie', 'Polka' and 'Poranna Rosa', and slightly increased fruit weight in cvs. 'Polana' and 'Poranna Rosa'. There was no attempt to quantify the effect of Goëmar BM 86 on the total amount of yield. Both Krok and Wieniarska (2008) and Ochmian et al. (2008) noted that biostimulant treatments tended to increase fruit weight mainly at the start of harvest, although in the latter study the effect of Acadian Seaplants on fruit weight was not significant. In blueberry, Loyola and Muñoz (2009) found that an *Ascophyllum nodosum* extract increased the diameter of the fruit, and there was a trend toward increased fruit weight.

In this study, while biostimulant preparations had no statistically significant effect on the fruit set or yield of arctic bramble, a statistically non-significant trend towards higher yield was observed with Kelpak, Cremalga and Kriss in Exp. 2 and with Kelpak in Exp. 3. Aside from the positive effect of Kriss on fruit weight, this trend was associated

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with statistically non-significant trends towards higher number of flowers in Exp. 2, and towards lower spoilage rate in Exp. 3. While any of these observations could be random variation, in particular the possible effect of Kelpak on the flowering and fruit yield of arctic bramble requires further research.

Ascophyllum nodosum (Lessoniaceae) is perhaps the most widely studied algal species for use as a biostimulant (Shukla et al. 2019). Both Acadian Seaplants and Goëmar BM 86 consist solely of *A. nodosum* extract, which is also one of the main ingredients in Cremalga, Kriss and Alginamin. Meawhile, Kelpak consists solely of *Ecklonia maxima* (Fucaceae) extract, which is also present in Cremalga. In this study, the closest indication of the possibility of yield increase was observed with Kelpak, while increased fruit weight and reduced flowering were observed only with Kriss and Alginamin. The biological mechanisms and optimal methods of use for algae-based biostimulants are still poorly understood (Shukla et al. 2019), and while there are some differences between the products used in this study in their claimed effects and recommended timing of application, it is not clear whether their biological mechanisms are much or at all different.

Conclusions

We found high RH during pollination to have a strong negative effect on arctic bramble fruit yield, mainly via reduced fruit set, and a negative effect on fruit weight via reduced number of drupelets per fruit. Thus, our first hypothesis on the effect of RH on yield formation was confirmed in all aspects. Of the two arctic bramble cultivars, ‘Mesma’ had lower RH optimum than ‘Alli’, and was generally much more prone to fruit spoilage in a greenhouse environment, while both performed best in the 40 to 60% relative humidity range. RH conditions during fruit development did also affect fruit spoilage in cv. ‘Mesma’, confirming our second hypothesis.

The use of algae-based biostimulant products during shoot growth reduced rather than increased the number of flowers in arctic bramble, refuting our third hypothesis. The use of same products during flowering and fruit development had no significant effect on the fruit yield, but an increase in fruit weight was observed after treatment with Kriss and Alginamin, mainly via increased weight of individual drupelets. Thus, our fourth hypothesis was confirmed in two aspects.

Based on these results, use of algae-based biostimulants on arctic bramble may provide some benefits in cultivation, such as increased fruit weight, but the evidence on yield increase is inconclusive. As for relative humidity, our results suggest that climatic control to prevent excessive humidity during flowering can be highly beneficial in protected cultivation.

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