Effect of shade treatment on the growth and vitality of cloudberry *Rubus chamaemorus*

L. Āboliņa^{1,2*}, A. Karlsons¹ and A. Osvalde¹

¹Latvia University of Life Sciences and Technologies, Faculty of Agriculture and Food technology, Lielā street 2, LV-3001 Jelgava, Latvia ²University of Latvia, Institute of Biology, O. Vaciesa street 4, LV-1004 Riga, Latvia *Correspondence: laura.abolina@lu.lv

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Abstract. Cloudberry Rubus chamaemorus is a promising new berry species for cultivation in Latvia. This study aimed to assess how different shade levels influence cloudberry growth and vitality in semi-controlled conditions. Cloudberries (variety 'Nyby') were planted in enclosed planting area and grown under four shading treatments, using shading nets: control (no shade), 30%, 50%, and 80% shade for two years. Non-destructive SPAD measurements were taken weekly during the growing season (from May to August) in both years. Leaf size was measured at the end of August in both years, while leaf density and leaf nutrient concentrations were determined at the end of August in 2024. The results revealed significant differences between treatments for all of the measurements, with the highest values observed in plants under the 80% shade in both years. In the second year, the 50% an 80% shade treatments had similar results. Overall, the highest plant vitality was observed under 50% and 80% shade, demonstrating that netting effectively protects cloudberries from excessive sunlight. While larger leaves might improve light capture, they also require additional energy, potentially reducing resources available for fruit production. Thus, we suggest the 50% shade to be the most effective for cloudberries in the Latvian climate, as it balances protection with optimal energy conservation. Additionally, optimal fertilizing in the field could improve plant health and yield, therefore further studies regarding the combined effects of shade and fertilization on cloudberry production are required.

Key words: berry cultivation, chlorophyll content, leaf nutrient content, netting, shade adaptation.

INTRODUCTION

Cloudberry *Rubus chamaemorus* is a perennial herbaceous plant. In Latvia, cloudberries are harvested in the wild, and their cultivation remains in the experimental stage. In northern regions, cloudberries can form abundant fields in ombrothropic bogs (Hébert-Gentile et al., 2011). Although Latvia has a milder climate, cloudberries are still found in sphagnum peatlands throughout the country. Their distribution in Latvia is concentrated in the northern and central regions, with significantly fewer records in the eastern continental areas (Laiviņš et al., 2009).

Rising annual temperatures, along with milder winters and longer summers, contribute to wild plant adaptations. During wild cloudberry field studies from 2020 to 2022 in Latvia, the authors observed that cloudberries predominantly grew in forested peat bogs with trees and low shrubs, rather than in fully exposed peatlands (Āboliņa et al., 2023). This suggested that in a moderate climate, cloudberries might prefer at least partial shade rather than full sun exposure.

Light conditions is one of the main ecosystem productivity drivers (Niinemets, 2010). However, prolonged periods of high temperatures and low precipitation during summer increase the risk of crop failure, particularly in fields with insufficient irrigation possibilities (Fatima et al., 2020). Drought and high temperatures significantly reduce plant photosynthetic activity, thus inhibiting carbon accumulation (Ashraf & Harris, 2013). Cloudberry cold hardiness and overall growth relies on sufficient carbon storage in rhizomes (Gauci et al., 2009). In the wild, cloudberries typically grow in high moisture ecosystems such as bogs, while cultivated cloudberries are often grown in cutover peat fields (Bussières et al., 2015), where irrigation can be challenging during droughts. Even in their natural habitat, climate change affects wild cloudberries in Northern regions, with events as higher temperatures at the beginning of the year and subsequent drought conditions (Crawford, 2008).

In forest ecosystems, the understorey tends to be cooler during the day, and warmer at night due to shade from plant canopies. In its natural habitat, wild cloudberry can reach 25 cm in height (Thiem, 2003). In Latvia, cloudberries are often found growing alongside bilberries *Vaccinium myrtillus* and lingonberries *Vaccinium vitis-ideae*, which can reach higher growth, respectively, 90 cm and 30 cm, thus potentially limiting light availability for smaller herbaceous species nearby (Gustavsson, 2001; Gailīte et al., 2019; Āboliņa et al., 2023).

Wild plants tend to require more light than those grown in controlled environments, due to the environmental complexities and variables that are not present in fully or partly controlled conditions (Valladares et al., 2016). While low light exposure can limit plant growth, both shade and non-shade species develop adaptations for growing in the shade, including increased leaf area to optimize light capture (Valladares & Niinemets, 2008; Gommers et al., 2013). Cloudberries exhibit phenotypic variations depending on their growing conditions. Large leaves and longer shoots are typically associated with shaded environment, while smaller plants are found in open areas (Ågren et al., 1989). Berry quality also depends on the level of exposure to sunlight. Cloudberries are known for their fruit high in anthocyannins and elagitannins (Hykkerud & Uleberg, 2018). Wild cloudberry fruits produced in shaded areas have been found to be sweeter and lighter coloured than fruits in open areas (Jaakkola et al., 2012).

The photosynthetic rate of plants fluctuates throughout the growing period and varies by species. Lingonberry was found to maintain relatively high photosynthetic rate until October, whereas blueberry photosynthetic rate levels declined in September, indicating photoinhibition (Lundell et al., 2008; Percival et al., 2012). High exposure to sunlight and drought stresses can lead to plant dehydration and photoinhibition, thus limiting plant performance (Akashi et al., 2008; Valladares & Niinemets, 2008). Plant protection mechanisms for light and drought stresses require significant resources. Netting can mitigate these stressors by reducing excessive soil temperatures and radiation, increasing minimum temperatures to protect flowers from frost, and shielding plants from hail and heavy rainfall (Shahak et al., 2004; Retamal-Salgado et al., 2017).

In Latvia, one of the concerns during the growing season is the combination of prolonged drought and high temperatures. Minimizing soil water evaporation in such conditions could be a significant factor in maintaining favourable conditions for berry cultivation. Additionally, cloudberries are susceptible to frost damage (Gauci et al., 2009). Considering that cloudberry flowering in Latvia coincides with potential late spring frosts in May (Latvian nature S.a.; LEGMC, 2025), netting might contribute to flower protection.

Nets differ not only by the shade level but also by the transmitted light wavelength, which vary depending on the net material and colour (Kotilainen et al., 2018). The overall current knowledge regarding the netting impact on plant physiology is limited, particularly on berry crops. The aim of this study was to assess how different shade levels influence cloudberry growth and vitality in partly controlled conditions, imitating cultivation in a peat field in temperate climate. The findings will be used in developing a growing technology for cloudberries in Latvia.

MATERIALS AND METHODS

Design and conditions of the experiment

The experiment was located in Riga, Latvia, at the Institute of Biology, University of Latvia, for two vegetation seasons from May to August of 2023 and 2024.

The mean temperature and monthly solar radiation data for May, June, July and August in Riga (Fig. 1) was provided by SLLC 'Latvian Environment, Geology and Meteorology Centre' archives (LEGMC, 2025).



Figure 1. Mean monthly solar radiation (W m⁻²) and temperature, (°C) for the vegetation seasons of 2023 and 2024 in Riga, Latvia.

Solar radiation total sum was similar between years (686,753 and 676,134 W m⁻², respectively). While in 2023 the trend for solar radiation was decreasing over the summer months, in 2024, July and August had similar total radiation. Temperatures were higher for May and July in 2024 than in 2023, other months were similar between years. Additionally, 2023 and 2024 both were on average hotter than the previous climatic norm (+1.0 °C and +1.9 °C, respectively) following the climatic warming trend.

Cloudberry cultivar 'Nyby' was used in the experiment. Substrate from combined milled raw peat and peat substrate for forest seedlings (Ltd. LaFlora, Latvia), in a ratio of 2:1, degree of decomposition H2–H5, was used for propagation. Cloudberries were propagated in spring of 2022: rhizomes were sectioned in 15 cm parts and planted in 1 L pots with the peat substrate. In autumn, cloudberries with visible living rhizomes were transplanted in enclosed planting area (beds) with milled raw peat. The area was divided in four sections, each section measuring 2 m in length, 0.80 m in width, and 0.50 m in depth. In each section 24 plants were taken out of the pots and planted with identical gaps between plants. Beds were isolated from surrounding soil with water-permeable agrotextile. Milled raw peat substrate agrochemical characteristics before transplantation outside are given in Table 1.

 Table 1. Milled raw peat substrate nutrient concentrations, pH and EC before shading experiment

 establishment

Plant available nutrient concentrations, mg L ⁻¹ (1 M HCl extraction)									aII	EC _{H2O} ,			
Ν	Р	Κ	Ca	Mg	S	Fe	Mn	Zn	Cu	Mo	В	- рп _{ксі}	EC_{H2O} , mS cm ⁻¹
7	<5	31	391	108	3.15	38.55	2.7	2.6	0.3	0.02	0.1	3.48	0.09

Green shading nets with shading factors of 30%, 50% and 80% were used in the experiment to assess the effect of shade on cloudberry growth and vitality. The percentages indicate the proportion of sunlight (solar radiation) that is blocked by the shading net. A control variant (C) was left fully exposed to sunlight. No other natural or artificial shade affected the area (Fig. 2).



Figure 2. Experimental cloudberry beds with nets of different shading factors (from left to right): A - control (full sun exposure) and 30% sunlight blocking net; B - 50% and 80% sunlight blocking nets (taken on May 18, 2023).

In May of 2023 and 2024, 100 g of complex fertilizer (NPK 12-8-16 + micronutrients) was added to each bed as a base fertilizer. During the vegetative months from May to August, watering frequency was adjusted based on soil moisture level and weather patterns. Once a week, peat samples from 5–10 cm below the surface were taken and squeezed by hand into a ball. Optimal moisture was assumed if the peat retained its shape and was moist without dripping water. If the peat crumbled, treatments were watered with tap water to increase moisture.

Nutrient analysis

To determine plant-available nutrient (N, P, K, Ca, Mg, S, Fe, Mn, Zn, Cu, Mo, B) concentrations in substrate, peat samples were extracted with 1 M HCl in a volume ratio of 1:5. Peat reaction (pH) was measured in 1 M KCl mixture (in a peat-extractant ratio of 1:2.5). The electrical conductivity (EC) of the substrate was measured in a distilled water extraction (in a peat-water ratio of 1:5). For leaf tissue nutrient analysis, approximately 30 g of cloudberry leaves were collected from each treatment at the end of vegetation season of 2024. Samples were fully dried at +60 °C in a drying oven, and finely ground using a laboratory mill. Ground samples were then dry-ashed in concentrated HNO₃ vapours, and then redissolved in 3% HCl to detect K, P, Ca, Mg, Fe, Cu, Zn, Mn, B, and Mo via microwave plasma atomic emission spectrometry (MP-AES Agilent 4210). Wet digestion was used to determine N (in H₂SO₄) and S (in HNO₃). The contents of P, Mo, N, and B were determined via colorimetry, S – via turbidimetry, as previously described in Karlsons et al. (2021). Nutrient content was determined in triplicate for all samples.

Plant measurements

The beginning of cloudberry growth in 2023 was recorded at the end of April. The first leaves were fully developed by the second decade of May, measurements were conducted from May 22 to August 31. For each treatment, leaf total *a* and *b* chlorophyll concentration was measured weekly on randomly selected leaves (n = 10) with a chlorophyll meter SPAD–502Plus. In 2024, SPAD was measured between May 23 and August 28.

For all treatments, leaf size (in cm) was measured at the end of the growing season in both years (in 2023 – on August 31; in 2024 – on August 30). Leaves were selected randomly and two measurements (width and length) for each leaf were taken to calculate the average size (n = 10).

At the end of summer 2024 we also measured leaves per 10×10 cm² quadrats (n = 6 for each treatment) to compare cloudberry density after two years of growth. Quadrats were placed randomly in each bed without overlapping.

Statistical analysis

Data were analysed and visualized with R programming language. To determine significant differences (P < 0.05) between shading treatments for SPAD, leaf size and density, and leaf tissue nutrient concentrations, one-way ANOVA with post-hoc Tukey HSD test, and descriptive statistics were conducted. Mann-Kendall's τ (tau) test was used to determine significant trends in SPAD readings throughout the vegetation season.

RESULTS AND DISCUSSION

In our previous studies in Latvia, less wild cloudberries were observed in areas that are fully exposed to the sun, than in shady or partially shaded areas (Åboliņa et al., 2023). In the northern Finland and Sweden, wild cloudberries have been found to have larger leaves in shaded conditions, as well as longer rhizomes and higher seed mass as compared to exposed areas (Ågren, 1989). Optimally reduced light and temperature conditions under protective covers have been reported to increase yield and quality of other berries grown in an acidic environment (Matamala et al., 2023). This led to the idea that in temperate climates, cloudberries might require at least partial protection from sunlight during the summer months. The issue is also relevant in the context of global warming. Although typical temperate climate conditions of Latvia are favourable for cloudberries, the warming climate might have its negative effect on local plant vitality. Generally, for the last years the average temperatures have been above, and precipitation levels below the climatic norm in Latvia (LEGMC, 2025).

At the beginning of the first year, the cloudberry shading experiment did not indicate any noticeable trends in cloudberry photosynthetic activity, however, significant differences (P < 0.05) were observed at the end of the season (Fig. 3).

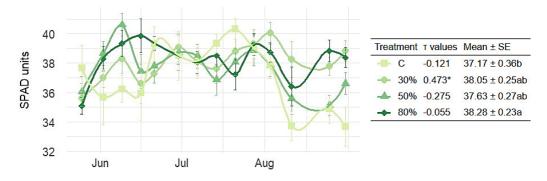


Figure 3. Shading level effect on chlorophyll content (in SPAD units) of cloudberry leaves from May to August 2023.

*Significant trend (P < 0.05). Means and standard errors (SE) of each treatment represent chlorophyll data of the whole season. Significant differences between treatments are indicated by small letters (P < 0.05; a > b).

Specifically, the last three weeks of SPAD measurements revealed significantly different results between the treatments. For these last three measurements, the control treatment had the lowest SPAD results, which differed significantly from treatments of 30% and 80% shade. The overall season means for each treatment revealed differences consistent with the end of the season results - control treatment had significantly lower SPAD indices than treatments 30% and 80%. Among the treatments, only the 30% shading showed a significant yet moderate positive trend in total chlorophyll content over the season.

In the second year, a trend was observed for the SPAD values to decrease over the season, as all four treatments showed strong negative trends over the observed period, as indicated by tau values (P < 0.05) (Fig. 4).

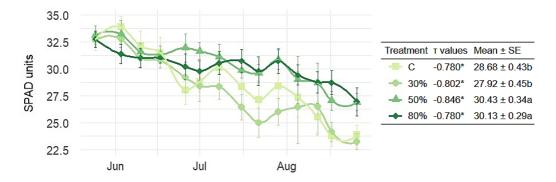


Figure 4. Shading level effect on chlorophyll content (in SPAD units) of cloudberry leaves from May to August 2024.

*Significant trend (P < 0.05). Means and standard errors (SE) of each treatment represent chlorophyll data of the whole season. Significant differences between treatments are indicated by small letters (P < 0.05; a > b).

It was also evident that for all of the treatments the chlorophyll content was lower in the second year, indicated by significantly lower SPAD results (weekly treatment means ranging 23.24–33.90) as compared to the first year (weekly treatment means ranging 33.68–40.61). Significant differences between groups were observed three times during the season, once at the end of July and then again at the last two weeks of August. In all three weeks, the 80% shade treatment had significantly higher SPAD indices than the 30% treatment. The overall season SPAD means were consistent with these differences, as control treatment and 30% SPAD results were significantly lower than for treatments 50% and 80%.

In the second year of our experiment, SPAD indices showed a consistent and significant decline in total chlorophyll content over the course of the season for all treatments. Decrease in total chlorophyll, also observed visually as yellowing of the leaves, was noticeable by second half of July 2024 for the two most exposed treatments – control and 30% shade. Thus, the visual indications generally corresponded to the SPAD readings. July and August 2024 had similar total sun radiation, which may have further contributed to late summer photodamage of cloudberries in treatments more exposed to the sun.

In both years of the experiment, the largest leaves corresponded to the darkest shade treatment of 80%. In the first year, the smallest leaves were observed in the control and 50% shade treatments, in the second year – in control and 30% shade treatments (Fig. 5). Noticeably, the second year revealed higher variation of leaf size in all of the treatments, as well as an overall decrease in size was observed. Size decrease in the second year was confirmed significant for the 30% shade treatment (P < 0.05).

Shade-tolerant plants have larger leaves, reduced chlorophyll a/b ratio, higher total chlorophyll content - adaptation responses to shade conditions, which contribute to carbon gain optimization (Lobos et al., 2012, Gommers et al., 2013, Lambers & Oliveira, 2019). Our study results were consistent with these responses as well, as the largest leaves were confirmed for the 80% shade treatment in both years, and for 50% shade treatment as similar on the second year.

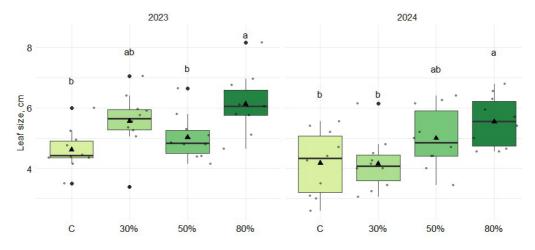


Figure 5. Cloudberry leaf size in different shading treatments for both years of the shading experiment (2023 & 2024). Triangles show group means, grey dots show individual measurements, letters indicate significant differences (P < 0.05; a > b) between treatments.

It was also evident that between treatments, the shaded plants had higher survival rates at the end of the experiment. Leaves per quadrat were measured at the end of 2024 season to assess the density of developed cloudberry ramets after a two-year period for each treatment (Figs 6 and 7). Differences were significant between the control and 80% shade treatments, thus following the overall trend for the 80% shade treatment to have higher results. The lower density observed for the control also corresponded to other plant health indicator results.

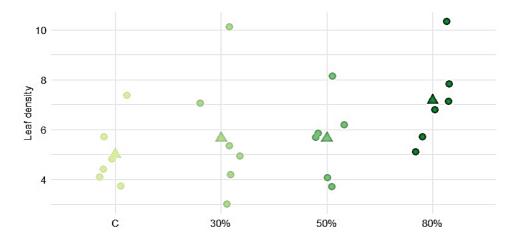


Figure 6. Cloudberry leaf density per 10×10 cm² quadrats in different shading treatments (n = 6), measured at the end of August 2024. Triangles show group means, dots show individual measurements.

The higher leaf density in late August for the shaded treatments is explainable by reduced exposure to sunlight, thus reducing high temperature and radiation stress.

Shade-tolerant plant leaves have a higher dry matter percentage and carbon concentration, which make the leaves more sufficient at resisting damage and they last longer in shady environments (Pons & Poorter, 2014). Longer surviving leaves allow the plant to photosynthesise continuously without replacing them frequently due to photoinhibition or combined damage. Thus, the study results suggest that in a typical summer, as the climate warms, radiation levels may be higher than optimal for cloudberries if they are exposed to full sun. Data on photosynthesis rates, leaf size and density confirms that cloudberry is a shade-tolerant plant and also suggests that physiological characteristics of the hermaphroditic variety 'Nyby' could generally correspond to wild cloudberry phenotypes in different habitats. Comparison between wild plants and the cultivated variety could initially help to develop a cultivation technology, particularly from the aspects of cloudberry nutritional requirements.



Figure 7. Visual comparison of cloudberry growth under different sun exposure levels: A – control (full exposure) and B – under 80% sunlight blocking net. Taken on July 28, 2024.

Plant nutrient content was analysed to compare shading treatments and additionally, cultivated cloudberries 'Nyby' with wild plants. Significant differences were observed between shading treatments for N, Fe and Cu (Table 2). The highest concentrations of these nutrients were determined for cloudberry leaves under the 50% and 80% shade treatments, although only the 80% shade treatment reached leaf N concentrations consistent with the range of wild cloudberry. P, K, Mg, Zn, Cu, and Mo concentrations of all treatments generally fell within the range observed for wild cloudberries. The concentrations of Ca, S, Fe, Mn, and B were higher for cultivated cloudberries in the shading experiment than for wild plants, which could be mainly due to the base fertilizer applied in both years of the experiment. The substrate used in the experiment was similar to previously described wild cloudberry peat in terms of decomposition level and nutrient concentrations described in Āboliņa et al. (2023).

	A. Shadii	ng treatments	B. Wild cloudberry nutrient				
Nutrient	K	30%	50%	80%	content (Āboliņa et al., 2023)		
Macronutri	ents, %						
Ν	1.31	1.20	1.83*	1.98*	1.90-3.00		
Р	0.09	0.08	0.09	0.10	0.08-0.27		
Κ	0.72	0.96	1.10	0.84	0.75-1.75		
Ca	1.44	1.41	1.3	1.44	0.15-0.90		
Mg	0.42	0.48	0.49	0.50	0.26-0.72		
S	0.30	0.31	0.31	0.30	0.07-0.23		
Micronutrie	ents, mg kg ⁻¹						
Fe	120	126	145	204*	34.67-129.00		
Mn	1,581	1,678	1,761	1,639	50.95-660.00		
Zn	109	112	111	126	43.61-121.00		
Cu	3.80	4.54	5.18	6.79*	2.50-17.20		
В	44	50	50	58	8.00-29.00		
Mo	0.20	0.25	0.20	0.20	0.10-0.75		

Table 2. (A) Mean nutrient concentration in air-dried leaves of cloudberries grown in different shading treatments (2024); (B) Nutrient concentration in air-dried wild cloudberry leaves in Latvia, 2020–2022

*Significantly higher concentrations than for other treatments (P < 0.05).

As nutritional status also affects every aspect of plant physiology, especially photosynthesis, we also consider the nutrient supply results as indicators of cloudberry vitality. Shading nets can reduce ambient and leaf temperatures and thus prevent leaf damage, which is important for CO_2 assimilation and thus photosynthesis (Lobos et al., 2012). Nitrogen use is optimized as it is allocated to light-harvesting complexes (Eichelmann et al., 2005). Strong positive N and chlorophyll index correlations have been reported in other berry species, even for different varieties (Pinzón-Sandoval et al., 2023). Soil N deficiency has been shown to significantly reduce total chlorophyll contents in berry leaves (Yang et al., 2023a; Yang et al., 2023b). However, the level of sensitivity to N deficiency depends on the cultivar (Yañez-Mansilla et al., 2015). According to Hallik et al. (2009), chlorophyll and N correlation is species specific among herbaceous plants, rather than universal. Considering the higher N and chlorophyll concentrations in cloudberry leaves under the shaded treatments could be an adaptation to enhance chlorophyll production and light-harvesting capacity. Studies have shown that this helps to maximize photosynthesis under limited light conditions (Lambers & Oliveira, 2019), further confirming cloudberry responses characteristic to a shadetolerant plant. In addition to N, higher Fe and Cu concentrations in cloudberry leaves were also determined in the 80% shading treatment. These microelements play a vital role not only in maintaining the overall health and vitality of plants - Fe is also directly involved in N fixation and chlorophyll development, and Cu acts as a catalyst for photosynthesis and respiration (Lambers & Oliveira, 2019).

Our study focused on the agronomic aspects of netting as a means of plant protection from overexposure to sunlight and its effects on cloudberries. As the most optimal plant status results were observed in the 80% shade treatment, we consider shade as an effective factor contributing to cloudberry vitality over the summer season in Latvian climate. However, we also consider the hidden aspects of netting on plant development and growth. For berry cultivation, it is important to understand how the plant \times environment interaction impacts potential yield size and quality, as well as overall management of the berry crop (Senger et al., 2022). Problems related to the use of netting on cultivated berries may include reduced pollinator activity and decreased plant water stress, both of which significantly influence the overall chemical composition and quality of the fruit (Brown & McNeil, 2009; Mikulic-Petkovsek et al., 2015; Karppinen et al., 2016). Habitat openness, temperature and exposure to sunlight were suggested as the main factors affecting yield and chemical composition of cloudberry fruits (Jaakkola et al., 2012). Lower stress levels during flowering and fruiting are associated with increased yield, but may lead to reduced secondary metabolite content in the fruits. Zoratti et al. (2015) found that shading increased antohcyannin content in bilberries, but decreased their content in blueberries. Considering this, the lowest yet effective shade factor might be applied to achieve desirable cloudberry growth and berry quality. Several studies have shown that, depending on the species, reducing solar radiation by 50% to 70% can improve plant vitality (Dai et al., 2009; Schwerz et al., 2017). As leaf size was confirmed significantly larger for the 80% shade treatment in both years, 80% shading for cloudberries could be excessive, as the plants might use the most energy for green mass growth at the expense of other physiological processes. Meanwhile, in 2024, leaf size between the other treatments did not differ, while SPAD results were significantly higher for plants under both 50% and 80% shade. This suggests that plants under 50% shade would not spend significant energy resources to develop larger leaves whilst maintaining optimal chlorophyll content. The mechanical protection is also considerable as a positive shading effect during the experiment. Netting considerably decreases the negative effects of insects and birds on berry crops (Kuesel et al., 2019). Reduced weed growth was also observed under the shaded treatments, as compared to the control.

Current study of shading effect on cloudberries revealed healthier plants for longer periods in shaded treatments as compared to the fully exposed control variant. Higher cloudberry vitality was indicated by SPAD results and leaf density, as well as leaf colour during on-site assessment. Based on the findings of this research, we consider the cloudberry to be able to maintain optimal photosynthetic activity and leaf growth under 50% shade netting, which will help maintain optimal temperature and irradiance for the plant in temperate climates. It is worth noting that optimal fertilizing would also improve plant vitality and possibly yield, therefore further studies regarding shade and fertilizer combined effect on cloudberry production are required.

CONCLUSIONS

Cloudberry is a promising new berry species for cultivation in Latvia, particularly given the vast areas of cutover peat bogs where it naturally occurs. Our study focused on the agronomic benefits of netting, which is known to mitigate extreme temperatures and protect plants from excessive solar radiation. The highest plant vitality was observed under 50% and 80% shade, demonstrating that netting effectively shields cloudberries from overexposure to sunlight and enhances overall plant health. However, we also considered the plant physiological adaptations to lower irradiance – increased leaf size, which were significant for cloudberries under 80% shade. While larger leaves may improve light capture, they also require valuable energy, potentially reducing resources

available for fruit production. Although both 50% and 80% shade treatments improved cloudberry vitality, we suggest the 50% shade netting to be most effective for cloudberries in the Latvian climate, as it balances protection with optimal energy conservation. These findings will contribute to the development of cloudberry cultivation technologies in Latvia.

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REFERENCES

- Akashi, K., Yoshimura, K., Nanasato, Y., Takahara, K., Munekage, Y. & Yokota, A. 2008. Wild Plant Resources for Studying Molecular Mechanisms of Drought/Strong Light Stress Tolerance. *Plant Biotechnology* 25, 257–263. 10.5511/plantbiotechnology.25.257
- Ashraf, M. & Harris, P.J.C. 2013. Photosynthesis under Stressful Environments: An Overview. *Photosynt.* **51**(2), 163–190. 10.1007/s11099-013-0021-6
- Äboliņa, L., Osvalde, A. & Karlsons, A. 2023. Habitat Characteristics and Mineral Nutrition Status of Rubus chamaemorus L. in Latvia. *Plants* 12, 528. doi:10.3390/plants12030528
- Ågren, J. 1989. Seed size and number in Rubus chamaemorus: between-habitat variation, and effects of defoliation and supplemental pollination. *The Journal of Ecology* **77**(4), 1080–1092. https://doi.org/10.2307/2260824
- Brown, A.O. & McNeil, J. N. 2009. Pollination ecology of the high latitude, dioecious cloudberry (Rubus chamaemorus, Rosaceae). *Am. J. Bot.* **96**, 1096–1107. doi: 10.3732/ajb.0800102
- Bussières, J., Rochefort, L. & Lapointe, L. 2015. Cloudberry Cultivation in Cutover Peatland: Improved Growth on Less Decomposed Peat. Can. J. Plant Sci. 95, 479–489. doi:10.4141/cjps-2014-299
- Crawford, R.M.M. 2008. Cold climate plants in a warmer world. *Plant Ecology & Diversity* 1(2), 285–297. https://doi.org/10.1080/17550870802407332
- Dai, Y., Shen, Z., Liu, Y., Wang, L., Hannaway, D. & Lu, H. 2009. Effects of Shade Treatments on the Photosynthetic Capacity, Chlorophyll Fluorescence, and Chlorophyll Content of Tetrastigma Hemsleyanum Diels et Gilg. *Environmental and Experimental Botany* 65, 177–182. https://doi.org/10.1016/j.envexpbot.2008.12.008
- Eichelmann, H., Oja, V., Rasulov, B., Padu, E., Bichele, I., Pettai, H., Mänd, P., Kull, O. & Laisk, A. 2005. Adjustment of Leaf Photosynthesis to Shade in a Natural Canopy: Reallocation of Nitrogen. *Plant, Cell & Environment* 28, 389–401. doi: 10.1111/j.1365-3040.2004.01275.x
- Fatima, Z., Ahmed, M., Hussain, M., Abbas, G., Ul-Allah, S., Ahmad, S., ... & Hussain, S. 2020. The fingerprints of climate warming on cereal crops phenology and adaptation options. *Sci Rep* 10, 18013. https://doi.org/10.1038/s41598-020-74740-3
- Gailīte, A., Gaile, A. & Ruņģis, D. 2019 Genetic diversity studies of Latvian Vaccinium Myrtillus L. populations for in situ conservation. *Agr* **4**(3), 53–59. doi:10.7251/AGRENG1903053G
- Gauci, R., Otrysko, B., Catford, J.-G. & Lapointe, L. 2009. Carbon Allocation during Fruiting in Rubus Chamaemorus. *Annals of Botany* **104**, 703–713. doi:10.1093/aob/mcp142
- Gommers, C.M.M., Visser, E.J.W., Onge, K.R.S., Voesenek, L.A.C.J. & Pierik, R. 2013. Shade Tolerance: When Growing Tall Is Not an Option. *Trends in Plant Science* 18, 65–71. https://doi.org/10.1016/j.tplants.2012.09.008
- Gustavsson, B.A. 2001. Genetic Variation in Horticulturally Important Traits of Fifteen Wild Lingonberry Vaccinium Vitis-Idaea L. Populations. *Euphytica* 120, 173–182. doi: 10.1023/A:1017550609218

- Hallik, L., Kull, O., Niinemets, Ü. & Aan, A. 2009. Contrasting Correlation Networks between Leaf Structure, Nitrogen and Chlorophyll in Herbaceous and Woody Canopies. *Basic and Applied Ecology* **10**, 309–318. https://doi.org/10.1016/j.baae.2008.08.001
- Hébert-Gentile, V., Naess, S. K., Parent, L. É. & Lapointe, L. 2011. Organo-mineral fertilization in natural peatlands of the Quebec North-Shore, Canada: Dispersion in soil and effects on cloudberry growth and fruit yield. *Acta Agriculturae Scandinavica, Section B — Soil & Plant Science* 61(1), 8–17. https://doi.org/10.1080/09064710.2011.603739
- Hykkerud, A.L. & Uleberg, E., Hansen, E., Vervoort, M., Mølmann, J. & Martinussen, I. 2018. Seasonal and yearly variation of total polyphenols, total anthocyanins and ellagic acid in different clones of cloudberry (Rubus chamaemorus L.). *Journal of Applied Botany and Food Quality* 91, 96–102. http://dx.doi.org/10.5073/JABFQ.2018.091.013
- Jaakkola, M., Korpelainen, V., Hoppula, K. & Virtanen, V. 2012. Chemical composition of ripe fruits of Rubus chamaemorus L. grown in different habitats. J. Sci. Food Agric. 92, 1324–1330. https://doi.org/10.1002/jsfa.4705
- Karlsons, A., Tomsone, S., Lazdāne, M. & Osvalde, A. 2021. Effect of Fertilization on Growth of Lingonberry (Vaccinium Vitis-Idaea L.). Agronomy Research 19(S2), 1039–1051. doi:10.15159/AR.21.041.
- Karppinen, K., Zoratti, L., Nguyenquynh, N., Häggman, H. & Jaakola, L. 2016. On the developmental and environmental regulation of secondary metabolism in Vaccinium spp. Berries. *Frontiers in Plant Science* 7, 655. https://doi.org/10.3389/fpls.2016.00655
- Kotilainen, T., Robson, T.M. & Hernández, R. 2018. Light Quality Characterization under Climate Screens and Shade Nets for Controlled-Environment Agriculture. *PLOS ONE* 13, e0199628. doi:10.1371/journal.pone.0199628
- Kuesel, R., Scott Hicks, D., Archer, K., Sciligo, A., Bessin, R. & Gonthier, D. 2019. Effects of Fine-Mesh Exclusion Netting on Pests of Blackberry. *Insects* 10, 249. doi: 10.3390/insects10080249
- Laiviņš, M., Bice, M., Krampis, I., Knape, D., Šmite, D. & Šulcs, V. 2009. *Atlas of Latvian woody plants*. Institute of Biology of the University of Latvia: Riga, Latvia, 476 pp. (in Latvian).
- Lambers, H. & Oliveira, R.S. 2019. Photosynthesis, Respiration, and Long-Distance Transport: Photosynthesis. In Lambers, H. & Oliveira, R.S., *Plant Physiological Ecology*. Springer, Cham, 11–114. https://doi.org/10.1007/978-3-030-29639-1_2
- Latvian nature. Cloudberry Rubus chamaemorus L. Available online: https://www.latvijasdaba.lv/augi/rubus-chamaemorus-l/ (accessed on 23 November 2024) (in Latvian).
- Lobos, G.A., Retamales, J.B., Hancock, J.F., Flore, J.A., Cobo, N. & Pozo, A. 2012. Spectral Irradiance, Gas Exchange Characteristics and Leaf Traits of Vaccinium Corymbosum L. 'Elliott' Grown under Photo-Selective Nets. *Environmental and Experimental Botany* 75, 142–149. https://doi.org/10.1016/j.envexpbot.2011.09.006
- Lundell, R., Saarinen, T., Åström, H. & Hänninen, H. 2008. The Boreal Dwarf Shrub Vaccinium Vitis-Idaea retains Its Capacity for Photosynthesis through the Winter. *Botany* 86, 491–500. doi:10.1139/B08-022
- Matamala, M.F., Bastías, R.M., Urra, I., Calderón-Orellana, A., Campos, J. & Albornoz, K. 2023. Rain Cover and Netting Materials Differentially Affect Fruit Yield and Quality Traits in Two Highbush Blueberry Cultivars via Changes in Sunlight and Temperature Conditions. *Plants* 12, 3556. https://doi.org/10.3390/plants12203556
- Mikulic-Petkovsek, M., Schmitzer, V., Slatnar, A., Stampar, F. & Veberic, R. 2015. A comparison of fruit quality parameters of wild bilberry (Vaccinium myrtillus L.) growing at different locations. J. Sci. Food Agric. **95**, 776–785. https://doi.org/10.1002/jsfa.6897
- Niinemets, Ü. 2010. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecol. Res.* **25**, 693–714. https://doi.org/10.1007/s11284-010-0712-4

- Percival, D., Kaur, J., Hainstock, L.J. & Privé, J.-P. 2012. Seasonal Changes in Photochemistry, Light Use Efficiency and Net Photosynthetic Rates of Wild Blueberry (Vaccinium Angustifolium Ait.). *Canadian Journal of Plant Science* **92**, 1135–1143. 10.4141/cjps2011-205
- Pinzón-Sandoval, E.H., Balaguera-López, H.E. & Almanza-Merchán, P.J. 2023. Evaluation of SPAD Index for Estimating Nitrogen and Magnesium Contents in Three Blueberry Varieties (Vaccinium corymbosum L.) on the Andean Tropics. *Horticulturae* 9, 269. https://doi.org/10.3390/horticulturae9020269
- Pons, T.L. & Poorter, H. 2014. The Effect of Irradiance on the Carbon Balance and Tissue Characteristics of Five Herbaceous Species Differing in Shade-Tolerance. *Frontiers in Plant Science* 5, 12. https://doi.org/10.3389/fpls.2014.00012
- Retamal-Salgado, J., Vásquez, R., Fischer, S., Hirzel, J. & Zapata, N. 2017. Decrease in Artificial Radiation with Netting Reduces Stress and Improves Rabbit-Eye Blueberry (Vaccinium Virgatum Aiton) 'Ochlockonee' Productivity. *Chilean J. Agric. Res.* 77, 226–233. 10.4067/S0718-58392017000300226
- Schwerz, F., Sgarbossa, J., Olivoto, T., Elli, E., Aguiar, A., Caron, B. & Schmidt, D. 2017. Solar Radiation Levels Modify the Growth Traits and Bromatological Composition of Cichorium Intybus. *Advances in Horticultural Science* **31**(4), 257–265. 10.13128/AHS-20832
- Senger, E., Osorio, S., Olbricht, K., Shaw, P., Denoyes, B., Davik, J., Predieri, S., Karhu, S., Raubach, S., Lippi, N., Höfer, M., Cockerton, H., Pradal, C., Kafkas, E., Litthauer, S., Amaya, I., Usadel, B. & Mezzetti, B. 2022. Towards smart and sustainable development of modern berry cultivars in Europe. *Plant J.* **111**, 1238–1251. doi: 10.1111/tpj.15876
- Shahak, Y., Gussakovsky, E.E., Gal, E. & Ganelevin, R. 2004. Colornets: crop protection and lightquality manipulation in one technology. In Cantliffe, D.J., Stoffella, P.J. & Shaw, N. (eds): Proc. VII IS on Prot. Cult. Mild Winter Climates, Acta Hort. 659, pp. 143–151.
- SLLC. Latvian Environment, Geology and Meteorology Centre (LEGMC). Climatic data. Available online: https://data.gov.lv/dati/dataset/klimatiskie-dati (accessed on 15 January 2024) (in Latvian).
- Thiem, B. 2003. Rubus chamaemorus L.—A Boreal Plant Rich in Biologically Active Metabolites: A Review. *Biol. Lett.* 40, 3–13.
- Valladares, F., Laanisto, L., Niinemets, Ü. & Zavala, M. A. 2016. Shedding light on shade: ecological perspectives of understorey plant life. *Plant Ecology & Diversity* 9(3), 237–251. https://doi.org/10.1080/17550874.2016.1210262
- Valladares, F. & Niinemets, Ü. 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. *Annual Review of Ecology, Evolution, and Systematics* **39**, 237–257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506
- Yañez-Mansilla, E, Cartes, P, Reyes-Díaz, M, Ribera-Fonseca, A, Rengel, Z. & Alberdi, M. 2015. Leaf nitrogen thresholds ensuring high antioxidant features of Vaccinium corymbosum cultivars. *Journal of Soil Science and Plant Nutrition* 15(3), 574–586. https://dx.doi.org/10.4067/S0718-95162015005000025
- Yang, H., Duan, Y., Wu, Y., Zhang, C., Wu, W., Lyu, L. & Li, W. 2023. Physiological and transcriptional responses of carbohydrate and nitrogen metabolism and ion balance in blueberry plants under nitrogen deficiency. *Plant Growth Regul* 101, 519–535. https://doi.org/10.1007/s10725-023-01038-5 Cited as: Yang et al., 2023a.
- Yang, Y., Huang, Z., Wu, Y., Wu, W., Lyu, L. & Li, W. 2023. Effects of Nitrogen Application Level on the Physiological Characteristics, Yield and Fruit Quality of Blackberry. *Scientia Horticulturae* 313, 111915. https://doi.org/10.1016/j.scienta.2023.111915 Cited as: Yang et al., 2023b.
- Zoratti, L., Jaakola, L., Häggman, H. & Giongo, L. 2015. Modification of Sunlight Radiation through Colored Photo-Selective Nets Affects Anthocyanin Profile in Vaccinium spp. Berries. *PLOS ONE* **10**(8), e0135935. https://doi.org/10.1371/journal.pone.0135935