

Drought effect on water relations and fruit yield in highbush blueberries

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Abstract — Introduction. The objective of our studies performed on the highbush blueberry plant (*Vaccinium corymbosum*) was to analyse the effects of (i) a drought cycle on key physiological processes, and (ii) moderate or strong water deficits on yield and harvest index. **Materials and methods.** Water potential, embolism, transpiration, photosynthesis and stem diameter variations were surveyed during a drought cycle and after rehydration (experiment 1). Two week-long dry periods (moderate and strong water deficits) occurring at different phenological stages (fruit growth, maturation and after picking) were analysed in relation to the fruit yield (experiment 2). **Results and discussion.** Blueberry is highly sensitive to a water deficit (i.e., stomata closure and decrease of photosynthesis occurred rapidly as water potential decreased); the rapid decrease of stomatal conductance efficiently restricts water loss and thus water potential decrease, which prevents embolism occurrence; blueberry exhibits a good recovery capacity after rehydration. The most critical stage was during fruit growth. A water stress occurring between late May and late June strongly affected fruit production by decreasing fruit size. **Conclusion.** Blueberries could be said to react quite "robustly" to water stress. Nevertheless, to assure high yield, they should be watered regularly. Detailed physiological studies (experiment 1) and more classical agronomics studies (experiment 2) were complementary to improve the species water relation knowledge and help cultural practices. © Éditions scientifiques et médicales Elsevier SAS

France / *Vaccinium corymbosum* / plant physiology / plant water relations / soil water deficit / plant response

Fonctionnement hydrique du myrtillier arbustif et élaboration du rendement.

Résumé — Introduction. L'objectif de nos études conduites sur le myrtillier (*Vaccinium corymbosum*) a été d'analyser (i) les effets d'un cycle de sécheresse sur certains stades physiologiques et (ii) ceux de déficits en eau plus ou moins forts sur le rendement et l'indice de récolte. **Matériel et méthodes.** Dans une première expérimentation, le potentiel hydrique, l'embolie, la transpiration, la photosynthèse et les variations du diamètre de la tige ont été suivis pendant un cycle de sécheresse, puis après réhydratation. Une deuxième expérimentation a permis d'analyser l'effet sur la production de 2 semaines de sécheresse, accompagnées de déficit en eau modéré ou élevé et appliquées à différents stades phénologiques (croissance du fruit, maturation et récolte). **Résultats et discussion.** Le myrtillier est très sensible au déficit hydrique, car la fermeture des stomates et la diminution de la photosynthèse interviennent rapidement lorsque le potentiel hydrique diminue. La baisse rapide de la conductance des stomates réduit efficacement les pertes en eau, entraînant une diminution du potentiel hydrique, ce qui prévient l'embolie des vaisseaux. Le myrtillier présente une bonne capacité de récupération après réhydratation. La période la plus sensible à la sécheresse se situe pendant le grossissement des fruits. L'application d'un stress entre fin mai et fin juin a de graves conséquences sur la production des fruits, leur taille étant fortement réduite. **Conclusion.** Le myrtillier peut être considéré comme robuste vis-à-vis du stress hydrique. Cependant, pour donner de hauts rendements, il devra être arrosé régulièrement. Les études physiologiques menées lors de la première expérimentation et celles, agronomiques, plus classiques, menées lors de la deuxième expérimentation ont été complémentaires pour approfondir les connaissances sur l'effet de l'irrigation sur l'espèce et ainsi aider à la conduite de sa culture. © Éditions scientifiques et médicales Elsevier SAS

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France / *Vaccinium corymbosum* / physiologie végétale / relation plante eau / déficit hydrique du sol / réponse de la plante

1. introduction

Highbush blueberry (*Vaccinium corymbosum*), originating from the Great Lakes region, in the United States, has been domesticated by Coville in 1906 [1] and introduced into France in 1980. These berry bushes are of increasing interest to farmers as a means of diversifying their production, or even for single crop cultivation. The blueberries under cultivation represent a new fruit in France. Annual consumption is only 2 g per person, compared to 500 g per person in the United States and 200 g per person in Germany. At present, 300 ha of orchard can be found, spread mainly across the Massif Central, the Landes, the Loire valley, the Vosges and Sologne. Scientific knowledge about this plant remains limited. This small-berry shrub is very rarely subject to conditions of water stress. On the contrary, major studies have dealt with anoxia resulting from root flooding [2, 3]. But, when grown in France, it can be confronted with such problems.

Few literature references contain data on the water relations of that species [4–6]. Nevertheless, Byers and Moore's [7] tentative application of cultivation coefficients permitted irrigation scheduling. Likewise, blueberry reaction in terms of gas exchanges [8, 9] indicates that the shrub reacts to water stress with sufficient recovery potential after stress.

This study on the water relations of this shrub was therefore conducted to provide answers regarding the development of highbush blueberry cultivation in Europe. For this reason, the *ministère de l'Agriculture, de la Pêche et de l'Alimentation* is financing a programme of training through research animated by Enita¹ (France) in collaboration with Inra² (France). This 5 year research project aims at furthering understanding of the development and functioning of the vegetative apparatus of the highbush blueberry and its water relations, as well as the technological value of the product and optimum conservation of the fruit. The work presented in this article concerns, firstly, the description of water relations of the bush under water stress conditions. We then study the impact of given levels of

water stress applied over a 20 d period (i.e., actual transpiration rate corresponding to 35% and 65% of the transpiration of control shrubs) on fruit production at various vegetative phases in order to identify the most sensitive stages during which irrigation is particularly necessary.

2. materials and methods

Our trials used 9 year-old var. Bluecrop blueberry bushes. Plants were about 1 m high, grown in 25 L containers in a mixed substrate composed of light peat (50%) and calibrated maritime pine bark (50%), with 2 L of gravel at the bottom of each pot to facilitate drainage. Plastic film was used to cover the surfaces of the containers to limit evaporation from the soil as completely as possible and to improve accuracy of the measurements of plant transpiration. Plants were watered with an acidophilic nutritive solution every 2 d. The weight at field capacity moisture of each container was determined prior to the running of the experiments.

The experimentation focusing on the effect of drought on water relations (experiment 1) was run in a greenhouse at a "controlled" temperature ranging from 20 to 30 °C by a cooling system. The experimentation on sensitive stages for fruit production (experiment 2) was run outside using a mobile shelter which could be installed over the containers in case of rain.

In experiment 1, a control group of six bushes, kept at near field capacity weight set to within approximately 1 kg of field capacity weight to limit the risks of hypoxia and leaching, was compared to six bushes without watering during 11 d, which constituted drought treatment.

In experiment 2, 30 pots were divided into six groups of five pots each, each group representing a specific treatment (*table I*). Three periods of water stress were chosen with one or two levels of stress, depending on the period. The "control" group was conditioned as explained above. We defined the level of stress in relationship to the transpiration rate. The water supply was

¹ Enita : *École nationale d'ingénieurs des travaux agricoles* located at Clermont-Ferrand, France).

² The laboratory which collaborates to this research is the *bioclimatologie-PIAF (Physiologie intégrative de l'arbre fruitier)* joined unity located at the Inra-université Blaise-Pascal and Inra Clermont-Ferrand agronomic center.

Table I.

Description of three periods of water restriction applied to 9 year-old blueberry bushes, with one or two levels of stress depending on the period (experiment 2). Each treatment was composed of five repetitions.

Water stress period	Phenological phase	Transpiration rate (%)	Treatment
Without restriction	–	100	C (control)
28 May–16 June	Growth of fruit	65	S ₁
		35	S ₁₊
18 June–7 July	Ripening-maturing	65	S ₂
		35	S ₂₊
10–29 July	Picking	65	S ₃

restricted so that the transpiration (T) of the bushes corresponded to 65% or 35% of the control group level.

Stress periods were determined in relationship to the various phenological phases of highbush blueberries and on the basis of preliminary experimental results [10]. At the end of each drought period, the pots were saturated with water and the plants regained an unlimited supply of water. In both experiments, daily transpiration of each bush was established by weighing (Mettler scale: accuracy to within 1 g for weights of up to 32 kg) and by measuring micro-variations in the diameters of a few stems for each treatment (Solartron sensor: accuracy to within 1 μm) [11, 12]. Leaf water potential was evaluated using a pressure chamber [13] before sunrise (Ψ_{Predawn}) and at mid-day, solar time (Ψ_{Min}), every day in experiment 1, and twice a week in experiment 2.

In experiment 1, complementary measurements of hydraulic conductance were made to characterize the plant vulnerability to embolism and to identify any presence of embolism under conditions of drought. To do so, we used hydraulic determination of embolism by measuring low pressure water flow [14]. The vulnerability curve was produced in laboratory by artificially drying stems by pressurisation [15]. In addition, measurement of leaf gas exchange (photosynthesis and transpiration) was made daily between 13:30 and 15:30 using a LICOR chamber (6400 model). This apparatus makes it possible to create a standardised

micro-climate around the measured leaf. In our work, we used a leaf temperature of 29 °C, a leaf irradiance of 1500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, a CO₂ concentration of 350 ppm, and a relative humidity between 75 and 78% (i.e., a vapour pressure deficit about 1 kPa).

In experiment 2, the fruit yield of the various treatments were determined. The numbers of floral buds per bush were counted before the experimentation; buds were then removed to give homogeneous subjects for the treatments (same number of flower buds per plant). Variance analysis and a rank test (Newman-Keuls) were run for yield components.

3. results

3.1. drought effects on water relations and leaf gas exchange

The evolution in the predawn water potential of the treated group in comparison to the control group showed differences between the two treatments, which were significant after 5 d without watering (*figure 1a*). The Ψ_{Predawn} of the treated plants reached -0.8 MPa at the end of the drought period.

The evolution of the Ψ_{Min} was similar for the two treatments and was strongly dependent upon climatic conditions (*figure 1b*). Significant difference between the treatments was observable from the third day. It should

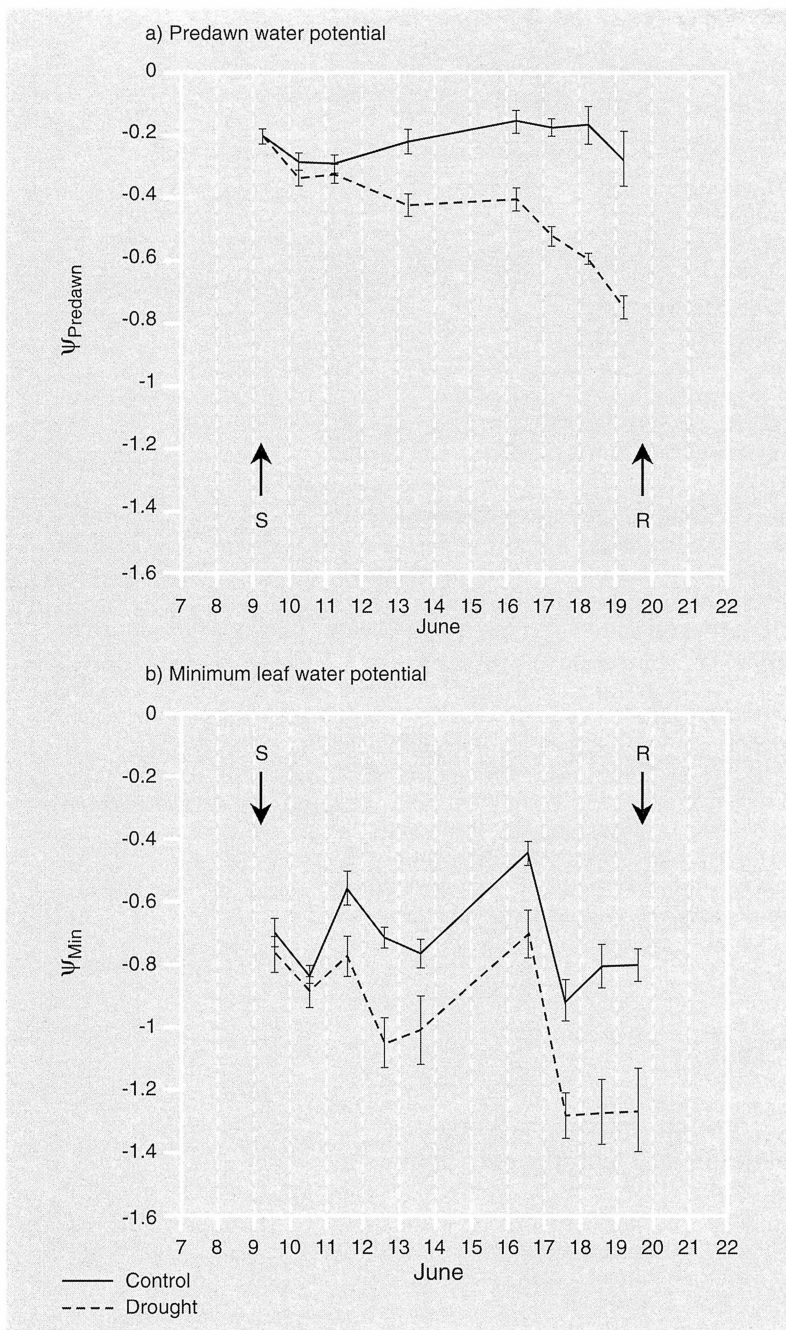


Figure 1. The effect of drought on blueberry water relations: evolution of a) the predawn water potential, b) the minimum leaf water potential during a period of water shortage, compared for a control group of six blueberry bushes, kept at near field capacity weight, and a drought treatment group of six bushes without watering during 11 d (experiment 1). The bars represent standard errors ($n = 6$). S: beginning of water shortage for treated plants; R: rehydration of treated plants.

be noted that the Ψ_{Min} did not drop below -1.4 MPa, but it remained at this value while, simultaneously, the Ψ_{Predawn} continued to drop. This behaviour, in which the Ψ_{Min} was maintained, is typical of ‘isohydric’ plants.

The evolution in stem diameter showed that growth was rapidly affected by drought, from the second day without water (figure 2). The amplitude of contraction rendered an account of the mobilisation of plant water reserves. A large increase could be seen in the amplitude of contraction for the treated group, expressing a higher level of mobilisation of plant water reserves. Upon bush rehydration (R), these higher levels of amplitude of contraction completely disappeared for a few days.

The net leaf photosynthesis, measured around 14:00 under standardised leaf micro-climate conditions, decreased very fast during the phase of water stress (figure 3). Eight days after rehydration (R) the treated plants regained the same level of photosynthesis as the control plants. In contrast, during the first 5 d following rehydration (20 to 25 June), the level of photosynthesis remained very low. This behaviour corresponds to the absence of growth on the one hand and to the lack of amplitude of contraction in stem diameter, mentioned earlier, on the other.

When the daily relative transpiration (transpiration of the treated group / transpiration of the control group, over the same period) is measured, transpiration of the treated plants represented only 35% of the transpiration of the control plants at the end of the stress phase (figure 4). This level of stress corresponds to that imposed in experiment 2 (sensitive phases: high stress). The plants were kept at this level of transpiration for 15 d in experiment 2. It should be noted that the plants returned to a rate of transpiration near to that preceding the pause in irrigation rapidly once the pause had ended (7–8 d).

The evolution in embolism (percentage loss of hydraulic conductance: LHC %) obtained by pressurisation at various pressures in laboratory made it possible to identify the cavitation threshold and to define

the evolution of conductance loss as a percentage. This curve (figure 5), which can be qualified as merely “physical” (in the sense that it does not denote the implementation of any physiological regulation), shows that, in this species, embolism increases very rapidly from -1.2 MPa. At -1.2 MPa hydraulic conductance, loss of the vessels was nil, whereas, at -1.4 MPa conductance, loss was at 50%. Above -2.1 MPa embolism was total. The water potentials obtained during stress were, thus, just at the threshold of cavitation. Maintaining the Ψ_{Min} around the cavitation threshold made it possible to protect the plant against strong embolism. Stomatal regulation is, therefore, very important for this plant since the threshold of cavitation is reached rapidly. The relative conductance evolution curve compared to the potential (figure 5) displays the efficiency of stomatal regulation. A very rapid decrease in relative stomatal conductance could be observed whenever the water potential dropped. The point of intersection with the vulnerability curve was observed for very low ψ values.

3.2. determination of sensitive stages in yield elaboration

As a more in-depth analysis has already been made [16], only global results on yield analysis are presented for each treatment: yield per bush, fruit quantities per bush and average weight of a single fruit (table II). The most sensitive periods corresponded to the phases of fruit growth (beginning of June) and of ripening-maturing (end of June). Moderate water stress (65% of the control transpiration level) resulted in a drop in yield. The most dramatic impact took place during the period of ripening under the strongest level of stress.

The quantity of fruit per bush remained unchanged (figure 6b). The drought treatment has no effect on fruit fall, but only on fruit size. The effect of water stress was felt mainly at the level of fruit filling, as it is showed by the fruit average weight. This point leads back to one of the previously presented results: photosynthesis was quickly affected whenever there was even a moderate level of water stress.

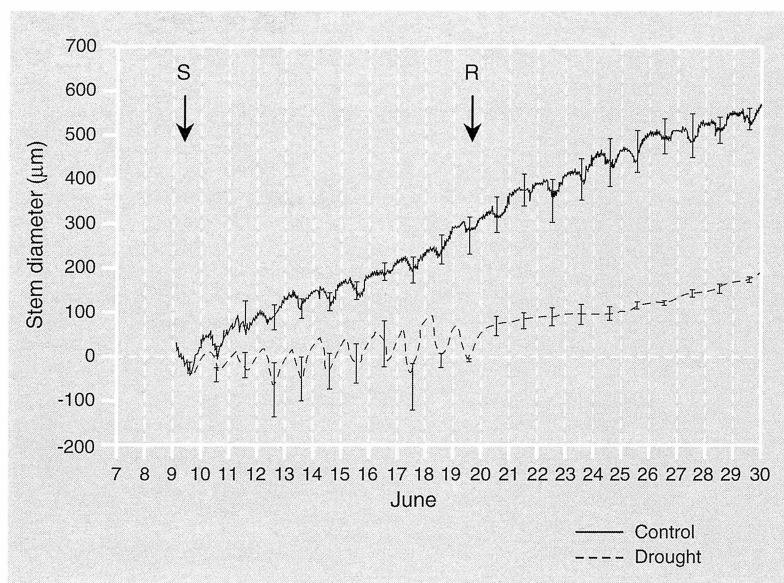


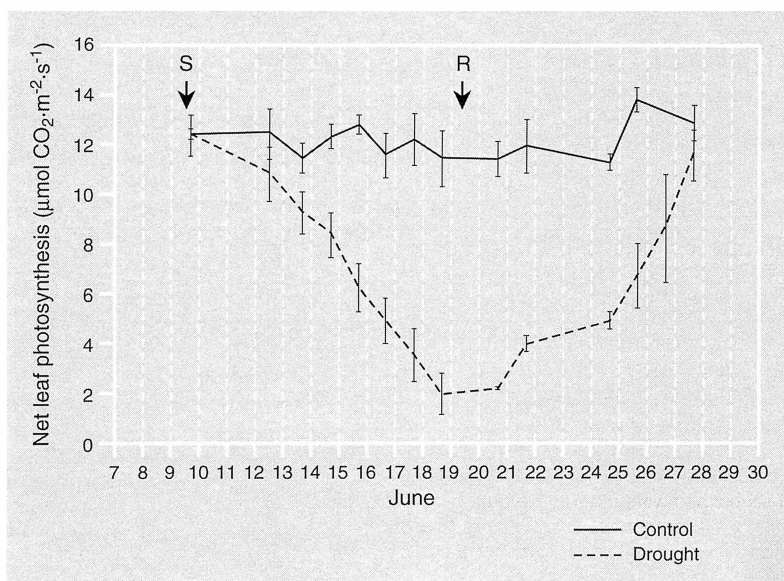
Figure 2.

The effect of drought on blueberry water relations: average evolution of stem diameter for control plants without drought treatment and treated plants (experiment 1). S: beginning of water shortage for treated plants; R: rehydration of treated plants. The bars represent standard errors ($n = 3$) at midday, solar time.

Figure 3.

Evolution of net leaf photosynthesis at midday (solar time) under standardised climatic conditions (29°C , irradiance = $1500\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $\text{CO}_2 = 350$ ppm, vapour pressure deficit = 1 kPa) for both blueberry control plants and plants without watering during 11 d (treated plants, experiment 1).

S: beginning of water shortage for treated plants; R: rehydration of treated plants. The bars represent standard errors ($n = 4$).



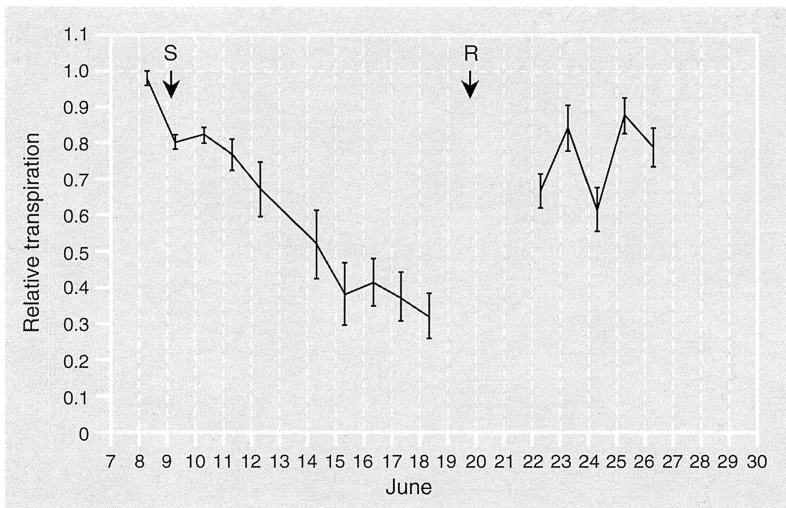
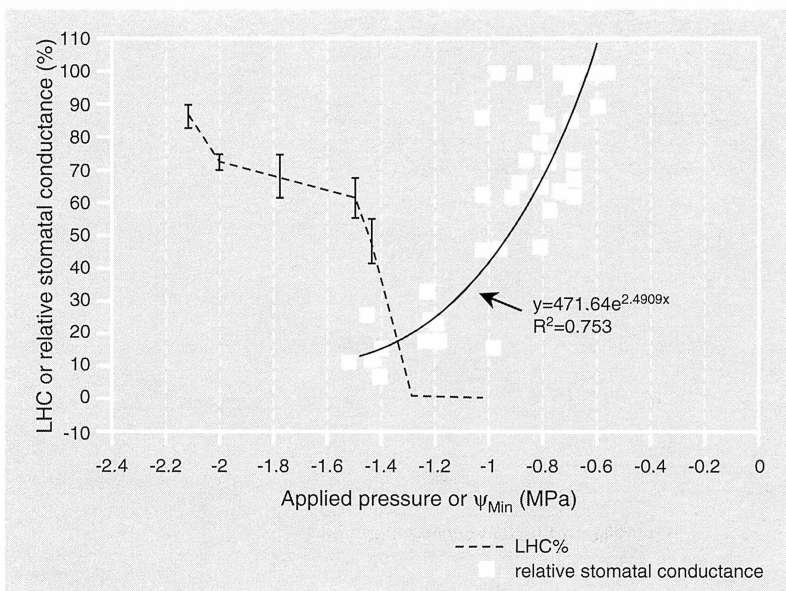


Figure 4. Evolution of daily relative transpiration of plants without watering during 11 d (treated plants) (i.e., transpiration of plants treated / transpiration of control plants, experiment 1). S: irrigation pause for treated plants. R: rehydration of treated plants. The bars represent standard errors ($n = 6$).

Figure 5. The effect of drought on blueberry water relations: evolution in the percentage of conductance loss (the bars represent standard errors; $n = 6$) and in relative stomatal conductance (i.e., values measured on treated plants normalized by values measured on control plants) as a function of water potential (leaf water potential for stomatal conductance, applied pressure for the vulnerability curve).



4. conclusion

In this study, we have shown that blueberries are highly sensitive to lack of water and that this sensitivity is displayed notably by rapid stomatal closure and, in parallel, by a significant reduction in photosynthesis. Regarding yield elaboration, no bloom or fruit fall was observed, nor was any fruit formation incident. The number of fruits borne by each individual shrub did not significantly differ between treatments. Therefore, the yield component altered was the fruit mean weight. Under moderate stress, the decrease varied between 15% (S_3 : picking) and 25% (S_1 : growth of fruit) whereas, under severe water restriction, it varied from 30% (S_1^+ : growth of fruit) to 40% (S_2^+ : ripening-maturing). Globally, it ensues that the marketing value of production can be significantly diminished by the reduction of fruit size in direct correlation with the fruit mean weight.

In contrast, the rapid stomatal closure makes it possible for the plant to limit its loss in water and, thus, avoid, in a large part, embolism of its vessels. In fact, blueberries would appear to be quite vulnerable to embolism, the cavitation threshold being reached at only -1.2 MPa, but the efficiency of their stomatal regulation protects them from both runaway embolism and shrub drying. This behaviour was the same as that which has been described for oak trees [17, 18]. There was, hence, efficient stomatal closure to protect the plant against embolism. This behaviour is somewhat different from that of walnut trees [19], in which embolism under conditions of water stress are limited to leaf petioles, thereby protecting the branches, as well as from that of peach trees that are very inefficient at closing their stomata and accept a high rate of embolism in their branches under drought conditions [20]. Furthermore, highbush blueberry presents a good aptitude at recuperating following rehydration. From this point of view, blueberries could be said to react quite “robustly” to water stress. Still, to assure high yield, they should be watered regularly.

The other interest of this study is to show the complementarity between detailed

Table II.

Effect of water stress on blueberry fruit production. The treatments C, S₁, S₁+, S₂, S₂+ and S₃ are those of the experiment 2, presented on *table I*.

Treatment	Yield per bush		Fruit per bush		Single fruit weight	
	Average weight (g)	% of control	Number	% of control	Average weight (g)	% of control
C	2 921.8 ± 89.44 a	100	3 178.8 ± 93.91	100	0.9246 ± 0.02 a	100
S ₁	2 279.4 ± 67.08 b	78	2 983.2 ± 49.19	94	0.7668 ± 0.02 ab	83
S ₁ +	2 030.2 ± 67.08 b	69	3 225.4 ± 178.89	101	0.6504 ± 0.03 bc	70
S ₂	2 312.4 ± 67.08 b	79	3 010.0 ± 125.22	95	0.7752 ± 0.01 ab	84
S ₂ +	1 490.6 ± 89.44 c	51	2 705.8 ± 53.67	85	0.5634 ± 0.04 c	61
S ₃	2 160.0 ± 44.72 b	74	2 860.4 ± 98.39	90	0.7692 ± 0.02 ab	83
Significance	**	—	ns	—	**	—

± standard errors with $n = 5$.

The different letters in a same column represent data with significant differences according to the Newman-Keuls test; ns, not significant; **, significant with $p = 0.05$.

physiological studies (experiment 1) and more classical agronomics studies (experiment 2). In particular, an in-depth knowledge of a species water relations is necessary to help cultural practices and improve the production of the species, particularly when quality criteria are sought.

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Funcionamiento hídrico del arándano arbustivo y elaboración del rendimiento.

Resumen — Introducción. El objetivo de nuestros estudios llevados a cabo sobre el arándano (*Vaccinium corymbosum*) fue analizar (i) los efectos de un ciclo de sequía en algunas fases fisiológicas y (ii) los de déficit de agua más o menos fuertes en el rendimiento y el índice de cosecha. **Material y métodos.** En una primera experimentación, se siguió vigilando el potencial hídrico, la embolia, la transpiración, la fotosíntesis y las variaciones del diámetro del tallo durante un ciclo de sequía, y luego después de rehidratación. Una segunda experimentación permitió analizar el efecto sobre la producción de 2 semanas de sequía, acompañadas de déficit de agua moderado o elevado y aplicados a diferentes fases fenológicas (crecimiento de la fruta, maduración y cosecha). **Resultados y discusión.** El arándano es muy sensible al déficit hídrico, dado que el cierre de los estomas y la disminución de la fotosíntesis ocurre rápidamente cuando el potencial hídrico disminuye. La baja rápida de la conductancia de los estomas reduce eficazmente las pérdidas de agua, produciendo una disminución del potencial hídrico, lo que previene la embolia de los vasos. El arándano presenta una buena capacidad de recuperación después de hidratación. El periodo más sensible a la sequía se sitúa durante el engorde de las frutas. La aplicación de un estrés entre finales de mayo y finales de junio tiene graves consecuencias en la producción de las frutas, su tamaño siendo fuertemente reducido. **Conclusión.** El arándano puede ser considerado como robusto frente al estrés hídrico. Sin embargo, para dar altos rendimientos, se tendrá que regar regularmente. Los estudios fisiológicos llevados a cabo en la primera experimentación y aquellos, agronómicos, más clásicos, desarrollados en la segunda experimentación fueron complementarios para indagar los conocimientos sobre el efecto del riego en la especie y asimismo ayudar al manejo de su cultivo. © Éditions scientifiques et médicales Elsevier SAS

Francia / *Vaccinium corymbosum* / fisiología vegetal / relaciones planta agua / déficit de humedad en el suelo / respuesta de la planta