UNIVERSITÉ DU QUÉBEC À CHICOUTIMI

DÉPARTEMENT DES SCIENCES FONDAMENTALES

DYNAMIQUE DE LA PHÉNOLOGIE, DE L'ALLOMÉTRIE ET DU RENDEMENT DES BLEUETIERS NAINS SAUVAGES DU QUÉBEC SELON L'ESPÈCE ET DIVERS TRAITEMENTS AGRICOLES

PAR

MARIE-PIER FOURNIER

B. Sc. (BIOLOGIE)

MÉMOIRE PRÉSENTÉ

À L'UNIVERSITÉ DU QUÉBEC À CHICOUTIMI

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN RESSOURCES RENOUVELABLES

RÉSUMÉ

Le rendement des plants de bleuets sauvages est étroitement lié à plusieurs caractéristiques intrinsèques et extrinsèques. Pour ainsi améliorer la productivité, une meilleure compréhension de l'influence de l'architecture des plants, de la phénologie spécifique aux espèces et des traitements de fertilisation et de fauchage sur la production de fruit serait importante pour faire de meilleur choix de pratiques agricole en zone nordique. Pour ce faire, la première partie de cette étude porte sur la comparaison des traits phénologiques, architecturaux et allométriques entre les deux espèces présentes au Saguenay-Lac-Saint-Jean, soit *Vaccinium angustifolium* Aiton et *Vaccinium myrtilloides* Michaux. Dans la seconde partie de l'étude, ce sont les effets combinés sur les traits allométriques et le rendement de deux pratiques agricoles, soit le fauchage et l'application d'engrais, qui sont comparés dans une bleuetière en zone nordique. L'expérience s'est déroulée du printemps 2017 à l'automne 2018 sur une bleuetière commerciale située au nord du Saguenay-Lac-Saint-Jean. La combinaison de fauchage – mécanique ou mécanique et thermique – et d'engrais – minéral, organique ou sans – a été appliquée sur les champs. La phénologie des bourgeons, la croissance en hauteur et en longueur, la masse des fruits par plant et par parcelle ainsi que le nombre d'éléments sur la plante (bourgeon, feuille, fleur, fruit, etc.) ont été notés selon le type de production en cours dans les champs, soit l'année après fauchage (*pruning year*) ou l'année de récolte (*harvesting year*). La surface foliaire spécifique, la biomasse hors-sol des plants, l'aire et la biomasse des feuilles ont été estimées à partir de la prise de donnée sur 192 plants récoltés.

La comparaison entre les espèces a permis de montrer des différences entre elles : d'abord leur phénologie diffère et le bourgeonnement des feuilles et des fleurs de *V. myrtilloides* est retardé, dû à un nombre plus important de composantes structurelles (bourgeon, fleur, feuille) comparativement à *V. angustifolium*. La biomasse des fruits est similaire entre les deux espèces : *V. myrtilloides* possède des fruits plus petits, mais en plus grande quantité, ce qui peut être expliqué par la limitation de la pollinisation et par une biomasse hors-sol importante. Par son retard dans la phénologie des fleurs, *V. myrtilloides* pourrait être l'espèce la mieux adaptée à la zone nordique pour résister au gel printanier, mais la pollinisation devrait être augmentée. Pour ce qui est des pratiques agricoles, l'application d'engrais, qu'il soit minéral ou organique, améliore la majorité des traits de la plante, dont la production de fruit après deux années. L'engrais organique n'a cependant réussi à atteindre les résultats de l'engrais minéral qu'après deux années, comme il a dû être dégradé avant d'être rendu disponible pour les plantes. Le fauchage thermique, appliqué en plus du fauchage mécanique, a accru certains traits végétatifs, comme la biomasse des feuilles et de la plante. D'ailleurs, deux modèles prévisionnels ont été produits et qui montre que le nombre de fleurs avec l'application d'engrais ainsi que la longueur des branches et la biomasse de la plante sont les facteurs qui expliquent le mieux le rendement en fruit. L'étude confirme que l'utilisation d'engrais dans les champs de bleuet en zone nordique est essentielle, mais une étude à plus long terme sur le fauchage thermique est nécessaire pour vérifier si ce type de fauchage amène réellement plus de bénéfices que de coûts.

AVANT-PROPOS

Ce mémoire a été réalisé dans le cadre du programme de maîtrise en ressources renouvelables de l'Université du Québec à Chicoutimi (UQAC). La directrice de maîtrise était Mme Annie Deslauriers de l'UQAC et le codirecteur était M. Maxime Paré, aussi de l'UQAC.

Cette recherche avait comme sujet l'impact des pratiques agricoles ainsi que des espèces sur la physiologie des plants de bleuets sauvages en zone nordique. Plus précisément, l'allométrie, l'architecture, la phénologie, la croissance ainsi que le rendement des plants ont été mesurés afin de comparer les espèces – soit *Vaccinium angustifolium* Aiton et *Vaccinium myrtilloides* Michaux – dans un premier temps, et aussi de décrire les effets de l'ajout d'engrais minéral ou organique, du fauchage mécanique seul ou mécanique et thermique et de l'interaction entre ses deux pratiques dans un second temps. Ainsi, ce mémoire se divise en deux chapitres écrits sous forme d'articles scientifiques en anglais, l'un portant sur la différence entre les espèces et l'autre portant sur l'effet de l'engrais, du fauchage et leur interaction sur la physiologie des plants de bleuets sauvages en zone nordique. Au cours de cette maîtrise, les résultats de recherche préliminaires ont aussi été présentés dans le cadre du *North American Blueberry Research and Extension Workers Conference* qui a eu lieu à Orono (Maine) aux États-Unis du 12 au 15 août 2018. Certains résultats ont aussi été rapportés aux partenaires agricoles par la Annie Deslauriers et Maxime Paré.

REMERCIEMENT

Tout d'abord, je tiens à remercier grandement Mme Annie Deslauriers et M. Maxime Paré pour d'avoir cru en mes capacités de mener à terme ce projet de recherche et de m'avoir dirigé tout au long de ma maîtrise. Votre dévouement envers moi a porté fruit et m'a permis d'acquérir des compétences qui me seront utiles dans les années à venir. Avec chacune de vos méthodes de travail et de vos différences, j'aurai eu un soutien varié qui m'a permis de devenir plus autonome tout au long de ma maîtrise. Un grand merci pour vos efforts et votre compréhension ! Je remercie aussi les partenaires financiers décrits dans l'avant-propos, car sans eux cette recherche n'aurait pas eu lieu.

De plus, sans aide, je n'aurais jamais réussi à accomplir mon terrain et mes laboratoires. Je dis merci à Claire Fournier et Mirelle Boulianne pour leur soutien en tant que technicienne au laboratoire de biologie de l'UQAC et d'avoir contribué, par votre travail impeccable et minutieux, aux travaux de recherche des étudiants. Sans vous, nous n'aurions personne vers qui nous tourner lors de problématiques dans le cadre de nos expériences, et votre aide nous est précieuse. Je veux aussi dire merci à toutes les personnes travaillant pour le laboratoire d'écologie animale et végétale de L'UQAC, particulièrement Léa Garcia et Quentin Lion pour avoir pris des donnés avec moi sur un terrain pas toujours convivial. D'ailleurs, je tiens à souligner les efforts des assistants de recherche et stagiaires qui m'ont aidé à accomplir ma tâche, soit Pénélope Blackburn, Jean-Benoît Tremblay, Maéva Julien, Félix Gagnon et Solène Brasseur. Sans eux, je n'aurais jamais réussi à récolter, mesurer, préparer et analyser 29 185 données phénologiques, 2305 données allométriques et 2328 échantillons de bleuetier. Un grand merci pour votre travail acharné !

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INTRODUCTION GÉNÉRALE

Le bleuet sauvage est sans contredit l'un des petits fruits les plus appréciés autant frais, congelé ou dans les produits transformés au Canada, ce qui en fait une industrie importante (MAPAQ 2016). Près du tiers des terres canadiennes dédiées à l'exploitation de ce petit fruit sauvage se retrouvent au Saguenay-Lac-Saint-Jean, une région caractérisée par un climat nordique qui limite les rendements en fruit par l'augmentation des risques de gel printanier (Strik and Yarborough 2005, MAPAQ 2016). D'autres facteurs peuvent influencer les rendements, comme les différentes pratiques agricoles, les maladies, la pollinisation, la pédologie et la physiologie des différents clones et espèces présents dans les champs (Hanson *et al.* 1982, Percival and Dawson 2009, Taulavuori *et al.* 2013). Peu d'études ont déterminé l'impact de ces différents facteurs en région nordique, il est donc nécessaire d'approfondir la recherche sur le sujet afin d'amener une meilleure gestion des bleuetières par les agriculteurs.

D'abord, le bleuet sauvage est un arbuste à rhizome endémique à l'Amérique du Nord de la famille des Éricacées (Eaton 1994, Penney *et al.* 1997). Il vit sur des sols podzoliques sablonneux d'origines éoliennes ou deltaïques, pauvres en éléments nutritifs, bien drainés et acides (Morin 2008). Deux espèces se retrouvent dans les champs du Québec, soit *Vaccinium angustifolium* Aiton – avec tiges et des feuilles glabres – et *Vaccinium myrtilloïdes* Michaux – avec des tiges et des feuilles pubescentes (Morin 2008, Gagnon *et al.* 2014). De plus, le cycle de culture du bleuet sauvage est habituellement de deux ans : les plants sont d'abord fauchés à la suite de la récolte des fruits à l'automne, ensuite ils entrent dans une année de croissance végétative, nommée « *pruning year* », et, l'année suivante, la production de fruits a lieu, soit l'« *harvesting year* » (Penney *et al.* 2008, Rioux 2011).

En général, la productivité d'un plant est grandement liée aux ressources intrinsèques et extrinsèques disponibles. Si la capacité photosynthétique ainsi que la disponibilité des nutriments et de l'eau sont améliorées, la productivité – c'est-à-dire la croissance des parties végétatives et productives – le sera aussi par l'augmentation des glucides non-structuraux produits par la photosynthèse (Jordan and Eaton 1995). Ces glucides, comprenant les sucres solubles et l'amidon, sont des molécules à la base du métabolisme, de la croissance structurale et de la formation des réserves (Körner 2003). Ainsi, si la plante alloue ses glucides dans la croissance de manière différentielle selon l'organe (Körner 2003), les croissances seront différentes en termes de productivité – ce que l'on nomme l'allométrie (Aarssen 2008) – ou dans le temps – on parlera plutôt de phénologie (Badeck *et al.* 2004). Par l'étude de l'allométrie et de la phénologie, il est donc possible de faire un portrait de la physiologie des plants et de pouvoir ainsi mettre l'emphase sur des différences structurales ou temporelles permettant l'augmentation des rendements. En liant la physiologie et les facteurs intrinsèques et extrinsèques pouvant modifier la productivité des plants, cela donnera un portrait clair des actions à prendre afin d'augmenter les rendements.

Chaque espèce possède comme facteur intrinsèque à sa physiologie des caractéristiques génomiques propres variant en fonction des clones et influençant leur productivité – *V. angustifolium* possèderait un meilleur rendement la première année de récolte alors que pour *V. myrtilloides* ce serait à la deuxième année (Chiasson and Agrall 1996, Morin 2008, Bell *et al.* 2010, Gagnon *et al.* 2014). Il serait donc pertinent de mettre en lumière comment les différences allométriques et phénologiques modifient la productivité des espèces afin de déterminer si l'une d'elles serait plus appropriée en zone nordique.

Les facteurs extrinsèques comme les pratiques agricoles peuvent aussi modifier la productivité, entre autres, le type de fauchage et d'engrais. D'une part, pour le type de fauchage, les plants sont d'abord coupés au ras du sol – fauchage mécanique seul, et peuvent ensuite être brûlés – fauchage mécanique et thermique. Le fauchage thermique est reconnu pour apporter des nutriments au sol par les cendres et d'éliminer les pestes – tels les insectes nuisibles, les champignons ou les mauvaises herbes, mais pourrait aussi causer une perte de matière organique du sol (Trevett 1956, Black 1963, Smith and Hilton 1971, Warman 1987, Kuwar 2012). Le fauchage mécanique seul augmenterait la ramification des plants, ce qui limiterait le nombre de bourgeons reproductifs par plant (Trevett 1966, Ismail *et al.* 1981).

Dans la culture du bleuet sauvage, le type d'engrais, la fertilisation minérale complète (N-P-K) contribuerait à une meilleure croissance et à une augmentation du nombre de bourgeons (Eaton 1994, Morin 2008, Lafond 2009) alors que la fertilisation organique démontrerait des effets inconstants selon les études (Gagnon *et al.* 2003, Warman *et al.* 2004, Warman *et al.* 2009, Fecondo *et al.* 2015, Rohloff *et al.* 2015, Koort *et al.* 2016, Stojanov *et al.* 2019). Bien que l'engrais organique doive être dégradé pour être accessible aux plantes, à long terme son application élèverait la quantité de matière organique dans le sol, augmentant du même coup son activité microbienne, sa rétention d'eau et sa capacité d'échange cationique (Gagnon *et al.* 2003, Warman *et al.* 2004). Cependant, la plupart des études n'ont pas mis en interaction le fauchage et la fertilisation ni déterminé leur influence sur les facteurs allométriques. Il serait donc pertinent d'étudier l'effet de ces pratiques agricoles sur les traits allométriques des plants dans le but de déterminer quel trait serait à améliorer afin d'accroître les rendements.

Ainsi, dans le premier chapitre, il sera question de l'effet des différences phénologiques et allométriques entre *Vaccinium angustifolium* et *Vaccinium myrtilloides* dans un but de prédire les traits à valoriser pour accroître les rendements.

Dans le deuxième chapitre, il sera plutôt question des effets du type de fauchage – mécanique ou mécanique et thermique – ainsi que du type de fertilisation – minéral ou organique – sur les trais allométriques et le rendement, et de comment le rendement peut être expliqué par des traits allométriques spécifiques.

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Chapitre 1: How plant allometry influences bud phenology and fruit yield in two vaccinium species

I. Abstract

Understanding how plant allometry, plant architecture, and phenology contribute to fruit production can identify those plant traits that maximize fruit yield. In this study, we compared these variables and fruit yields for two shrub species, *Vaccinium angustifolium* and *Vaccinium myrtilloides*, to test the hypothesis that phenology is linked to the plant allometric traits, which are predictors of fruit production. We measured leaf and flower phenology, allometric traits of shoots and fruit attributes of both *Vaccinium* sp. in a commercial wild lowbush blueberry field (Quebec, Canada) over a two-year crop cycle; one year of pruning followed by one year of harvest. During the harvesting year, the leafing and flowering of *V. angustifolium* occurred earlier than that of *V. myrtilloides* whereas for the pruning year, their phenology was similar. This difference was related to the allometric characteristics of the buds due to variation in carbon partitioning by the plants during the pruning year. *V. myrtilloides* produced more, yet smaller, fruits than *V. angustifolium*, and, as such, both plants had a similar fruit biomass production. A reduced pollination success and a different carbon partitioning strategy explains the fruit attribute of *V. myrtilloides*. Also, despite differences in reproductive allometric traits, the vegetative biomass still determined the reproductive biomass in a log-log scale model. Growing buds are competing sinks for nonstructural carbohydrates: the differences between the two *Vaccinium* species in both number and characteristics, e.g., number of flowers per bud, influence levels of fruit production and explain some of the phenological differences observed. For similar aboveground biomass, both *Vaccinium* species had similar reproductive outputs in terms of fruit biomass, despite differences in reproductive traits such as fruit size and number.

I.1.   Introduction

How a plant allocates carbon for reproduction is fundamental for explaining fruit yields. The allometry of biomass partitioning—the differential growth of plant parts (Aarssen 2008)—and the trade-off between vegetative and reproductive growth are at the base of the life strategies of plants and are species-specific. Carbohydrates, produced via photosynthesis, are allocated for metabolism, the growth of aboveground or belowground structures, the formation of reserves, and reproduction (Körner 2003, Park *et al.* 2009, Hartmann and Trumbore 2016); thus, the plant partitions carbon among different growing structures. Reproductive biomass—fruit yields in commercial species—match plant biomass (Weiner *et al.* 2009) and the allometry of leaf traits (Chang et al. 2017). These characteristics reflect both potential energy and the photosynthetic capacity for reproduction. In commercial blueberries (*Vaccinium* sp.) where fruit yield is important, excess available carbohydrates are first allocated to reproduction and then to vegetative growth (Swain and Darnell 2001, Chang *et al.* 2017).

A better understanding of plant phenology—the developmental stages of plant parts in time (Badeck *et al.* 2004)—physiology, and architecture, i.e., the organization of the different plant parts (Barthélémy and Caraglio 2007), is necessary to provide information on how to maximize fruit yields. The meristems, represented by both vegetative, i.e., growth, and reproductive buds, form a population of functional units or elements that compete for resources (Bonser and Aarssen 2003). As resource allocation is allometric in a broad sense (Weiner 2004), resource partitioning within plants can differ depending on the number of elements (size-dependent effect) influencing phenology (Mason *et al.* 2014, Barbier *et al.*

2015), growth, and reproductive outputs (Bonser and Aarssen 2003). For example, flower bud abundance, leaf surface area, and plant biomass are three plant traits that can affect fruit production; however, their relative importance can be altered through agricultural practices (Yarborough 2004, Yarborough 2012).

In commercial wild blueberry fields, crop management consists of a two-year crop cycle. The cycle begins with mechanical pruning in late fall, about two months after fruit harvesting. The following growing season—the pruning year—is used for vegetative growth where shoot development occurs from rhizomes to produce both leaf and flower buds for the second year. During the second year—the harvesting year—both fruit production and fruit harvesting occur (Chiasson and Agrall 1996b). In the pruning year, new shoot growth is driven by the translocation of root carbohydrates that supply carbon and nutrients to the vegetative buds (Loescher *et al.* 1990, Morin 2008, Kaur *et al.* 2012). In the harvesting year, however, carbon allocation is controlled mainly by the abundance and type of buds (Gauci *et al.* 2009, Kaur *et al.* 2012), as well as characteristics of the fruit (Li *et al.* 2015). Depending on the strength of the carbon sink, a trait that varies between species, vegetative growth can be slowed, sped up, or delayed (Kaur *et al.* 2012). Species allometry and phenology modify the presence and abundance of fruit as the number of reproductive units, such as buds, alters patterns of carbon allocation and partitioning (Lacointe 2000, Marcelis and Heuvelink 2007).

In North America, two endemic blueberry species are found in wild lowbush blueberry commercial fields. *Vaccinium angustifolium* Aiton, the lowbush blueberry, is a tetraploid species (24 bivalent chromosomes) marked by a glabrous foliage and stems that can attain 50 cm in height (Hall *et al.* 1979, Tirmenstein 1991, Chiasson and Agrall 1996a, Gagnon *et*

al. 2014). *Vaccinium myrtilloides* Michaux, the velvet leaf blueberry, is a diploid species (12 bivalent chromosomes) having pubescent foliage and stems that can reach 75 cm in height (Vander Kloet and Hall 1981, Tirmenstein 1990, Chiasson and Agrall 1996a, Gagnon *et al.* 2014). *V. angustifolium* is the most common species found in blueberry cultures and produces higher yields during the first harvesting year (Chiasson and Agrall 1996a). In contrast, *V. myrtilloides* produces a higher yield during the second harvesting year (Gagnon *et al.* 2014). A three-year crop cycle is rare, however, because of lower yields overall when compared to the two-year cycle. However, no studies have demonstrated the physiological reasons for the differences in fruit yield between the two species.

Earlier phenology is precarious in northern regions for both *Vaccinium* species because of the possibility of spring frosts, the main factor reducing wild blueberry fruit yield (Randall *et al.* 2001, Strik and Yarborough 2005, MAPAQ 2016). Although some commercial blueberries demonstrate cold hardiness and adaptation, temperatures below -2 °C during flower bloom can seriously injure reproductive structures and reduce fruit development and yield (Olson and Eaton 2001, Yarborough 2015). The timing of plant phenology is determined by both the genetic characteristics of species and the local climate (Badeck *et al.* 2004, Bell 2009, Anna and Rufus 2012). This leads to earlier or later phenological events in leaves or flowers that can influence a plant's susceptibility to frost (Smith 1969, Lin and Pliszka 2003, Hancock 2008) and thus affect fruit yield.

Most studies of plant physiology and phenology of wild blueberry (Hall *et al.* 1972, Swain and Darnell 2001, Morin 2008, Li *et al.* 2016, Drummond 2019) have taken place in maritime areas of coastal Maine, Nova Scotia, and New Brunswick. Furthermore, these

studies did not compare the phenology of *V. angustifolium* and *V. myrtilloides* or evaluate how phenology relates to the architectural aspects and allometric traits that are linked to fruit production. As both *Vaccinium* species have various phenotypes and genotypes, and produce variable amounts of fruit between years (Hall *et al.* 1979, Vander Kloet and Hall 1981, Tirmenstein 1990, Tirmenstein 1991, Chiasson and Agrall 1996a, Gagnon *et al.* 2014), comparing these species is important for understanding how much of these differences can be attributed to phenological and allometric traits and, eventually, determine the optimal conditions associated with higher fruit productivity.

In this study, we investigated the phenological and allometric characteristics of two wild lowbush blueberry species, *V. angustifolium* and *V. myrtilloides*, grown in commercial fields in the Lac-Saint-Jean region of Quebec, Canada. We aimed to understand how these phenological and allometric traits influence fruit yield. Specifically, we tested the hypothesis that (1) the leaf and flower phenology are linked to the plants' allometric traits and species; and (2) both phenology and plant allometry are predictors of fruit production.

I.2. Material and Methods

I.2.1. Experimental design

We conducted our study from spring 2017 to autumn 2018 in a commercial wild lowbush blueberry field at the *Bleuetière d'Enseignement et de Recherche* (BER) of *Corporation d'Aménagement Forestier de Normandin* (CAFN) in Normandin Quebec, Canada (48°49′35″N; 72°39′35″W). We established an experimental design that included 2 adjacent sites composed of 2 fields at each site and 4 blocks of 12 experimental units (EU) in each field arranged in a split-plot design (Supplementary Figure SM.1). Each site contained 96 EU, each 15×22 m (330 m^2), separated by 3-m buffer zones. All EU received 1 of 12 different treatments (see Table II.7 in chapter 2). These treatments were combinations of mechanical or mechanical and thermal pruning, with or without fungicide application, and mineral, organic or without fertilization (Supplementary Figure SM.1, see Table II.8 in chapter 2). Site 1 was pruned thermally in fall 2016 and mechanically in spring 2017. Site 1 was harvested in 2018. Site 2 was pruned mechanically and thermally in fall 2017. Site 2 was in a pruning year in 2018 and a harvesting year in 2019 (after the completion of this study, Supplementary Figure SM.1). However, the effects of these various treatments are not presented in this paper, but see chapter 2 p.48. As well, 52 beehives were used in spring 2018 to ensure sufficient flower pollination during harvesting year (see Table II.8 in chapter 2).

I.2.2.   Data collection

Immediately before the beginning of the growing season, eight shoots per EU were selected at random. As we wished to record early phenological changes, our initial measurements were recorded on shoots. We based our selection criteria on the observation of a primary leaf bud having reached Stage 1 to avoid buds showing no development (Supplementary Figure SM.2 and Figure SM.4). The same eight shoots in each EU were then monitored periodically throughout the growing season, for phenological measurements. We noted the species, *V. angustifolium* (VA) or *V. myrtilloides* (VM) when we observed and measured plant characteristics. In total, we monitored 604 plants of *V. angustifolium* and 164 plants of *V. myrtilloides* during the Site 1 pruning year (2017). During the Site 1 harvesting year (2018), we monitored 606 and 162 plants of *V. angustifolium* and *V. myrtilloides*, respectively. During the pruning year of Site 2 (2018), we monitored 585 *V. angustifolium* and 183 *V. myrtilloides* plants. We recorded leaf bud phenology over the pruning and harvesting years at both sites using the same shoot, with measurements every 3 to 4 days (see Table II.8 in chapter 2) following a six-stage leaf development protocol (Supplementary Figure SM.2, Figure SM.4 and Figure SM.5). Floral and fruit bud phenology were also recorded for Site 1 (every 3 to 4 days) during the harvesting year using an eleven-stage development protocol (Supplementary Figure SM.2, Figure SM.6, Figure SM.7).

We recorded several allometric traits of the blueberry shoots (Supplementary Figure SM.2). In pruning years, we noted the number (nb) of leaves and ramifications and plant height (cm). In the harvesting year (only Site 1), we recorded the number of leaf buds, flower buds, apical and total flowers, leaves, branches and ramifications, plant height (cm), and

branch length (mm). We measured these characteristics when they had attained their maximum values; thus, we noted these values once during the growing season. We then hand-harvested the fruit of each monitored plant to determine the number of fruits—apical and total number—and fruit biomass (BM) (g of fresh biomass (FM)) (Supplementary Figure SM.2). At the end of the harvesting year, a quarter of the monitored plants in Site 1 were cropped (192 plants in total; 145 *V. angustifolium* and 47 *V. myrtilloides*) to collect and determine leaf BM (g of dry biomass (DM)) and leaf area (cm^2) as well as the aboveground plant BM (g DM), excluding fruits (Supplementary Figure SM.2). Leaf area (cm^2) was measured with a planimeter (Li-3100, Li-Cor, Lincoln, NE, USA). Based on these collected data, aboveground plant BM, leaf BM, and the measured leaf area were extrapolated for all plants at both sites ($n = 1534$) using regressions of plant leaf number and height (Annexe 2, p.97). We calculated the specific leaf area (SLA) as:

$$SLA\left(\frac{m^2}{kg}\right) = \frac{leaf\ area\ (cm^2)}{dry\ leaf\ mass\ (mg)} * 100$$

.   **(I.1)**

I.2.3.   Meteorological data

We installed a meteorological station on Site 1 to record meteorological data, such as temperature (°C) and precipitation (mm), at 5-min intervals. Table I.1 presents the meteorological data for both years of our study.

I.2.4.   Statistical analysis

We assessed leaf and floral bud phenology as qualitative ordinal variables. The stages were expressed by their frequency for each sampling day, expressed as day of the year (DOY) (Deslauriers *et al.* 2019). We calculated the average date ($\bar{x}$), standard deviation ($s_{\bar{x}}$), and standard error of the mean ($se_{\bar{x}}$) at which the E_i stage occurred using:

$$\bar{x} = \frac{\sum_{i=1}^{k} f_{E_i} \times x_i}{n} ,$$

(I.2)

$$s_{\bar{x}} = \sqrt{\frac{\sum_{i=1}^{k}(x_i - \bar{x})^2}{n-1}} ,$$

(I.3)

$$se_{\bar{x}} = \frac{s_{\bar{x}}}{\sqrt{n}} ,$$

(I.4)

where x_i is the date expressed in DOY, f_{Ei} is the frequency of the E_i stage, and k is the number of sampling dates, as adapted from Scherrer (2007).

We developed a generalized multinominal logistic model to compare bud phenology between species (GENLINMIXED procedure in SPSS Statistics). The input data for the generalized multinominal logistic model was a frequency table where the E_i stage was expressed by their frequency of observation for each sampling day (DOY). In the model, species, year, and the date at which the Ei stage occurred were fixed variables, while fields, blocks (nested in fields), and EU (nested in fields, blocks, and species) were run as random

variables. We used the LINK option of LOGIT (SPSS Statistic) for the linkage function between the probabilities of the phenological response—linked to DOY—and fixed variables. This procedure produces logistic regressions, also known as logit probability models, where the explanatory variable, phenological stage, is a qualitative ordinal variable. The covariance structure in the RANDOM argument was determined as autoregressive (AR1) by the COVTYPE option (GENLINMIXED procedure in SPSS Statistic). The produced main logit probability model then determined the differences between species for both the leaf and productive buds; flowers and fruit were in the same logistic model. The $P(E_i)$ probability, which represents the probability of observing a phenological stage E_i at a given DOY x, was calculated separately by species using the estimate E_{st}. E_{st} is the sum of all fixed model coefficients (b) included for a specific combination, such as stage (b_{Ei}), species (s) and, if applicable, year (y), giving us:

$$E_{st} = -(b_{E_i} + b_s + b_y) \tag{I.5}$$

Also, $P(b_{Ei})$ represents the DOY when there is a 50% probability of passing through stage E_i; thus, $P(50)$ is similar, but it includes the effects of species and, if applicable, year. Those elements were calculated by these equations:

$$P(b_{E_i}) = \frac{b_{E_i}}{b_{DOY}} \tag{I.6}$$

$$P(50) = \frac{E_{st}}{b_{DOY}} + 2P(b_{E_i}) \tag{I.7}$$

Generalized linear mixed models were performed using IBM SPSS Statistics 25 (IBM Corp. (2017), Armonk, NY, USA).

We ran canonical discriminant analysis (CDA) to observe dissimilarities between *V. angustifolium* and *V. myrtilloides*. CDA was based on the dataset generated using the phenological *P(50)* calculations and the allometric traits of each plant (CANDISC procedure in SAS). We applied Wilk's λ and the Mahalanobis squared distance to evaluate the significance of the CDA. Using the STEPDISC procedure in SAS, we performed a preliminary discriminant stepwise analysis to select a subset of the quantitative variables among the measured allometric traits to discriminate the two species.

Using the PROC MIXED procedure in SAS, we developed linear mixed models to compare the two species in terms of the measured variables and allometric traits, as illustrated in Supplementary Figure SM.2 (except for phenology). We used species and year (if applicable) as fixed factors, and blocks (nested in fields) and EU (nested in blocks, fields, and species) as random factors.

We used linear regressions, as described by Weiner *et al.* (2009), to fit the R-V model for both *V. myrtilloides*, using reproductive biomass (R or fruit BM) as the dependent variable and the vegetative biomass (V or aboveground plant BM) as the independent variable. The two variables were transformed by $\log_{10}$ to improve normality. A mixed-effect model linked the two variables and species. Random effects included fields, blocks (nested in fields), and EU (nested in blocks, fields, and species). Mixed-effect models were built using a backward process (PROC MIXED procedure in SAS), where nonsignificant ($P > 0.05$) factors were removed from the models. The normality of the residual predicted values was verified. All CDA, linear mixed models, and mixed-effect models were developed using SAS 9.2 (SAS Institute, Cary, NC, USA).

I.3. Results

I.3.1. Phenological differences between species

The leaf, flower, and fruit phenology of *V. angustifolium* and *V. myrtilloides* were monitored in 2017 and 2018 (Supplementary Figure SM.4 to Figure SM.7). During the pruning year, the two species showed no differences in leaf phenology (Table I.3, Figure I.1a, b). The timing of the phenological phases ($P_{(50)}$) of the leaves between species differed by only 1–2 days. Year also had a significant effect as the overall timing of leaf phenology began at the same time in both species; however in 2017, leaf bud development finished earlier in both species by about 8 days compared to 2018 (Table I.2 and 3, Figure I.1a, b).

Phenological differences between the two blueberry species during the harvesting year were greater; relative to *V. myrtilloides,* the timing of leaf and flower phenology for *V. angustifolium* occurred about 10 and 8 days earlier, respectively (Table I.3, Figure I.1d, e,). We observed significant phenological differences between species in the harvesting year for leaf bud and flower bud (Table I.2). Flowering occurred later than leaf bud burst even though we observed increases in the size and swelling of the flower buds earlier than that for the leaf buds. Leaf buds opened five days prior to flower buds in *V. angustifolium* and two days in *V. myrtilloides* (Table I.3, Figure I.1d, e). We modeled a difference of eight days between the two species for the probability of open flowers (Stage 6); we observed open flowers on DOY 171 for *V. angustifolium* and DOY 179 for *V. myrtilloides* (Table I.3). This delay is important given that *V. angustifolium* flowers were open at that time (DOY 171) while *V. myrtilloides* flowers remained closed (Stage 5, Table I.3), thereby limiting cross-pollination between the two species.

The observed earlier flower bud phenology in *V. angustifolium* was maintained for most of the fruit development (Figure I.1c). However, the date at which we observed the first mature fruit was similar (Figure I.1c): about half of the *V. myrtilloides* plants had reached the last stage of fruiting when 80% of the *V. angustifolium* plants had attained the same stage. This indicates a faster fruit maturation toward the end of fruit development in *V. myrtilloides*.

I.3.2.   Species effect on allometric characteristics

During the pruning years, both species had similar plant heights (Figure I.2a, Table I.4), ramification numbers (Table I.4), plant BM (Figure I.2d), and SLA (Figure I.2j, Table I.4). In the pruning years, however, we observed significantly higher leaf numbers for *V. myrtilloides* than for *V. angustifolium* (Figure I.2h, Table I.4). Furthermore, we also observed a significant difference between years for leaf number (Table I.4) and SLA (Table I.4) in the pruning years, with both traits lower in 2018. We observed no significant year and species interactions (Table I.4).

During the harvesting year, plant BM (Figure I.2e), branch length (Figure I.2c), ramification numbers, SLA (Figure I.2j), and fruit BM (Figure I.2o) did not differ between the two species (Table I.4). All other characteristics differed significantly between the two blueberry species; for example, *V. angustifolium* had a greater flower bud number (Figure I.2k) and BM per fruit (Figure I.2r) than *V. myrtilloides*. All other allometric traits had higher values for *V. myrtilloides* (Table I.4), including plant height (Figure I.2b), number of leaf buds (Figure I.2f), leaves (Figure I.2i), branches (Figure I.2e), apical flowers (Figure I.2m), total flowers (Figure I.2l), flowers by bud (Figure I.2n), apical fruits (Figure I.2q), and total fruits (Figure I.2p). Branch growth slowed around the DOY 185, as fruits began to develop.

I.3.3.   Link between species, phenology, and allometric characteristics

Canonical axis 1 (Can 1) represented 96% of the between-class variation, and it discriminated the two blueberry species (Table I.5, Figure I.3). In the CDA, Wilk's λ was highly significant ($P < 0.001$), and the Mahalanobis squared distance separated the two species ($P < 0.0001$). Positive correlation (Table I.5) along the first canonical axis indicates smaller values for *V. angustifolium* than for *V. myrtilloides*. There was no separation along the CAN2 axis between the two blueberry species.

V. angustifolium had an earlier leaf phenology (correlation of 0.897 with CAN 1), associated with a lower leaf bud number (positive correlation of 0.307). *V. angustifolium* also had an earlier flower phenology. However, unlike leaf buds, the earlier phenology was not related to flower bud number that was negatively related (-0.135) with the *P(50)* of flowers. The earlier phenology of *V. angustifolium* was linked to a lower apical flower number (0.435) and a lower number of flowers per bud (0.333). The differences between species in flowering were therefore related to the allometric characteristics of the buds. Due to the lower apical flower numbers, *V. angustifolium* had fewer apical blueberries compared to *V. myrtilloides*.

For both species, the vegetative BM significantly determined the reproductive BM on a log-log R-V mixed-effect model (Table I.6, Figure I.4). Species and the interaction between species and vegetative BM were not significant and were thus removed from the model (Table I.6). The predicted log of reproductive BM increased with the log of vegetative BM (Table I.6) with a positive intercept (0.7667). For both species, several points fell well below the regression lines, indicating a very low reproductive biomass for these values of vegetative plant BM having a broad single point distribution (Supplementary Figure SM.3).

I.4. Discussion

In this study, we assessed the phenological differences of two species of *Vaccinium* and the links between phenology and plant allometry, including the allometric traits of fruit. In the harvesting year, we observed marked differences in leaf and flower phenology between *V. angustifolium* and *V. myrtilloides*; phenological events occurred later for *V. myrtilloides*. We highlighted the importance of plant allometry, especially bud allometric traits, to explain some of these phenological differences, in agreement with our first hypothesis. Despite differences in terms of bud number and bud characteristics, e.g., the number of flowers per buds and total flower number that influence phenology and the number of produced fruits, reproductive biomass was similar for both species. Plant aboveground biomass determined fruit biomass (Weiner *et al.* 2009, Wenk and Falster 2015); therefore, we only partially accept our second hypothesis. Delayed phenology can increase reproductive biomass indirectly by protecting flower buds from spring frost and favor reproductive success due to improved pollination (Jackson *et al.* 1972, Olson and Eaton 2001). Thus, allometric traits, determined by specific plant architecture and phenology, influence the production of fruit, and *V. myrtilloides* represents a promising species due to its delayed phenology, slightly greater vegetative biomass, and greater number of flowers relative to *V. angustifolium*.

I.4.1. Link between species, phenology, and allometric characteristics

We only observed phenological differences between *V. angustifolium* and *V. myrtilloides* during the harvesting year, not during the pruning years, even under the dissimilar environmental conditions between 2017 and 2018 (Table I.1). Smith (1969) highlighted the later leaf and flower phenology of *V. myrtilloides* in northern regions but did

not cite any explanation apart from genetic differences. Although these species have distinct genetics and chromosome numbers, *V. angustifolium* being tetraploid with 48 chromosomes and *V. myrtilloides* being diploid with 24 chromosomes (Smith 1969, Vander Kloet 1988, Sakhanokho *et al.* 2018)—elements that could, in part, explain the phenological differences—we observed no major phenological differences in the emerging leaf buds during the pruning years. This similar phenology between *Vaccinium* species during the pruning years suggests that this process depends highly on the mobilization of stored carbohydrates in the plant rhizomes, i.e., starch and sugars, made available for new shoot production following the stress of pruning (Hall *et al.* 1972, Janes 2004, Morin 2008). The delayed phenology observed for *V. myrtilloides* during the harvesting year, however, possibly indicates an effect of carbon partitioning through plant allometry, e.g., the number of leaf buds, total flower number, and flower per bud. The meristems number partially influenced the phenological timing of the two species and their fruit production.

During the pruning years, when the photosynthetic structures are ready, carbohydrate production in *Vaccinium* sp. is used preferentially to increase plant biomass and produce both flower and leaf buds (Swain and Darnell 2001, Petridis *et al.* 2018). The production of reserves in stems and rhizomes occurs toward the end of summer until leaf senescence (Kaur *et al.* 2012). Thus, while the two species shared similar plant allometric traits, such as biomass, height, the number of ramifications, and SLA, the observed differences in bud allometry during the harvesting year originated in the bud formation during the pruning year and was not related to a difference in reserves within the rhizomes. The interspecific allometric differences in flowering are established when flower buds are developed and

where several pre-flowers are produced for the flower and fruit production of the following year (Vander Kloet and Hall 1981, Kovaleski *et al.* 2015). Even if *V. myrtilloides* produces fewer flower buds, this species produces more flowers per bud, thereby allowing the species to have a greater number of total flowers during the harvesting year and thus increased fruit numbers. Similarly, compared to *V. angustifolium, V. myrtilloides* produced more vegetative buds at the end of the pruning year, allowing a greater branch production during the harvesting year. Although we did not record any photosynthetic data, we assume that both species had similar photosynthesis rates due to their comparable SLA, given the strong correlation between SLA and photosynthesis rate (Reich *et al.* 1997, Wright *et al.* 2004).

Sugar allocation has a direct role in bud phenology. In herbaceous and shrub plants, such as peas (*Pisum sativum* L.) (Mason *et al.* 2014) and roses (*Rosa hybrida* L.) (Barbier *et al.* 2015), respectively, decapitation of the apex leads to a rapid auxiliary bud release because of a reduced sink competition between the apex and the lower dormant buds that receive more sucrose after the excision. Moreover, at high levels of sucrose, auxiliary rosebuds open more rapidly, whereas low levels of sucrose result in a three-day lag (Barbier *et al.* 2015). Although rhizome growth and biomass may have differed between the species (to date, we are not aware of any studies that compare their belowground biomass), the starch reserves are shared between different developing shoots. In general, rhizomes act more as a carbon source (Hall *et al.* 1972, Janes 2004, Morin 2008), especially during shoot growth where starch reserves are severely depleted but are quickly refilled when growth is complete. Therefore, assuming a similar mobilization of stored carbohydrates from the plant rhizomes, such as during pruning years, the nonstructural carbon partitioning in the buds of the two

species differed, in part, because of their aboveground allometry. *V. angustifolium* had fewer leaf buds leading to a decreased sink competition and thus a higher sugar allocation per bud. As observed for other plant species (Mason *et al.* 2014, Barbier *et al.* 2015, Deslauriers *et al.* 2019), a greater amount of carbohydrates per bud could explain the earlier bud burst. However, unlike leaf buds, flower phenology seems not to be related to flower bud number. The number of flowers per bud influenced more the phenology rather than flowers number: a lower number of flower units per bud anticipated phenology. That corresponds with the delayed phenology in *V. myrtilloides* (Smith 1969), a specie having more flowers per bud.

Due to resource, partitioning between reproductive and vegetative meristems also differed between the *Vaccinium* species. During the harvesting year, the first phases of flower phenology occurred earlier than leaf phenology; in both species, however, leaf bud burst occurred prior to the first flower opening (Stage 6, Supplementary Figure SM.5 and Figure SM.6). The ability to quickly grow green leaves that assimilate CO_2 and speed up growth probably explain this observation (Shipley 2002, Weraduwage *et al.* 2015). During the harvesting year, the reproductive parts compete for carbohydrates with vegetative parts of the plant, although reproduction often has priority with respect to the other sinks (Swain and Darnell 2001, Chang *et al.* 2017). The more active and reproductive buds will develop into fruits, and this will be reflected in the sink competition and carbon allocations (Gauci *et al.* 2009, Kaur *et al.* 2012). Our results showed that vegetative growth, e.g., leaves, branches, slowed when fruit growth occurred, as the plant preferentially allocated carbohydrates to fruit development. Similar patterns have been observed for other species, including coffee, peach, cucumber, and tomato (Marcelis 1993, Heuvelink 1996, Génard *et al.* 2008).

I.4.2.   How plant allometry determines fruit attributes

While the total number of produced fruits was higher in *V. myrtilloides*, the fruits were smaller than those of *V. angustifolium*. Pollination success can explain this difference. Production of more flowers leads to a higher total fruit number and a higher fruit biomass per plant, in agreement with Usui (1994) and Usui *et al.* (2005). Thus, the number of fruits strongly and directly influences fruit biomass. However, although *V. myrtilloides* has many fruits, this specie had a biomass similar to *V. angustifolium* because of smaller fruits. This effect can be explained by an early flower phenology that may have a great and direct influence on fruit biomass by the period when the flowers were accessible for pollination; in our study, the number of added bees present in the field decreased sharply after the removal of the hives on June 28, 2018. Pollination was likely to have been greatly reduced after this date, meaning that flowers having a later phenology, e.g., *V. myrtilloides,* may not have had maximal pollination, thereby limiting ovule fertilization success by pollen vectors and thus the number of formed seeds vectors (Aalders and Hall 1961, Myra *et al.* 2004). As fruit size is well correlated with seed number (Weiner *et al.* 2009, Wenk and Falster 2015), delayed flower phenology by a lower bee presence can limit fruit biomass, in addition to limiting fruit development time in the growing season. Other than the time for development reflected by phenology, insect pollinators, such as bees, are critical for seed production success and fruit biomass. This relationship only holds when there are no early frost events; late reproductive phenology can protect flower buds against early spring frosts, which are a major factor affecting wild blueberry yields between years (Olson and Eaton 2001, Strik and Yarborough 2005, Gagnon *et al.* 2014).

Another factor can limit the pollination of *V. myrtilloides* was the lowest number of individuals (i.e. density) of this species in our study fields, decreasing the likelihood of a bee to bring pollen from one plant of *V. myrtilloides* to another. Moreover, because of only three days of overlap in flower phenology between both species, *V. myrtilloides* could not benefit from a large seed production by cross-pollination with *V. angustifolium*. Hybridization between species, however, can reduce reproductive biomass, and evidence of this was the several points lying below the regression line in our R-V model (Supplementary Figure SM.3), i.e., very low reproductive biomass relative to aboveground biomass. As proposed by Weiner *et al.* (2009), these represent cases of unsuccessful or aborted hybrid reproductive growth. In more southern regions, multiple studies have shown a deleterious effect on fruit production with the presence of both blueberry species in the same field due to this cross-pollination or inbreeding effect (Aalders and Hall 1961, Schott 2000, Bell *et al.* 2010).

Smaller fruits of *V. myrtilloides* can also be explained by carbon allocation. Plant allometry is linked directly to plant allocation, and this is essentially size-dependent (Gauci *et al.* 2009, Jorquera-Fontena *et al.* 2016, Jorquera-Fontena *et al.* 2018). In shrubs such as *Vaccinium* sp., the aboveground vegetative biomass is represented mainly by the photosynthetic biomass, i.e., leaves, while shoots and twigs are less important contributors. However, belowground biomass represents more than 90% of the total plant biomass (Marty *et al.* 2019) and contributes to the carbon requirements, especially at the time of shoot growth. The belowground reserves are shared between the different developing shoots, thus limiting the effect on a single shoot (Morin 2008). Reproductive biomass increases with aboveground biomass in a log-log allocation model, the R-V model (Weiner *et al.* 2009). When plant

biomass increases, potential reproduction output also increases, but there is also a greater structural and metabolic cost that limits maximizing carbon allocation to reproduction, depending on the source–sink carbon ratio (Gauci *et al.* 2009, Jorquera-Fontena *et al.* 2016, Jorquera-Fontena *et al.* 2018). In our R-V model, this pattern was represented by a slope < 1 (Weiner *et al.* 2009, Wenk and Falster 2015) with no minimum size of reproduction (negative *x*-intercept). For a similar aboveground biomass, both species had similar reproductive outputs in terms of fruit biomass, despite differences in fruit size and number. Yet, a large reproductive allocation was observed for a given vegetative biomass (large point distribution around the regression lines in Supplementary Figure SM.3). According to Bonser and Aarssen (2009), reproductive output also integrates environmental, developmental and genotypic factors, creating a large reproductive allometry, represented here by fruit biomass.

Drought can also modify plant allometry and limit reproductive output. Drought effects were observed in the pruning year of 2018, as plants received three times less rain than in 2017 (Table I.1). This resulted in a slower bud development and a lower leaf number and SLA. Water deficit limits carbon gain and development of organs such as buds, thus limiting the plant growth and the potential to produce vegetative biomass (Anadon-Rosell *et al.* 2017, Beauvieux *et al.* 2018). The hydraulic strategy of *Vaccinium* species to maintain stomatal conductance and photosynthesis during drier periods involves reducing leaf area by producing fewer leaves and increasing leaf protection, thereby reducing the SLA (Moola 1997, Hartley *et al.* 1999, Glass 2000, Anadon-Rosell *et al.* 2017). As drought limits vegetative biomass and alters leaf characteristics, the reproductive output is affected through less bud development: consequently, fruit yields are reduced the following harvest year.

I.5. Conclusion

We demonstrated that the difference in allometric traits between two *Vaccinium* species can modulate both phenology and fruit production. Plants having a greater vegetative biomass, characterized by a greater plant height, branch length, and number of leaves, produce more flowers and thus a higher fruit biomass. These findings are of great importance because a plant architecture having more vegetative and reproductive structures is going to present a sink competition in those structures that reduced carbon allocation and a delayed leaf and flower bud phenology protected buds from early spring frosts. *V. myrtilloides* has an architecture that promotes both greater fruit production, in terms of number, and a delayed phenology. This study provides new perspectives on how to improve the reproductive output of *Vaccinium* by enhancing both the vegetative biomass and plant architecture.

I.6.   Reference

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Table I.1. Mean monthly minimum, mean, and maximum temperature (°C) and total monthly rain (mm) for May–August for the two years (2017–2018) of the study.

Month (DOY)	Temperature (°C)			Total rain (mm)
	Minimum	Mean	Maximum	
2017				
May (121–151)	5.53 ± 3.50	12.90 ± 2.62	19.82 ± 3.92	16.6
June (152–181)	8.37 ± 3.98	15.87 ± 3.63	22.40 ± 4.52	115.4
July (182–212)	9.06 ± 4.06	17.51 ± 2.60	24.82 ± 3.10	72.6
August (213–243)	9.31 ± 3.45	15.62 ± 2.39	21.98 ± 3.40	123.6
2018				
May (121–151)	-0.13 ± 5.10	9.26 ± 5.24	17.57 ± 7.26	41.4
June (152–181)	6.60 ± 4.67	15.73 ± 4.44	23.00 ± 5.68	36.6
July (182–212)	15.66 ± 4.57	21.45 ± 2.70	28.30 ± 3.47	26.4
August (213–243)	12.92 ± 2.81	20.04 ± 2.17	27.08 ± 1.90	75

Table I.2. Generalized linear mixed models and pairwise tests of the effect of species and year on bud phenology. The results include the F-statistic, degrees of freedom (df_{nom}, df_{denom}), and P-value (P): $F_{df1, df2}$ (P). Significance of P-values is based on $\alpha = 0.05$; P-values in bold are significant in the main model.

Crop cycle	Type of bud	Effect	$F_{df1, df2}$ (P)
Pruning	Leaf	Model	$1201.827_{4, 8573}$ (**$P < 0.001$**)
		Species	$3.303_{1, 8573}$ ($P = 0.069$)
		Year	$223.749_{1, 8573}$ (**$P < 0.001$**)
		Species*Year	$1.494_{1, 8573}$ ($P = 0.222$)
		DOY	$4790.709_{1, 8573}$ (**$P < 0.001$**)
Harvesting	Leaf	Model	$2304.741_{2, 6425}$ (**$P < 0.001$**)
		Species	$249.490_{2, 6425}$ (**$P < 0.001$**)
		DOY	$4599.925_{1, 6425}$ (**$P < 0.001$**)
	Flower	Model	$4808.430_{2, 10402}$ (**$P < 0.001$**)
		Species	$173.725_{1, 10402}$ (**$P < 0.001$**)
		DOY	$9610.803_{1, 10402}$ (**$P < 0.001$**)

Table I.3. Day of the year (DOY) corresponding to 50% probability (P$_{(50)}$) of reaching the following stage for leaf (L) or flower (F) buds of *V. angustifolium* and *V. myrtilloides* in the pruning years of 2017 (Pr17) and 2018 (Pr18) or the harvesting year (Hy).

Stage	*V. angustifolium*				*V. myrtilloides*			
	L – Pr17	L – Pr18	L – Hy	F – Hy	L – Pr17	L – Pr18	L – Hy	F – Hy
0	-	-	132	126	-	-	142	134
1	146	154	139	134	147	155	150	142
2	153	161	148	146	154	162	158	154
3	158	167	152	152	160	167	162	160
4	162	170	155	157	163	171	165	165
5	166	174	158	163	167	174	169	171
6	-	-	-	172	-	-	-	179
7	-	-	-	181	-	-	-	188
8	-	-	-	189	-	-	-	196
9	-	-	-	203	-	-	-	211
10	-	-	-	213	-	-	-	220

Table I.4. Mixed model testing of the effect of species and years on allometric traits. The results include the *F*-statistic, degrees of freedom of the numerator (df1) and denominator (df2), and the *P*-value (*P* > F). The significance of the *P*-value is based on α = 0.05. Probability (*P*) is not significant (NS) when *P* > 0.05 while the other degrees of significance correspond to *P* < 0.001 (***), *P* < 0.01 (**), and *P* < 0.05 (*). BM = biomass, SLA = specific leaf area, nb = number, abov. = aboveground.

Organ	Traits	Type of year			
		Pruning			Harvesting
	Effect	Species	Year	Species × Year	Species
Plant	Plant abov. BM	$2.54_{1, 459}$ (NS)	$0.52_{1, 459}$ (NS)	$0.02_{1, 459}$ (NS)	$3.46_{1, 243}$ (NS)
	Plant height	$3.25_{1, 445}$ (NS)	$0.70_{1, 445}$ (NS)	$0.00_{1, 445}$ (NS)	$\mathbf{5.31_{1, 235}}$ (*)
	Branch length	-	-	-	$0.55_{1, 277}$ (NS)
	Branch nb	-	-	-	$\mathbf{7.70_{1, 104}}$ (**)
	Ramification nb	$1.38_{1, 410}$ (NS)	$0.44_{1, 128}$ (NS)	$0.20_{1, 403}$ (NS)	$0.84_{1, 285}$ (NS)
Leaf	Leaf bud nb	-	-	-	$\mathbf{24.52_{1, 225}}$ - (***)
	Leaf nb	$\mathbf{7.91_{1, 440}}$ (**)	$\mathbf{88.26_{1, 92.4}}$ (***)	$1.95_{1, 435}$ (NS)	$\mathbf{15.40_{1, 255}}$ (***)
	SLA	$1.42_{1, 562}$ (NS)	$\mathbf{44.74_{1, 181}}$ (***)	$0.26_{1, 553}$ (NS)	$0.01_{1, 760}$ (NS)
Flower	Flower bud nb	-	-	-	$\mathbf{6.42_{1, 304}}$ (*)
	Apical flower nb	-	-	-	$\mathbf{55.27_{1, 188}}$ (***)
	Total flower nb	-	-	-	$\mathbf{7.54_{1, 266}}$ (**)
	Flowers per bud	-	-	-	$\mathbf{33.59_{1, 184}}$ (***)
Fruit	Apical fruit nb	-	-	-	$\mathbf{61.28_{1, 228}}$ (***)
	Total fruit nb	-	-	-	$\mathbf{21.76_{1, 293}}$ (***)
	Fruit BM	-	-	-	$2.56_{1, 281}$ (NS)
	BM per fruit	-	-	-	$\mathbf{15.85_{1, 481}}$(***)

Table I.5. Correlation between variables and the first two axes in the canonical discriminant analysis. All correlations are significant ($n = 683$, $P < 0.05$), except for the correlation marked by an asterisk.

Organ	Variables	CAN 1	CAN2
Leaf	Leaf $P_{(50)}$	0.897	-0.413
	Leaf bud number	0.307	0.339
Flower	Flower $P_{(50)}$	0.790	-0.006*
	Flower bud number	-0.135	-0.140
	Flowers per bud	0.333	0.460
	Apical flower number	0.435	0.470
Fruit	Apical blueberry number	0.385	0.216

Table I.6. Complete and simplified mixed-effect model built for reproductive biomass (fruit BM). The results include estimation, standard error (SE), and test of effects with t-statistics, degrees of freedom (df), and P-value (tdf (P-value)). Significance of the P-value is based on α = 0.05; values in bold are significant in the main model. BM = biomass, VA = *V. angustifolium,* VM = *V. myrtilloides*.

Model	Effet	Species	Estimation (SE)	Test
Complete	**Intercept**	-	0.8381 (0.4137)	**2.03_{50} (0.0481)**
	Vegetative BM	-	0.6519 (0.1492)	**4.37_{475} (< 0.0001)**
	Species	VA	-0.0880 (0.4309)	-0.20_{475} (0.8383)
	Species	VM	0.0000 (0.0000)	
	Vegetative BM* Species	VA	0.0321 (0.1676)	0.19_{475} (0.8481)
	Vegetative BM* Species	VM	0.0000 (0.0000)	
Simplified	**Intercept**	-	0.7667 (0.2280)	**$3.36_{5.03}$ (0.0198)**
	Vegetative BM	-	0.6780 (0.0674)	**10.05_{477} (< 0.0001)**
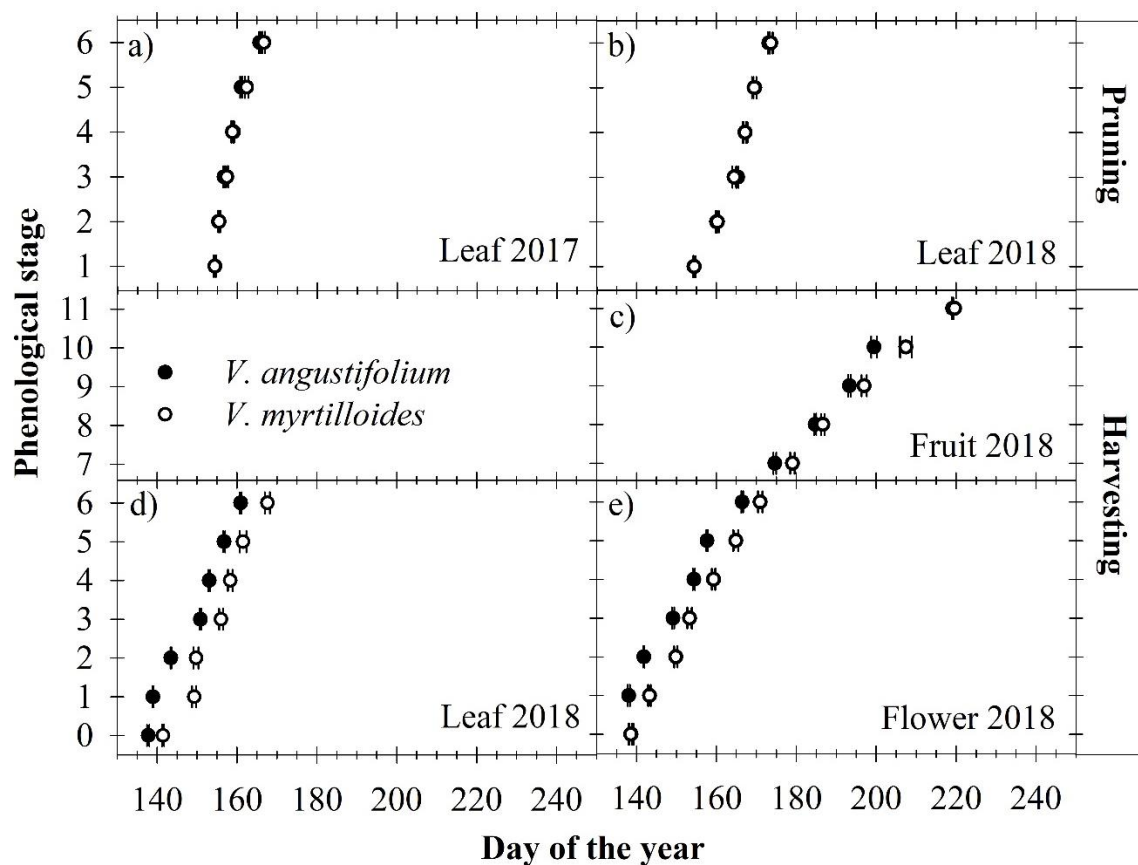
Figure I.1. Mean timing of the phenological stages of *V. angustifolium* and *V. myrtilloides* leaf buds in the vegetative years and the mean timing of the leaf, flower, and fruit buds in the pruning and harvesting years. Error bars represent the standard error of the mean.
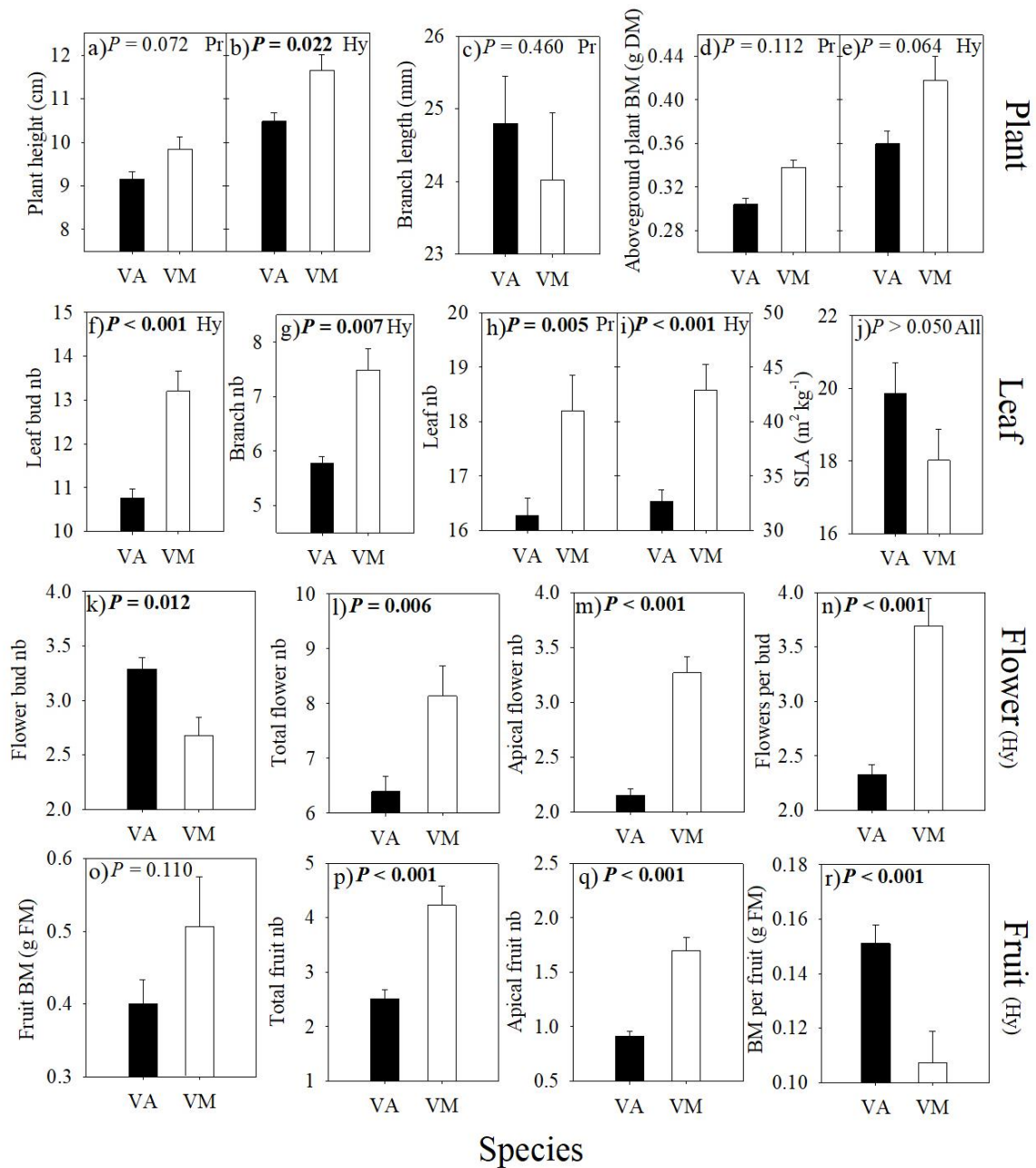
Figure I.2. Mean of the allometric traits per plant of the two *Vaccinium* species. Traits are presented for the different organs: plant, leaf, flower, and fruit. Data was collected in the pruning year (Pr), harvesting year (Hy), or both (All). Error bars represent the standard error of the mean. VA = *V. angustifolium,* VM = *V. myrtilloides*, nb = number, BM = biomass, DM = dry BM, and FM = fresh BM.
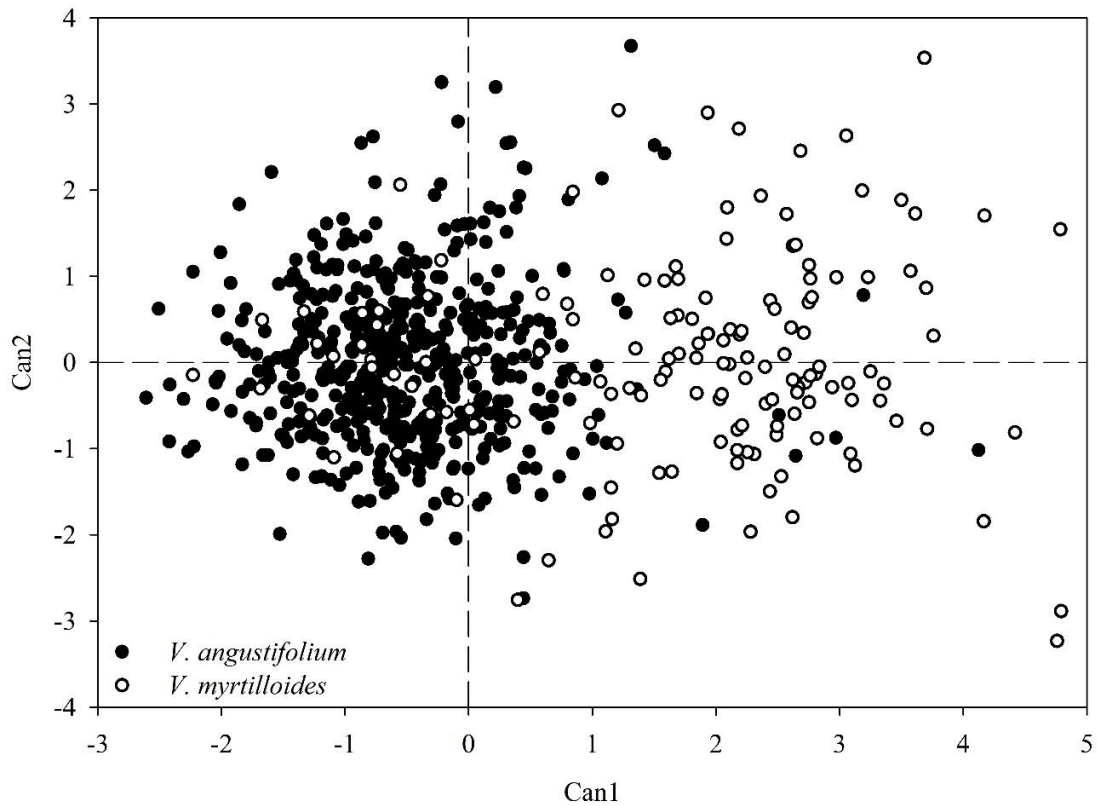
Figure I.3. Canonical discriminant analysis of the calculated distances based on the allometric parameters of *V. angustifolium* and *V. myrtilloides*. The distribution of the two species differs significantly ($P < 0.0001$).
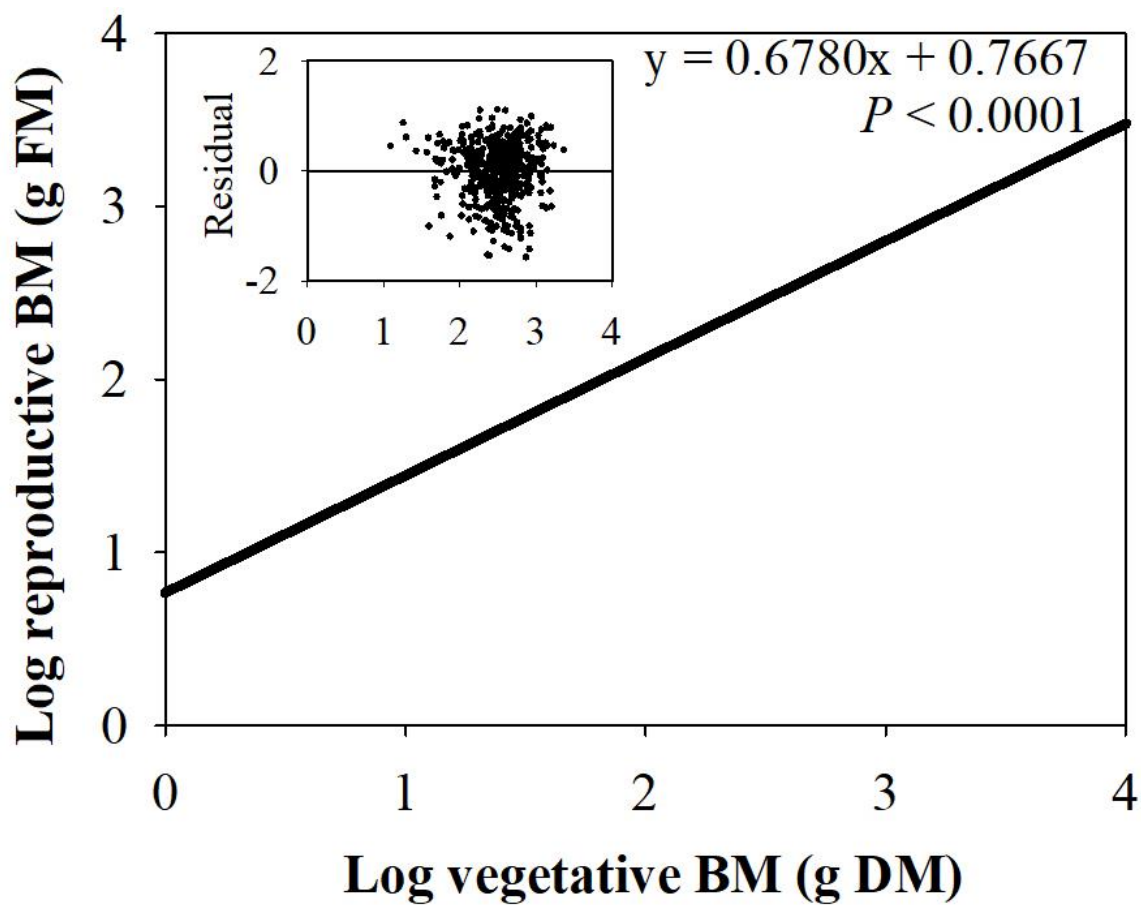
Figure I.4. Change in the log of reproductive biomass (g FM), i.e. fruit BM - R, predicted by the R-V mixed-effect model according to log of vegetative BM (g DM), i.e. aboveground plant BM - V. BM: biomass, FM: fresh BM, DM: dry BM.

Chapitre 2: Mineral or organic fertilizers and thermal pruning improve allometric traits related to fruit yields in a wild blueberry field

II. Abstract

Optimizing agricultural practices is an effective way to increase fruit productivity in commercial wild lowbush blueberry (*Vaccinium angustifolium* Aiton*; V. myrtilloides* Michx) fields but results from northern regions are scarce. In this study, we assessed the effect of a combination of pruning and fertilization practices on allometric traits and fruit yields in a commercial wild lowbush blueberry field from northern Quebec, Canada. We also targeted allometric traits that could be useful for predicting fruit yields. The experiment was conducted from fall 2016 to autumn 2018 where the combination of pruning – mechanical only or mechanical and thermal – and fertilizer – mineral, organic or without – was applied on two sites. Allometric traits, including fruit number and mass were measured on eight shoots per experimental unit (EU). The aboveground plant biomass, leaf biomass and leaf area were also measured on 192 monitored plants. Our results show that mineral and organic fertilizers improved most allometric traits in both pruning and harvesting years, including productive traits and fruit yields. During the pruning year, organic fertilizer led to lower plant allometric traits (i.e. plant aboveground biomass, leaf biomass, plant height) compared to mineral fertilizer, but similar traits were measured during the harvesting year, indicating a delayed effect of organic fertilizer. During harvesting year, compared to mechanical pruning used alone, thermal pruning improved some vegetative traits, such as plant and leaf biomass, leaf area, and plant height, but to a lesser extent than fertilizer applications. Furthermore, we modeled fruit yields as a function of productive or vegetative traits and showed that flower number, branch length and aboveground plant biomass positively explained fruit yields. All these traits were improved by fertilizer applications. Long-term studies must be performed to determine if the beneficial effect of thermal pruning will significantly improve fruit yields.

II.1. Introduction

Wild lowbush blueberry, an endemic shrub of North America, is an important crop in the Canadian agri-food industry. Canada is a major wild blueberry producer with exports exceeding about 200 million dollars per year. One third of this is produced in Quebec, and more than 80% of the Quebec wild blueberry fields are located in the northern regions of Saguenay-Lac-Saint-Jean (Vander Kloet 1988, MAPAQ 2016). However, compared to other southern areas, Quebec presents lower fruit yields (1.5 t ha^{-1}) compared to New Brunswick (3.4 t ha^{-1}), Nova Scotia (2.4 t ha^{-1}) or Maine (4.9 t ha^{-1}) (MAPAQ 2016, Yarborough 2017). To increase fruit yields, researchers, agronomists and farmers are looking for better agricultural practices. In Maine, many practices have been identified that improve fruit yield (Yarborough 2004), such as herbicide and fertilizer applications, pollination, integrated pest control, irrigation, pruning and harvesting methods (Yarborough 2004, Drummond *et al.* 2012). Although favorable practices are known, few researches have demonstrated their effectiveness in Saguenay-Lac-Saint-Jean contexts of northern climate.

Wild blueberries normally have a two-year crop cycle: after fruit harvesting, farmers prune plants mechanically and/or thermally in fall (Chiasson and Agrall 1996, Gagnon *et al.* 2014). During the first growing season, named as pruning or vegetative year, plant growth occurs from rhizomes (Gagnon *et al.* 2014). At the end of the pruning year, leaf and flower buds are produced for the following year and those buds remain dormant during fall and winter, when no agricultural practices are performed (Eaton and Nams 2006). During the second year, named as harvesting or production year, the fruits are harvested and the plants are pruned thereafter (Chiasson and Agrall 1996, Gagnon *et al.* 2014).

Two types of pruning are used by producers: mechanical or thermal. Mechanical pruning is widely performed technique in blueberry fields to stimulate stem refreshment and fruit production (Gagnon *et al.* 2014). However, if not performed adequately (i.e. > 1 cm above ground level), it could increase plant ramifications and branch number per stem (Ismail *et al.* 1981), and ramified plants may produce fewer flower buds and less fruit (Trevett 1966). In addition to mechanical pruning, thermal pruning may be also commonly done to add available and essential plant nutrients to soil in the short term by ash production (Hanson *et al.* 1982). This method is also known to increase fruit yields, plant height, density, biomass and mycorrhizal colonisation while reducing weed competition and plant diseases such as blueberry maggots (*Rhagoletis mendax* Curran) (Black 1963, Smith and Hilton 1971, Ismail *et al.* 1981, Hanson *et al.* 1982, Warman 1987, Penney *et al.* 1997, Kuwar 2012).

Nevertheless, thermal pruning is more expensive than the mechanical pruning and may also reduce the depth of soil organic horizons, which could limit soil nutrient pools and growing space for rhizomes and roots (Trevett 1956, Smith and Hilton 1971). However, a reduction in the soil organic matter depth was only observed when intense burning methods were used (Trevett 1956, Smith and Hilton 1971). Considering the cost difference between these types of pruning, blueberry production in Maine became more efficient after adoption of mechanical pruning only (Yarborough 2004), but the cost-benefit balance could be different in northern fields such as those in Saguenay-Lac-Saint-Jean where pest controls are easier – less pest species survive to northern climate. Thus, local and long-term studies are still needed to adequately choose which type of pruning method is best adapted for northern wild blueberry production.

Fertilizer applications are known to increase fruit yields, but only when weeds are controlled (Ismail *et al.* 1981, Eaton 1994, Penney and McRae 2000, Rojas 2010); wild blueberry is less effective than most weeds in assimilating nutrients from fertilizers (Eaton 1994, Marty *et al.* 2019). Moreover, fertilizer applications – specifically nitrogen (N) – increase the plant productivity (Lafond and Ziadi 2011, Jiao *et al.* 2017), but a too tall plant can increase the risk of winter frosts (Ismail *et al.* 1981), since 30 cm depth of snow has been identified as a threshold in order to protect the plants from winter frosts in northern Quebec (Girona *et al.* 2019). Also, adding too much fertilizer, specifically N, may substantially favor plant vegetative biomass and significantly reduce fruit yields (Lafond 2009). Since thermal pruning may increase soil nutrients availability (Smith and Hilton 1971), it remains unclear if fertilizer practices interact with the pruning method in Saguenay-Lac-Saint-Jean region.

The literature contains extensive researches on different agricultural practices linked to fruit yields (Black 1963, Ismail *et al.* 1981, Warman 1987, Eaton 1994, Penney *et al.* 1997, Eaton and Nams 2006, Morin 2008, Lafond 2009, Smagula *et al.* 2009, Lafond and Ziadi 2011, Rioux 2011). However, most of these studies were not conducted in northern areas and did not take into consideration interactions between pruning and fertilizer management practices. Also, no studies linked the fruit production with most allometric traits of plants (i.e. differential growth of plant parts (Aarssen 2008)) to determine which traits need to be targeted in order to increase fruit yields. Indeed, Trevett (1959) and Lafond and Ziadi (2011) found that flower bud number, plant height and density were positively correlated to fruit yields, but their predictive models did not include other traits that may control fruit yields such as plant biomass (BM), second year plant growth, and number of vegetative buds.

In this study, we investigated the combined effects of two major agricultural practices – pruning and fertilization – on allometric traits and fruit yields in northern blueberry fields (*Vaccinium* sp.). Since about 10% of wild blueberry lands in northern Quebec are now under organic management (Villeneuve 2018), we also investigated and compared the efficiency of a much-used organic fertilizer (poultry manure) with conventional mineral fertilizers and a control. We expected that fertilizer applications (mineral or organic) in combination with thermal pruning would improve most allometric traits and fruit yields.

II.2. Material and Methods

II.2.1. Experimental Design

The experiment took place from fall 2016 to autumn 2018 on a commercial wild lowbush blueberry field at the *Bleuetière d'Enseignement et de Recherche* (BER) in Normandin, Quebec, Canada (48°49′35″N; 72°39′35″W). The first fruit production on the field was harvested in 2008. Two adjacent sites were sampled, each totalling 96 experimental units (EU) of 15 x 22 m (330 m^2), including a 3 m border (buffer zone) between each EU. One site was composed of 2 fields, each inclued 4 blocks of 12 experimental units (EU) arranged in a split-plot design (Figure II.5, Supplementary Figure SM.1). All EU received a 1 of 12 combined treatments defined as pruning, fungicide, and fertilizer (Table II.7). Beehives (*Apis mellifera* L.) were used to ensure sufficient flower pollination (Table II.8).

Pruning treatments were defined as mechanical (M) or mechanical and thermal pruning (MT) (Table II.7). M was applied to all EU with a blueberry mower (model TB-1072, JR Tardif, Rivière-du-Loup, Canada) while MT was only applied to half of the EU with a high-pressure propane burners towed by a tractor (home-made liquid propane burner from *Bleuets du Canton S.E.N.C*, Dolbeau-Mistassini, Canada). The home-made burner includes fours individual propane burners that were placed 10 cm above soil surface. Burners consumed together about 140 kg of propane ha^{-1} (pressure of 15 psi and tractor speed of 1.5 km/hr). Considering net heating value of propane of 47 MJ kg^{-1} (Linstrom and Mallard 2001), this fuel consumption represents about 6 580 MJ ha^{-1}. Similar to Vincent *et al.* (2018), soil temperatures increased by less than 10 °C several minutes after thermal pruning (data not shown). Dates of pruning and details are presented in Table II.8.

Three fertilization treatments were defined as control (CF, no fertilizer applied), mineral fertilizer (MF) and organic fertilizer (OF). MF consisted of an application of nitrogen (N) (50 kg of N ha^{-1} as ammonium sulfate), phosphorus (P) (15 kg of P_2O_5 ha^{-1} as super triple phosphate), potassium (K) (15 kg of K_2O ha^{-1} as potassium sulfate) and boron (B) (0.7 kg of B ha^{-1} as borate) (Table II.7). Identical amounts of N (50 kg of N ha^{-1}) and B (0.7 of B kg ha^{-1}) were applied in OF EU with 1 000 kg ha^{-1} of granulated chicken manure (Pure Hen Manure, Acti-Sol Inc., Notre-Dame-du-Bon-Conseil, Canada) and borate (Table II.7). OF also provided P (30 kg P_2O_5 ha^{-1}), K (20 kg K_2O ha^{-1}), Ca (70 kg ha^{-1}) and organic matter (710 kg ha^{-1}). Dates of treatment applications are reported in Table II.8. All fertilizers were applied at soil surface using small broadcast spreader before plants emerging. Fungicide information (data not shown) was described in Table II.8.

II.2.2.   Data Collection

Allometric traits of 8 blueberry shoots per EU were selected at random and monitored – i.e. number (nb) of vegetative buds, flower buds, flowers, leaves, branches and ramifications, plant height (cm) and branch length (mm) (Supplementary Figure SM.2). The number of fruits and their biomass (BM) (g FM – i.e. fresh BM – per plant) were measured after being harvested by hand (Supplementary Figure SM.2). At the end of the harvesting year, a quarter of followed plants in Site 1 were cropped to measure their aboveground plant BM (g of dry BM or DM) that excluded fruits, leaf BM (g DM) and leaf area (cm^2) (Supplementary Figure SM.2). Dry BM of plant materials were obtained after oven drying at 60 °C for 48 hours.   The leaf area (cm^2) of these 192 plants was measured with a planimeter (Li-3100, Li-Cor, Lincoln, NE, USA). With the information from these plants, the

aboveground plant BM, leaf BM and leaf area were estimated for all other plants of the two

site with regressions based on plant height and leaf number per plant (Annexe 2, p. 97). The

specific leaf area (SLA, m^2 kg^{-1}) was then calculated according to equation I.1.

$$SLA\left(\frac{m^2}{kg}\right) = \frac{leaf\ area\ (cm^2)}{dry\ leaf\ mass\ (mg)} * 100 \tag{I.1}$$

Fruit yields (t ha^{-1}) from each EU were measured with a commercial blueberry

harvester (picker of 60 inch, *Les équipements D.H. Inc.*, Albanel, QC, Canada, on a F3680

tractor, Kubota, Osaka, Japan). Plant density in each EU was also estimated by counting all

stems in a quadrat of 50 cm by 50 cm (0.25 m^2) repeated four times on a transect diagonal

line.

II.2.3. Meteorological Data

A meteorological station, located directly on the experimental site, monitored

temperature (°C) and precipitations (mm) every 5 minutes. Supplementary Figure SM.8

presents the mean data from May to August in 2017 and 2018.

II.2.4. Statistical Analysis

Linear mixed models were developed to compare allometric traits and fruit yields

between treatments by the type of years (PROC MIXED procedure in SAS). Treatments

(pruning, fungicide, and fertilizer) and years (for the pruning cycle only) were considered as

fixed variables, while blocks (nested in fields) and EU (nested in fields and blocks) were

considered as random variables. Fungicide effects were included in the statistical analysis

but are not presented in this manuscript. Two mixed-effect models were created to link fruit

yields to treatments and allometric traits of leaves and plants, and flowers. In hierarchical order, presented in Figure II.5, fixed effects included allometric traits (Level 1), fertilizer treatments (MF, OF and CF, Level 2), fungicide treatments (FUN and CFUN, Level 3) and pruning treatments (M and MT, Level 4). Allometric traits were put in interaction with those last treatments. Random effects included blocks nested in fields (Level 5), and fields (Level 6). The mean of allometric traits were done by EU and an upscaling (to have data per hectare) was used on discrete variable (i.e. number of elements) to correct values according to the plant density of each EU. Variance inflation factors (VIF, Belsley *et al.* (1980)) – were verified to detect multicollinearity among the predictors of models. The leaf-plant model included the numbers of leaf buds, leaves, ramifications and branches, SLA, leaf area, branch length, plant height, aboveground plant BM and leaf BM. The flower model included the numbers of flower buds, flowers and flowers by bud. VIFs were generally lower than the accepted value of 4 (O'Brien 2007) in the flower model and in the leaf-plant model, but in this latter, the number of leaves, plant height, leaf BM and leaf area were removed because of their high collinearity and correlation with the aboveground plant BM and SLA; due to their presence in estimated equations of these traits. Mixed-effect models were built with a backward process (PROC MIXED procedure in SAS) starting from a null model and then gradually extended to the lower levels. Not significant (P value > 0.05) allometric traits or treatments were removed from models. Fitting was calculated with Akaike information criterion (AIC), AIC for small sample (AICC) and Bayesian information criterion (BIC) values, where lower values denoted a better model when the models were compared with each other. Normality of residual predicted values was verified and validated with Shapiro-Wilk test. Statistical analyses were performed in SAS 9.2 (SAS Institute, Cary, NC, USA).

II.3. Results

II.3.1. Fertilizer Effects

In the pruning year, compared to CF, adding MF and OF increased plant height (Figure II.6e), aboveground plant BM (Figure II.6f), ramification number (Supplementary Table SM.1), leaf number (Figure II.6a), leaf area (Figure II.6c) and leaf BM significantly (Figure II.6d). On the contrary, SLA was significantly reduced by adding fertilizers, and this effect was more pronounced with MF compared to OF (Figure II.6b).

In the harvesting year, adding MF and OF increased plant height (Figure II.6g), aboveground plant BM (Figure II.6h), leaf BM (Figure II.6j), and fruit yields (Figure II.7a). Adding MF also increased the flower bud number (Figure II.8a), flower number (Figure II.8b) and branch length (Figure II.6i). However, in most of these traits, the effect of OF was like those of MF or CF.

II.3.2. Pruning Effects

Pruning method had no significant effect on fruit yields (Figure II.7b). However, compared to M, MT slightly but significantly improved several allometric traits by reducing plant ramification in the pruning year and increasing plant height and BM during the harvesting year (Figure II.9). Interactions between fertilizers and pruning were only significant for leaf area and plant height during the harvesting year (Figure II.10, Supplementary Table SM.1 and Table SM.3). However, the only useful information we can extract from these results is that using M and CF produced shorter plants (Figure II.10).

II.3.3.   Relationships Between Allometric Traits and Fruit Yields

For both plant-leaf and flower models, the null mixed-effect model presented significant residual effects of random variables, so random variables – i.e. blocks nested in fields, and fields – were kept in the models. We chose the best models according to the minimum AIC, AICC and BIC to predict fruit yields (Table II.9). Because no treatment had a significant effect on plant density (P > 0.05, results not shown), upscaling was done in order to predict fruit yields (t ha^{-1}) EU scale with plant-based allometric traits.

For the leaf-plant mixed-effect model, the aboveground plant BM and branch length were significant variables, whereas SLA, number of leaf buds, ramifications and branches were not significant so were removed from the model (Table II.9, Figure II.11). Treatments were not significant because aboveground plant BM proportionally increased with fertilizer, from CF to MF (Table II.9, Figure II.11). The predicted fruit yield linearly increased with aboveground plant BM and branch length (Figure II.11). For the flower mixed-effect model, fertilizer and flower number effects were used in the model after building a backward process that removed flower bud number and flowers by bud to predict fruit yields (Table II.9, Figure II.12). The predicted yields increased linearly as a function of the number of flowers per plant (Figure II.12). A lower predicted fruit yield was observed for control fertilizer CF while OF and MF increased the predicted yield in a similar manner (Figure II.12).

II.4. Discussion

This study sheds new light on the effect of both fertilizers and pruning methods on blueberry plant allometry and fruit yield in Saguenay-Lac-Saint-Jean wild blueberry production. The fertilizer application was the only treatment that directly affected productive plant traits (i.e. flower and fruit allometric traits) and most vegetative traits, thus confirming our first hypothesis. Both fertilizer treatments produced higher fruit yields than the control, regardless of fertilizer form, as already demonstrated by several studies (Smagula *et al.* 2009, Drummond *et al.* 2012, Caspersen *et al.* 2016). Even if MF and OF differently affected plant allometry over the two-year cycle, both fertilizers led to similar fruit yields (Gagnon *et al.* 2003). On the contrary, pruning had no effect on the productive plant traits, like fruit yield, thus rejecting our second hypothesis (Hanson *et al.* 1982, Warman 1987). Aboveground plant BM, branch length and flower number were traits that best predict fruit yields. Those traits were improved by fertilizer, regardless of fertilizer form.

II.4.1. Fertilizer Effects

MF increased the productive traits during the pruning year by improving flower bud number and flower number per plant. The flower number per bud was not affected by treatments, but it had no effect on the number and BM of fruit. Conversely, OF did not affect the flower traits but instead increased plant fruit BM during the harvesting year in addition to raising blueberry numbers by about 20% compared to the control. Blueberry plants need large amounts of nutrients to support primary growth and reproductive bud development during the pruning year, as well as vegetative growth and fruit development in the harvesting year (Bryla *et al.* 2012). As a result, all accessible nutrients in the soil are rapidly assimilated

by plants, especially inorganic forms of N and some simple organic forms of N (Persson *et al.* 2003, Lupi *et al.* 2013). Furthermore, nutrients in excess may be stored in the plant rhizomes for future growth (Hicks and Turkington 2000).

Thus, as no fertilizer was applied in the harvesting year, our results showed that MF was mainly assimilated by blueberry during the pruning year, and less during the harvesting year, mainly because nutrients from MF (ammonium sulfate, and inorganic N forms) were rapidly used by the crop. No significant difference related to soil fertility (N and K) between MF and CF EU in the harvesting year (P > 0.05, data not shown) supports this hypothesis. The positive effects of MF on plant allometric traits were observed in both years, such as plant height, aboveground plant BM, ramification number, leaf number, leaf area and leaf BM, as already demonstrated by other studies (Eaton and Nams 2006, Lafond and Ziadi 2011). Improvements in leaf traits and aboveground plant BM by MF applications likely increased photosynthesis (i.e. carbon source) and carbon reserves capacities during the pruning year, allowing the plant to produce more flowers and have more resources to achieve high fruit yields during the harvesting year (Swain and Darnell 2001, Weiner *et al.* 2009, Kaur *et al.* 2012).

During the pruning year, allometric traits after OF applications did not increase as much as for MF applications but were still higher compared to CF treatment. However, from a two-year cycle perspective, OF applications showed similar allometric traits during the harvesting year as well as similar fruit yields as compared to MF applications, suggesting a delayed effect of OF. Indeed, OF contains high proportions of organic N materials (e.g. proteins, amino acids, etc.) and nutrients trapped in organic materials that become available to plants

after being mineralized/degraded by soil microorganisms (Näsholm and Persson 2001, Persson *et al.* 2003, Caspersen *et al.* 2016). Furthermore, Ericaceae like *Vaccinium* sp. have a symbiotic interaction with ericoid mycorrhizae that improves both the mineralization and assimilation of organic N materials (Marschner and Dell 1994, Schimel and Bennett 2004, Näsholm *et al.* 2009, Caspersen *et al.* 2016). Nonetheless, all these soil processes need time, thus explaining the delayed effect of OF as compared to MF.

Our results also suggest that wild blueberries assimilate nutrients according to fertilizer type. In this way, wild blueberries are an "opportunist" species that, with the help of soil microorganisms and ericoid mycorrhizae, can successfully grow and assimilate soil nutrients from different types of availability. Nevertheless, OF has several other benefits over MF. First, compared to MF, OF provides more macronutrients that are required for plant growth such as P, K, and Ca. Second, OF can increase soil organic matter (OM) content which may, in return, increases soil bio-fertility (Gagnon *et al.* 2003, Warman *et al.* 2004, Caspersen *et al.* 2016). Improving OM content of wild blueberry soils is important because roots grow mainly in the soil organic horizons (Hall *et al.* 1979, Gagnon *et al.* 2003, Morin 2008, Caspersen *et al.* 2016). Second, the addition of OM through OF inputs may increase microbial decomposition activities and lead to better soil fertility in the long term (Tilman and Wedin 1991, Näsholm and Persson 2001, Percival and Sanderson 2004). Third, increasing soil OM content can also enhance soil water retention capacity (Caspersen *et al.* 2016). A severe drought occurred during the harvesting year (Supplementary Figure SM.8) and higher water retention capacities, particularly in our sandy soil, might better protect plants through decreasing fruit abortion or shrivelling (Glass 2000, Gagnon *et al.* 2003,

Gagnon *et al.* 2014). This latter hypothesis may explain the higher but non-significant fruit numbers per plant measured with OF (Figure II.8c). However, as application rates of OF added tiny amounts of OM (710 kg of OM ha^{-1} or 71 g of OM m^{-2}), we believe that this latter hypothesis less explains our results.

II.4.2.   Pruning Effects

Compared to M treatment, MT slightly but significantly increased leaf surface, plant height and aboveground plant BM during the harvesting year only. As compared to fertilizer treatments, the effects of pruning method on those allometric traits were less important. Although MT may increase soil nutrients availability (Naylor and Schmidt 1989, Huang *et al.* 1992, Lafond 2004), we found no significant effect of MT on soil nutrient status for both years (P > 0.05 for N-NO$_3^-$, N-NH$_4^+$, P, K, Ca, Mg, data not shown), suggesting that MT had a very minimal effect on soil fertility. Other hypotheses may explain the beneficial effects of MT during the harvesting year only.

First, M significantly increased the ramification number by 7% during the pruning year (Figure II.9a), as already observed in another study (Ismail *et al.* 1981). Although M plants had slightly more stems, leaf characteristics (i.e. SLA, surface area and BM) were similar between the pruning treatments, suggesting a similar photosynthesis capacity and therefore similar carbohydrate production during the pruning year (Reich *et al.* 1997, Wright *et al.* 2004). Consequently, with more stems to support, plant metabolism costs are higher for M than for MT. With an increase of carbohydrate demand (i.e. sink competition) but no improvement in plant photosynthesis capacity (carbon source), the carbon allocation for each flower of M plants was likely lower than for the MT plants.

Second, mechanical pruning of site 1 was done in spring 2017 (during the week of May 15th, day of the year (DOY) 135), whereas MT was performed in fall 2016 (Table II.8). In spring, Table I.3 of chapter one showed that bud development began before DOY 132 and reach stage 2 (bud elongates and becomes pointed) on DOY 139. The mechanical pruning therefore took place during the beginning of bud development (personal observation), unlike burned EUs that had their buds broken by the thermal pruning performed in the previous fall (2016). In this context, blueberry plants from mechanical pruning alone (M treatment) had already started to use their carbon reserves to grow, and the pruning would have caused them to lose this carbon investment. Therefore, considering the decrease in reserves through late pruning and the increase of plant ramification during the pruning year, a relative reduction of plant carbohydrates may have occurred during the harvesting year for M treatment, explaining the decrease in vegetative growth of blueberry plants for M treatment during the harvesting year. An early pruning in spring or late in the previous fall would therefore be suitable to limit negative impacts of M pruning during the harvesting year (Yarborough 2012) and this could lead the M treatment being similar to MT.

In the literature, a number of studies showed improvements in fruit yields after MT treatment as compared to not-burned controls (Black 1963, Ismail *et al.* 1981, Warman 1987, Penney *et al.* 1997). Nevertheless, MT treatment has several disadvantages and advantages compared to mechanical pruning. Indeed, costs related to MT treatment (e.g. burning and tractor fuels, extra times, etc.) are much higher than for mechanical pruning alone (Hanson *et al.* 1982, Morin 2008). Furthermore, MT may reduce soil OM content/depth over time (Smith and Hilton 1971). However, thermal pruning can also be used as organic control

strategies against weeds, insects and fungal diseases (Black 1963, Ismail *et al.* 1981, Penney *et al.* 2008). More years of results will be needed to highlight the effects of MT compared to M – and its interaction effects with other treatments such as fertilizer applications – to better advise producers on the best agricultural practices to use in the northern contexts of Quebec. In view of the two interactions between pruning and fertilization for leaf area and plant height during the harvesting year (Figure II.10), it would simply not be advisable to prune mechanically only without addition of fertilizers.

II.4.3.   Relation Between Allometric Traits and Fruit Yields

The two models created to predict fruit yields are in accordance with the literature. For the leaf-plant model, aboveground plant BM and branch length were the best vegetative traits that can predict fruit yields. For example, Lafond and Ziadi (2011) reported that the plant height was positively correlated to fruit yields, which is in agreement with our model, as the aboveground plant BM had been estimated from plant height (Annexe 2, p.97). Also, aboveground plant BM and branch length were linked to leaf surface and leaf BM; nearly 50% of aboveground BM is constituted of leaf BM. Thus, a better photosynthetic capacity by improving leaf BM increased the carbon allocation capability for fruit production. Therefore, our leaf-plant model suggests that the reproduction allocation of wild blueberry is size dependent (Swain and Darnell 2001, Weiner *et al.* 2009, Wenk and Falster 2015). Unlike others that showed good predictions of fruit yields using flower bud number per plant (Trevett (1959) and Lafond and Ziadi (2011)), our model demonstrated that the number of flowers per plant estimated fruit yields with more accuracy, simply because the number of flowers may vary among buds (Drummond 2019). Fruit development from flower(s) depends

on the available carbon allocation, but also on pollination success and many other environmental factors related to climatic and edaphic conditions (Petridis *et al.* 2018). Nevertheless, although the models proposed here show ideal situations, promoting treatments that increase flower number per plant, the aboveground plant BM and branch length may indeed improve overall fruit yields, such as observed after thermal pruning and fertilizer applications, in either mineral or organic form.

II.5. Conclusion

In this study, we showed that pruning and applying fertilizers had significant effects on allometric traits of wild blueberry plants. Indeed, the fertilizer applications had the strongest beneficial effects on plant productivity. These effects are confirmed and explained by the models that we developed to predict fruit yields: we highlighted that flower number, branch length and aboveground plant BM significantly explained fruit yields, and all of these three allometric traits were improved by fertilizer applications, regardless of the form that was used. In fact, our results showed that mineral fertilizer benefits allometric traits on a short-term basis (the pruning year), whereas organic fertilizer reaches similar results in the harvesting year. Our results also demonstrated that compared to mechanical pruning only, the addition of thermal pruning slightly improved aboveground plant BM, but no significant differences were detected for fruit yields. Hence, long-term researches are still needed to clearly assess the question of whether thermal pruning is profitable compared to mechanical pruning over time. In addition, pruning treatments should be compared in the future with an application at similar times to confirm our result. Much more work remains to be done to increase fruit yields in northern Saguenay-Lac-Saint-Jean blueberry production, but with a better understanding of which allometric traits need to be targeted and improved, namely aboveground plant BM, branch length, and number of flowers, agricultural practices should be undertaken to improve these.

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Table II.7. Example of a block with twelve EU, each having a specific combination of treatments. The combinations were randomly established for each eight blocks. Fungicide effects were included in the statistical analysis but are not presented in this paper. There are 12 different combinations of treatment per block, 8 blocks per site and two sites, making a total of 192 EU.

Treatment	Pruning	Fungicide	Fertilizer	Abbreviation
1	Mechanical	Without	Mineral	M×CFUN×MF
2	Mechanical	Without	Without	M×CFUN×CF
3	Mechanical	Without	Organic	M×CFUN×OF
4	Mechanical	With	Mineral	M×FUN×MF
5	Mechanical	With	Without	M×FUN×CF
6	Mechanical	With	Organic	M×FUN×OF
7	Mechanical and thermal	With	Without	MT×FUN×CF
8	Mechanical and thermal	With	Organic	MT×FUN×OF
9	Mechanical and thermal	With	Mineral	MT×FUN×MF
10	Mechanical and thermal	Without	Without	MT×CFUN×CF
11	Mechanical and thermal	Without	Mineral	MT×CFUN×MF
12	Mechanical and thermal	Without	Organic	MT×CFUN×OF

Table II.8. Crop management calendar, treatment information and date of data collection for each studied sites.

Crop management	Site 1	Site 2	Treatment information
Pruning year	2017	2018	**-**
Harvesting year	2018	2019 (not presented)	**-**
Mechanical pruning	Week of May 15, 2017	Week of October 17, 2017	Blueberry mower (model TB-1072, JR Tardif)
Thermal pruning	November 7, 2016	October 24, 2017	High-pressure burner (home-made propane burner)
Fertilizer application	June 13, 2017	June 6, 2018	**Mineral:** 50 kg of N ha^{-1} as ammonium sulfate, 15 kg of P$_2$O$_5$ ha^{-1} as super triple phosphate, 15 kg of K$_2$O ha^{-1} potassium sulfate and 0.7 kg of B ha^{-1} borate
			Organic: 50 kg of N ha^{-1} of granulated chicken manure (Acti-sol 5-3-2) and 0.7 kg of B ha^{-1} borate
Fungicide application	July 13, 2017	July 16, 2018	Proline © (Bayer)
Beehives	4 beehives, early May in 2017 and 2018 to end of season, 48 beehives per hectare, 5 June to 28 June 2018		
Data collection in pruning year	**Phenology:** 154, 157, 160, 165, 170, 177, 183.	**Phenology:** 150, 155, 159, 163, 171, 178, 185, 200.	**Conversion DOY to date** : 135: May 15th, 140: May 20th, 145: May 20th, 150: May 30th, 155: June 4th, 160: June 9th,
Data collection in harvesting year	**Phenology:** 135, 137, 142, 145, 149, 152, 156, 158, 164, 171, 178, 185, 192, 220.		165: June 14th, 170: June 19th, 175: June 24th, 180: June 29th 185: July 4th, 190: July 9th, 195: July 14th, 200: July 19th,
	Allometry: 220.		220: August 8th.

Table II.9. Null, leaf-plant and flower mixed-effect model built for the predicted fruit yields. The results include estimation, standard error (SE), and test of effects with F or Z statistics (fixed and random effects respectively), degrees of freedom of numerator (df1) and denumerator (df2), and P value (F or $Z_{df1, df2}$ (P-value)). Fitting of the model was also included. P-value obtained according to $\alpha = 0.05$.

Models	Effects		Estimation (SE)	Test	Fitting	
Null	Residual		719494.000 (116245.000)	6.19 (< 0.0001)	-2 log Likelihood	1369.9
	Field		1855496.000 (2692098.000)	0.69 (0.2453)	AIC	1375.9
	Block (Field)		119185.000 (105186.000)	1.13 (0.1286)	AICC	1376.2
	Intercept		1649.200 (975.650)	1.69_1 (0.3401)	BIC	1372.0
Leaf-Plant	Residual		593053.000 (97144.000)	6.10 (< 0.0001)		
	Field		1451992.000 (2122917.000)	0.68 (0.2470)	-2 log Likelihood	1356.9
	Block (Field)		118675.000 (99845.000)	1.19 (0.1173)	AIC	1362.9
	Intercept		206.460 (932.440)	-	AICC	1363.2
	Aboveground plant BM (g m^{-2})		0.004 (0.001)	$7.37_{1,\ 78.2}$ (0.0081)	BIC	1359.0
	Branch length (mm)		30.383 (14.433)	$4.43_{1,\ 79.4}$ (0.0384)		
Flower	Residual		564403.000 (93085.000)	6.06 (< 0.0001)		
	Field		1622922.000 (2347714.000)	0.69 (0.2447)		
	Block (Field)		87235.000 (80041.000)	1.09 (0.1379)	-2 log Likelihood	1325.8
	Intercept		686.780 (934.950)	-	AIC	1331.8
		MF	637.040 (212.650)		AICC	1332.2
	Fertilizer	OF	502.840 (202.840)	$5.09_{2,\ 73.8}$ (0.0085)	BIC	1327.9
		CF	0 (.)			
	Flower number per m^2		0.168 (0.060)	$7.73_{1,\ 77.4}$ (0.0068)		

Year - Level 7 (fixed)   2017   2018

Site (not compared)   1   2

Field - Level 6 (random)   1   2

Block - Level 5 (random)   1   2   3   4

Pruning treatment - Level 4 (fixed)   M   MT

Fungicide treatment - Level 3 (fixed)   FUN   CFUN

Fertilizer treatment - Level 2 (fixed)   MF   OF   CF

Observations on 8 plants - Level 1 (Supplementary Figure 2)
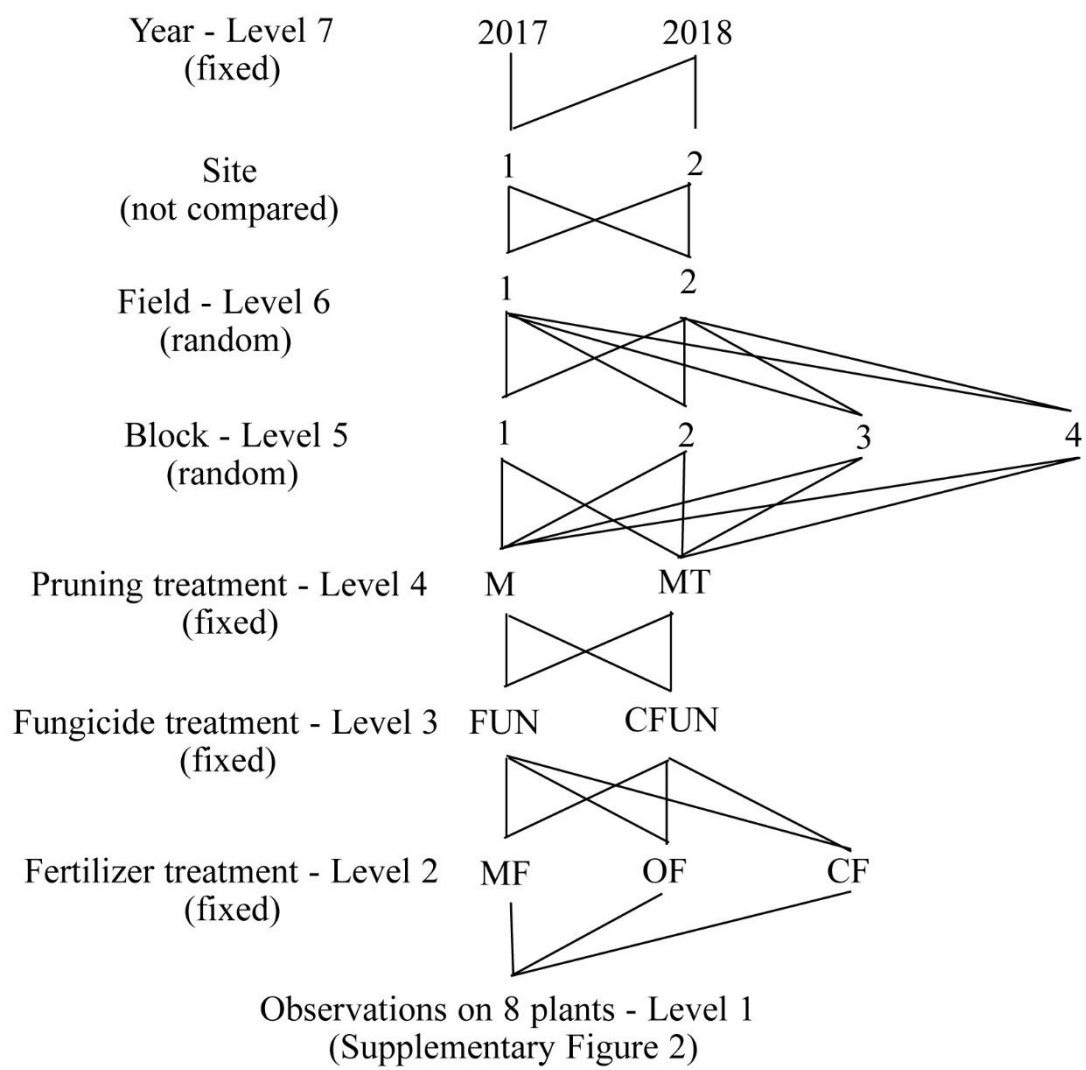
Figure II.5. Diagrams of the split-plot design with levels and statistic variable types (fixed or random), for a total of 192 EU. Observations of the level 1 are presented in Supplementary Figure SM.2.
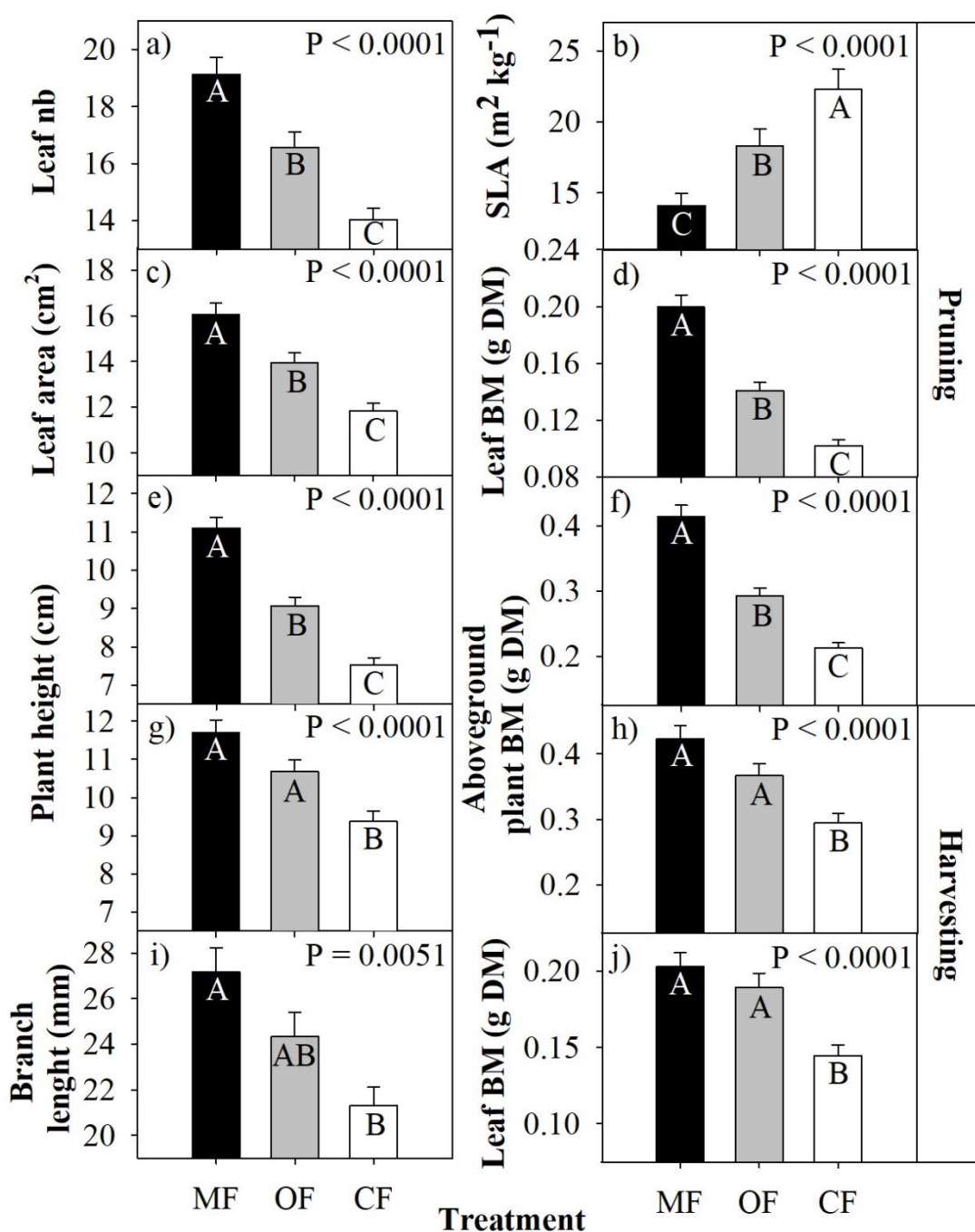
Figure II.6. Mean per plant of allometric traits of plants and leaves by fertilizer treatments. Data were collected in the pruning and harvesting years. Error bars represent the standard error of mean and P-value obtained according to α = 0.05: different letters represent significant difference. MF = mineral fertilizer, OF = organic fertilizer (poultry manure), CF = without fertilizer, nb = number, SLA = specific leaf area, BM = biomass and DM = dry BM.
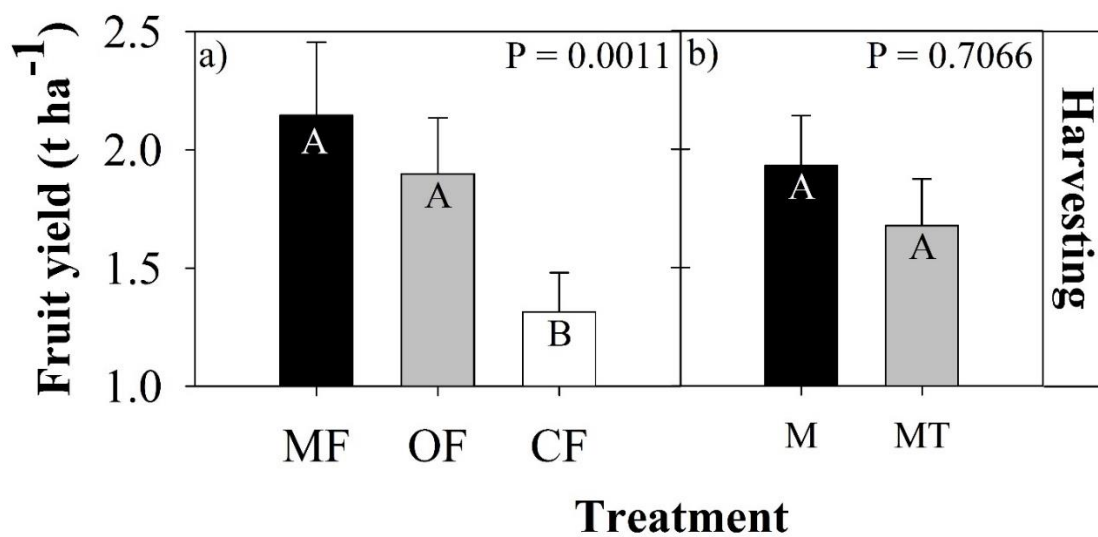
Figure II.7. Mean of fruit yields by a) fertilizer and b) pruning treatments. Data were collected in the harvesting year. Error bars represent the standard error from the mean. Different letters represent significant difference at a level α = 0.05. MF = mineral fertilizer, OF = organic fertilizer (poultry manure), CF = without fertilizer, M = mechanical pruning, MT = mechanical and thermal pruning.
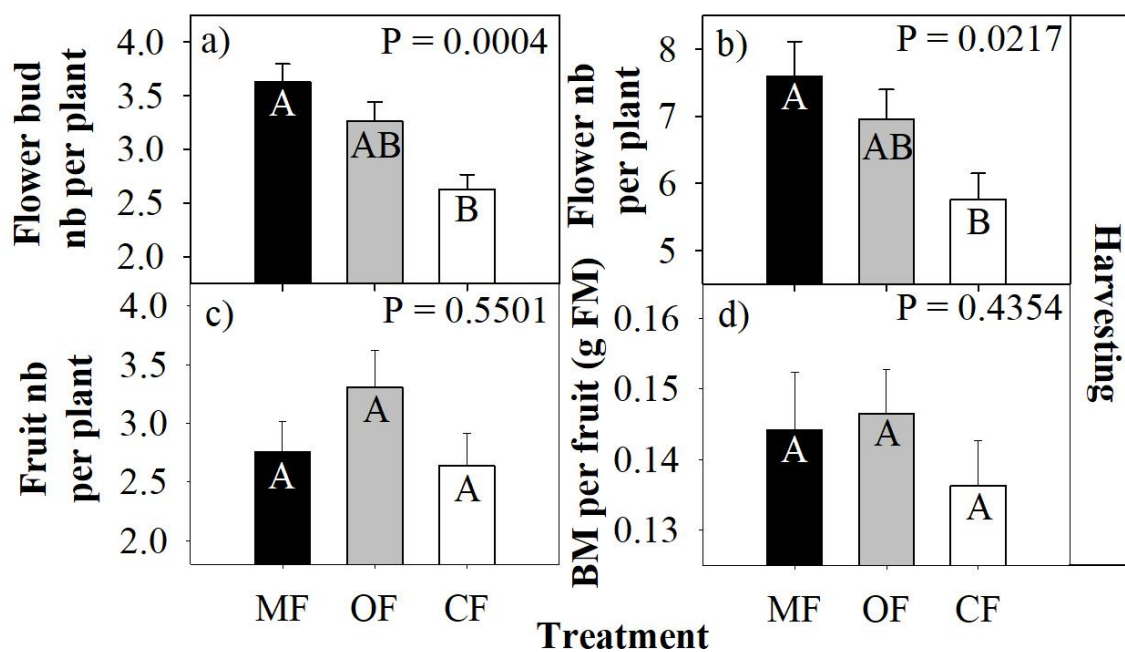
Figure II.8. Mean of allometric traits of flowers and fruits by fertilizer treatments. Data were collected in the harvesting year. Error bars represent the standard error from the mean. Different letters represent significant difference at a level α = 0.05. MF = mineral fertilizer, OF = organic fertilizer (poultry manure), CF =without fertilizer, nb = number, BM = biomass and FM = fresh BM.
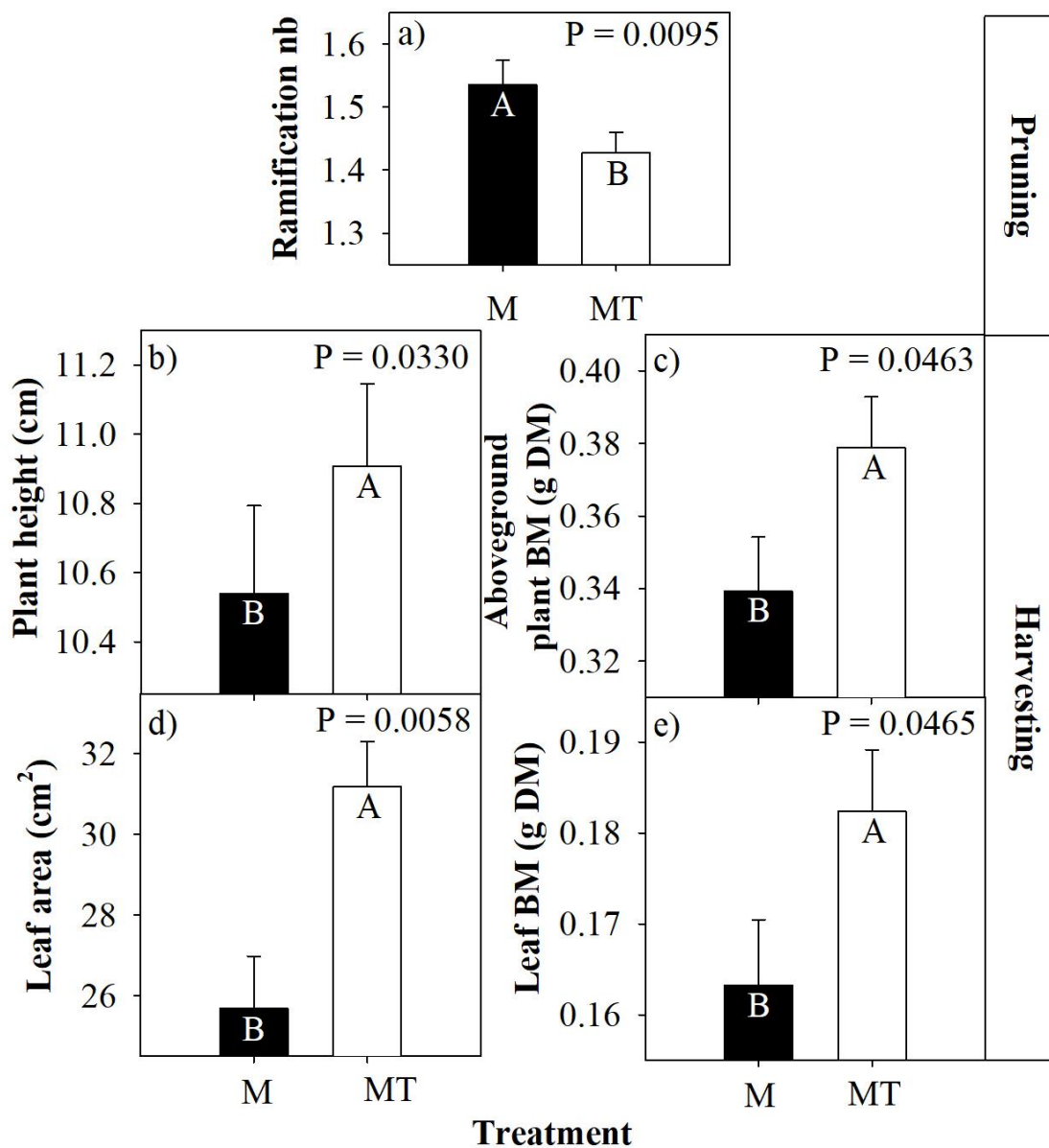
Figure II.9. Mean per plant of allometric traits by pruning treatments. Data were collected in the pruning or harvesting year. Error bars represent the standard error from the mean. Different letters represent significant difference at a level α = 0.05. MF = mineral fertilizer, OF = organic fertilizer (poultry manure), CF =without fertilizer, nb = number, BM = biomass and FM = fresh BM.
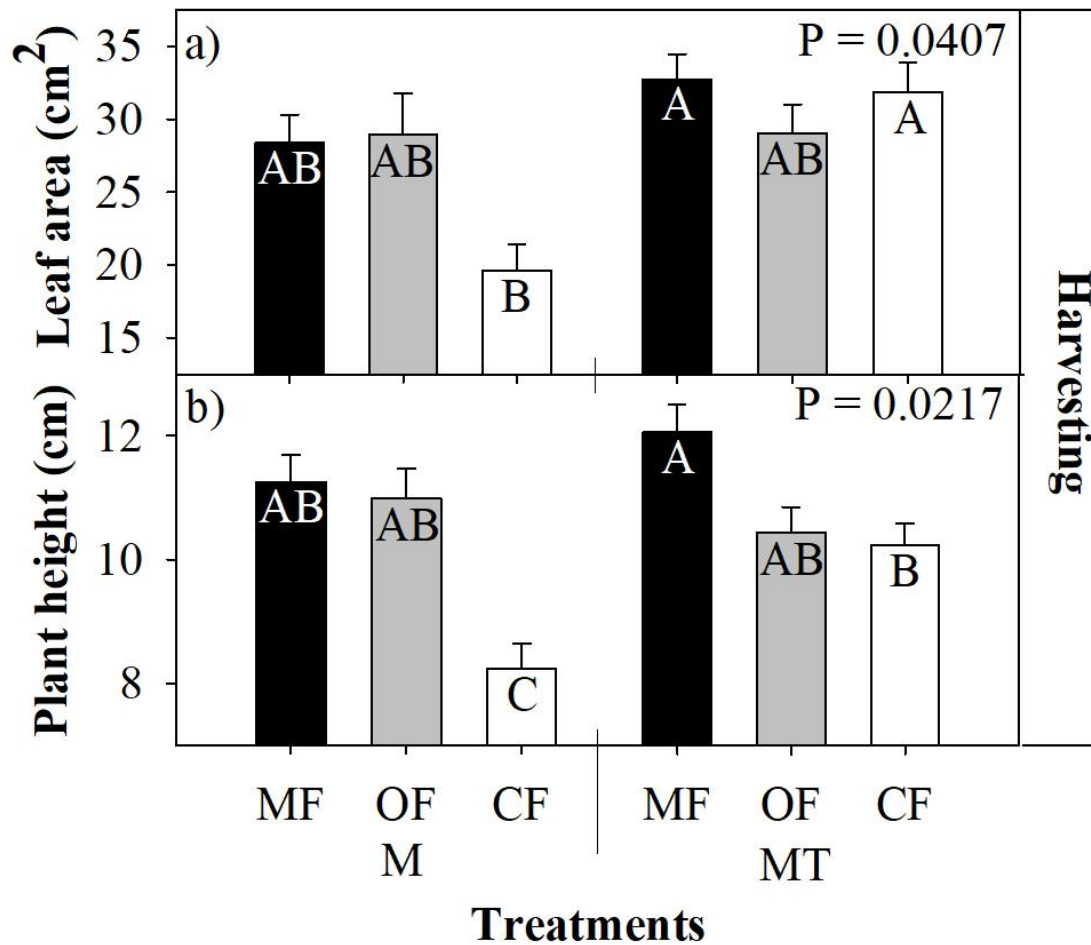
Figure II.10. Mean per plant of allometric traits by pruning and fertilizer treatments. Data were collected in the harvesting year. Error bars represent the standard error from the mean. Different letters represent significant difference at a level α = 0.05. MF = mineral fertilizer, OF = organic fertilizer (poultry manure), CF =without fertilizer.
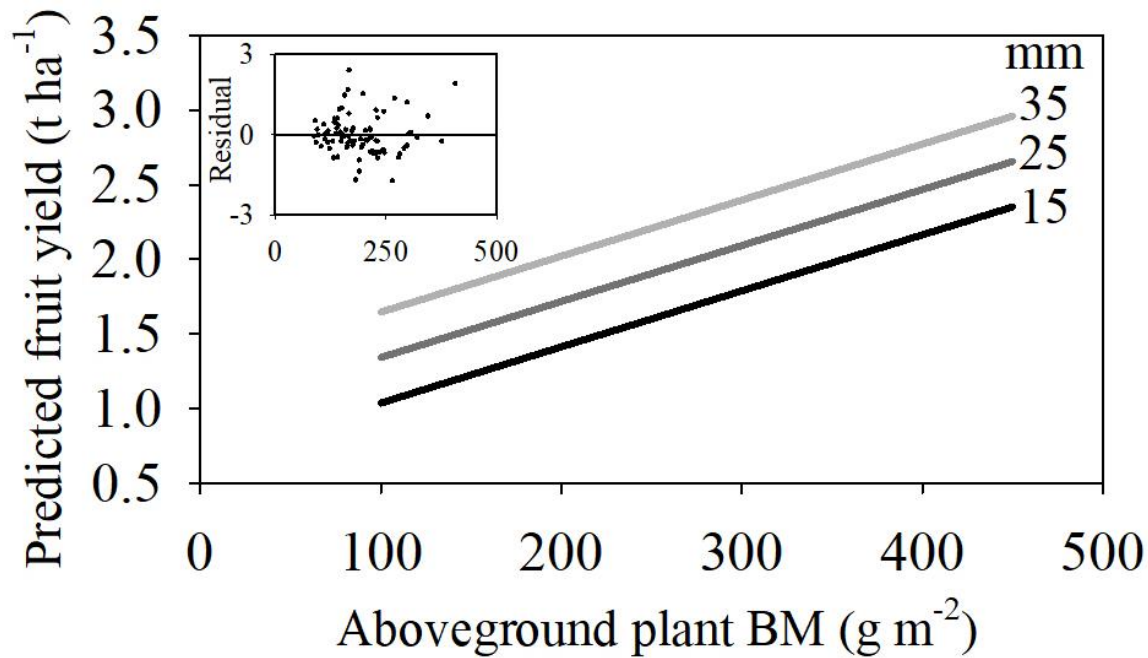
Figure II.11. Change in fruit yields predicted by leaf-plant mixed-effect model according to aboveground plant biomass (g m^2) and branch length modelled at 15, 25 or 35 mm.
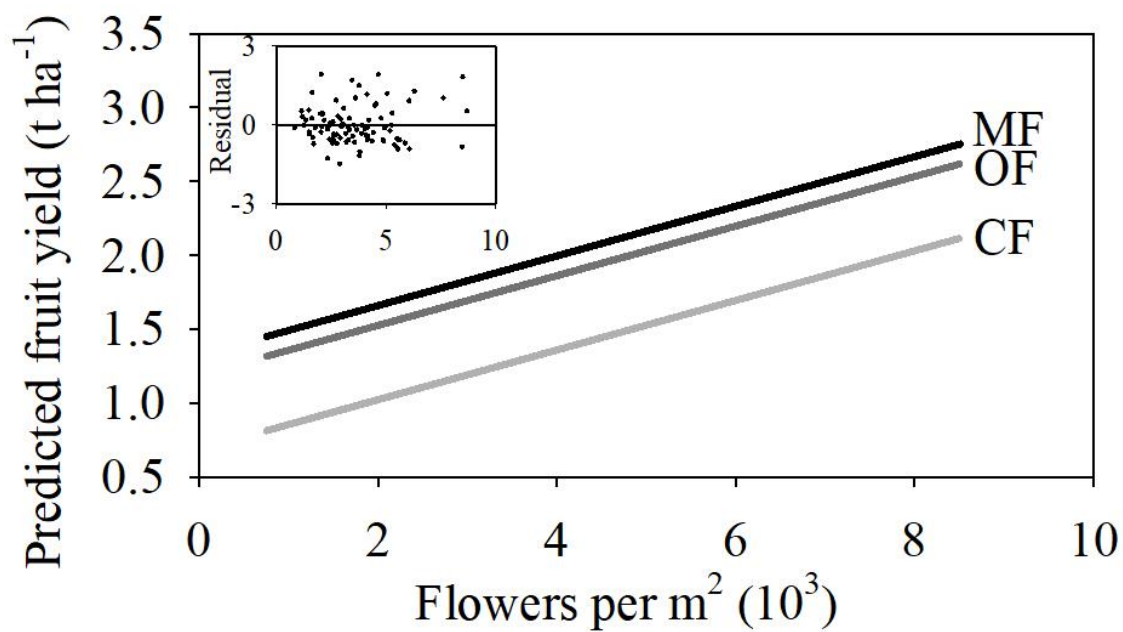
Figure II.12. Change in fruit yields predicted by flower mixed-effect model according to thousand flowers per m2 and fertilizer – CF: control, OF: organic fertilizer or MF: mineral fertilizer.

CONCLUSION GÉNÉRALE

Dans ce mémoire, les deux objectifs ont été atteints. Dans un premier temps, il a été déterminé que la phénologie et l'architecture des espèces modulent leur productivité en fruit. Dans un second temps, il a été déterminé que les deux pratiques agricoles étudiées – le fauchage et la fertilisation – ont eu des effets significatifs sur l'allométrie des plants. Ainsi, de deux manières différentes, il a été démontré que la présence d'une grande biomasse végétative de la plante (en excluant les racines) accroît la capacité de productivité en fruit des plants de bleuets sauvages en zone nordique. De ce fait, les facteurs augmentant la biomasse végétative hors-sol du plant, dont l'ajout de fertilisant (sans tenir compte du type d'engrais après deux ans), le fauchage thermique en supplément au fauchage mécanique et l'espèce *V. myrtilloides*, devraient être mieux exploités.

Dans le cas de *V. myrtilloides*, sa production en fruit en milieu nordique pourrait être augmentée grâce à une ouverture des fleurs retardée, protégeant les structures florales des gels printaniers tardifs. Dans ce cas, les cultivateurs devraient augmenter leurs efforts de pollinisation à la fin du printemps. De plus, en poursuivant les recherches sur cette espèce, les raisons qui l'amènent à disparaître des champs en culture pourraient être mieux connues et il serait possible de vérifier les allégations de Gagnon *et al.* (2014) et de Chiasson and Agrall (1996) qui avancent que *V. myrtilloides* serait encore plus productif en troisième année de culture, des informations ayant une valeur substantielle pour un cultivateur afin d'améliorer ses pratiques en zone nordique.

Cette étude a confirmé que l'ajout d'engrais est très efficace pour améliorer la production de fruit, mais a aussi démontré plus spécifiquement que l'engrais organique a un effet semblable, mais retardé par rapport à l'engrais minéral sur la majorité des caractéristiques des plants. Pour les deux types de fauchage, le fauchage mécanique et thermique a amélioré uniquement des facteurs végétatifs comparativement à l'utilisation du fauchage mécanique seul. Afin de pouvoir mieux conseiller les agriculteurs, les effets à long terme de ces pratiques – fauchage et fertilisation – devront être étudiés pour mieux déterminer les meilleures pratiques en zone nordique. De plus, cette étude a amené des précisions sur les traits des plants à mesurer pour estimer les rendements en fruit, soit, en plus de la biomasse végétative du plant, la croissance (hauteur du plant, longueur des branches) et la quantité de fleurs sur un plant en fonction du type d'engrais.

Il est aussi évident que comme les données ont été prises dans les mêmes dispositifs, des analyses combinées des effets espèces et traitements agricoles avaient été effectués, mais les résultats étaient complexes et il en ressortait en majorité les mêmes conclusions que ceux de ce mémoire. Il demeure que la poursuite de la recherche dans le domaine, particulièrement avec des études à long terme, est nécessaire pour mieux comprendre les interactions entre les espèces et les pratiques agricoles, et ce, toujours dans un objectif global d'amélioration des rendements des bleuets sauvages au Saguenay-Lac-Saint-Jean. Et cela passe par une meilleure compréhension des dynamiques phénologiques et allométriques des plants, afin de mieux cibler les processus physiologiques visant une productivité fruitière optimale.

Références

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Annexe 1. Supplementary figures and tables

Table SM.1. Mixed model with test of effect on allometric traits of plant parts by year type – pruning (Pr) and harvesting (Hy). Effects considered were year and treatment combination of pruning, fungicide (data not shown) and fertilizer. The results include F statistic, degrees of freedom of numerator (df1) and denumerator (df2), and P value ($F_{df1, df2}$ (P-value)). P-value obtained according to α = 0.05: bold font was significant in the main and pairwise model. BM: biomass, nb: number.

Part	Variable	Type	Year	Pruning	Fertilizer	Pruning×Fertilizer
Plant	Plant BM	Pr	$0.00_{1, 56.4}$ (0.9527)	$1.00_{1, 173}$ (0.3198)	$40.88_{2, 149}$ **(< 0.0001)**	$1.73_{2, 167}$ (0.1809)
		Hy		$4.11_{1, 71.3}$ **(0.0463)**	$13.50_{2, 65.9}$ **(< 0.0001)**	$3.09_{2, 65.9}$ (0.0523)
	Plant height	Pr	$0.09_{1, 58.5}$ (0.7639)	$0.72_{1, 173}$ (0.3972)	$44.97_{2, 149}$ **(< 0.0001)**	$1.96_{2, 167}$ (0.1442)
		Hy		$4.73_{1, 71.5}$ **(0.0330)**	$15.02_{2, 66}$ **(< 0.0001)**	$4.06_{2, 66}$ **(0.0217)**
	Branch length	Hy		$3.04_{1, 71}$ (0.0854)	$5.69_{2, 70.8}$ **(0.0051)**	$0.29_{2, 70.8}$ (0.7457)
	Ramification nb	Pr	$1.71_{1, 55.3}$ (0.1964)	$6.89_{1, 165}$ **(0.0095)**	$14.00_{2, 144}$ **(< 0.0001)**	$3.02_{2, 159}$ (0.0516)
	Branche nb	Hy		$1.85_{1, 132}$ (0.1757)	$1.15_{2, 132}$ (0.3184)	$4.32_{2, 132}$ (0.0153)

Table SM.2. Mixed model with test of effect on allometric traits of flower and fruit parts in the harvesting year. Factors considered were year and treatment combination of pruning, fungicide (data not shown) and fertilizer. The results include F statistic, degrees of freedom of numerator (df1) and denumerator (df2), and P value ($F_{df1, df2}$ (P-value)). P-value obtained according to $\alpha = 0.05$: bold font was significant in the main and pairwise model. BM: biomass, nb: number.

Part	Variable	Pruning	Fertilizer	Pruning×Fertilizer
Flower	Flower bud nb	$0.05_{1,\,72}$ (0.8319)	$8.64_{2,\,72}$ **(0.0004)**	$1.74_{2,\,72}$ (0.1821)
	Flower nb	$1.13_{1,\,68.9}$ (0.2912)	$4.07_{2,\,65.2}$ **(0.0217)**	$1.89_{2,\,65.3}$ (0.1599)
	Flowers per bud	$0.01_{1,\,579}$ (0.9034)	$0.09_{2,\,587}$ (0.9126)	$0.33_{2,\,587}$ (0.7191)
Fruit	Fruit nb	$0.36_{1,\,71.1}$ (0.5501)	$2.10_{2,\,71}$ (0.1301)	$4.00_{2,\,71}$ (0.0227)
	Fresh fruit BM	$0.05_{1,\,71.2}$ (0.8262)	$3.82_{2,\,71.2}$ **(0.0265)**	$2.63_{2,\,71.2}$ (0.0789)
	Fresh BM per fruit	$0.61_{1,\,428}$ (0.4354)	$0.55_{2,\,427}$ (0.5781)	$0.87_{2,\,427}$ (0.4193)
	Fruit Yields	$0.14_{1,\,69.1}$ (0.7066)	$7.53_{2,\,65.2}$ **(0.0011)**	$0.14_{2,\,65.2}$ (0.8668)

Table SM.3. Mixed model with test of effect on allometric traits of leaf parts by year type – pruning (Pr) and harvesting (Hy). Effects considered were year and treatment combination of pruning, fungicide (data not shown) and fertilizer. The results include F statistic, degrees of freedom of numerator (df1) and denumerator (df2), and P value ($F_{df1, df2}$ (P-value)). P-value obtained according to $\alpha = 0.05$: bold font was significant in the main and pairwise model. BM: biomass, nb: number.

Part	Variable	Type	Year	Pruning	Fertilizer	Pruning×Fertilizer
Leaf	Leaf bud nb	Hy		$3.55_{1,\ 71.3}$ (0.0635)	$3.00_{2,\ 65.6}$ (0.0566)	$0.44_{2,\ 65.6}$ (0.6483)
	Leaf nb	Pr	$132.92_{1,\ 158}$ **(< 0.0001)**	$1.47_{1,\ 175}$ (0.2267)	$22.58_{2,\ 158}$ **(< 0.0001)**	$2.9_{2,\ 175}$ (0.0575)
		Hy		$8.08_{1,\ 71.5}$ **(0.0058)**	$2.13_{2,\ 71.5}$ (0.1260)	$3.35_{2,\ 71.5}$ **(0.0407)**
	Leaf area	Pr	$132.92_{1,\ 158}$ **(< 0.0001)**	$1.47_{1,\ 175}$ (0.2267)	$22.58_{2,\ 158}$ **(< 0.0001)**	$2.9_{2,\ 175}$ (0.0575)
		Hy		$8.08_{1,\ 71.5}$ **(0.0058)**	$2.13_{2,\ 71.5}$ (0.1260)	$3.35_{2,\ 71.5}$ **(0.0407)**
	Leaf BM	Pr	$0.00_{1,\ 56.3}$ (0.9486)	$1.00_{1,\ 173}$ (0.3191)	$40.81_{2,\ 149}$ **(< 0.0001)**	$1.73_{2,\ 167}$ (0.1813)
		Hy		$4.10_{1,\ 71.3}$ **(0.0465)**	$13.47_{2,\ 65.9}$ **(< 0.0001)**	$3.08_{2,\ 65.9}$ (0.0528)
	SLA	Pr	$56.30_{1,\ 67.1}$ **(< 0.0001)**	$0.34_{1,\ 177}$ (0.5621)	$10.95_{2,\ 155}$ **(< 0.0001)**	$1.76_{2,\ 173}$ (0.1755)
		Hy		$0.00_{1,\ 471}$ (0.9938)	$0.87_{2,\ 650}$ (0.4209)	$1.99_{2,\ 651}$ (0.1369)

Figure SM.1. Schematic diagrams of the experimental design. Each site contained 96 experimental units (EU) of 15×22 m (330 m^2) separated by a 3-m buffer zone, for a total of 192 EU. M, mechanical pruning; MT, mechanical and thermal pruning; MF, mineral fertilizer; OF, organic fertilizer (poultry manure); CF, without fertilizer (see Table II.8 for details).
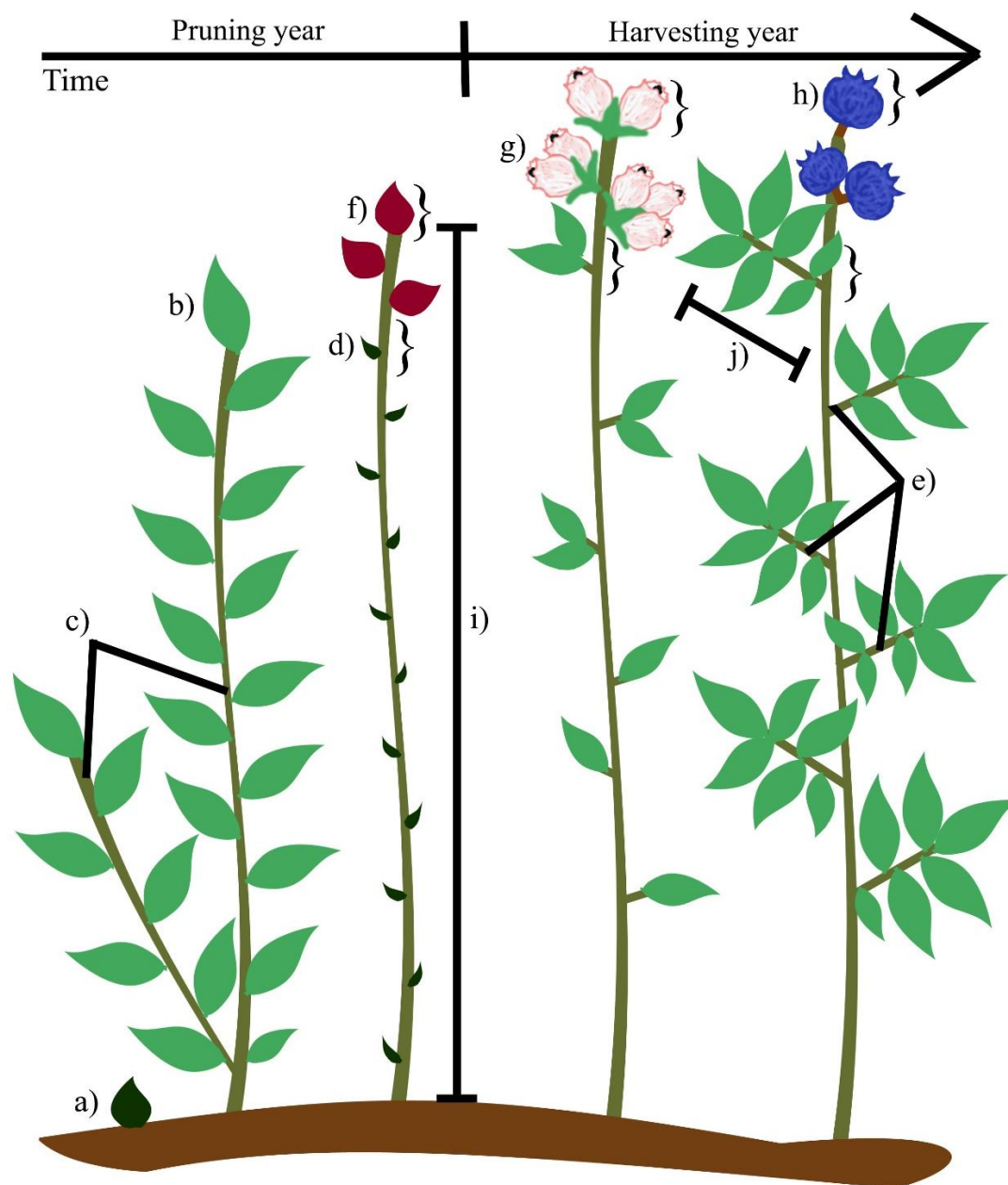
Figure SM.2. Development of allometric traits of a blueberry plant over time. Apical traits are illustrated with a parenthesis (}), and total traits are all structures present on a plant. Each plant measured plant part is represented by a letter and the measured data are included in parentheses (BM for biomass, *N* for number, *N*/1 for number by bud, mm, or cm for size, g DM or g FM for dry or fresh BM respectively, cm^2 for area): a) primary leaf bud (phenology), b) leaves (*N*, g DM, cm^2), c) ramifications (*N*), d) leaf buds (apical phenology, *N*), e) branches (*N*) and its j) apical length (mm), f) flower buds (apical phenology, *N*), g) apical and total flowers (*N*, *N*/1), h) apical and total blueberries (*N*, *N*/1, g FM), i) aboveground plant height (cm) and BM (g DM).
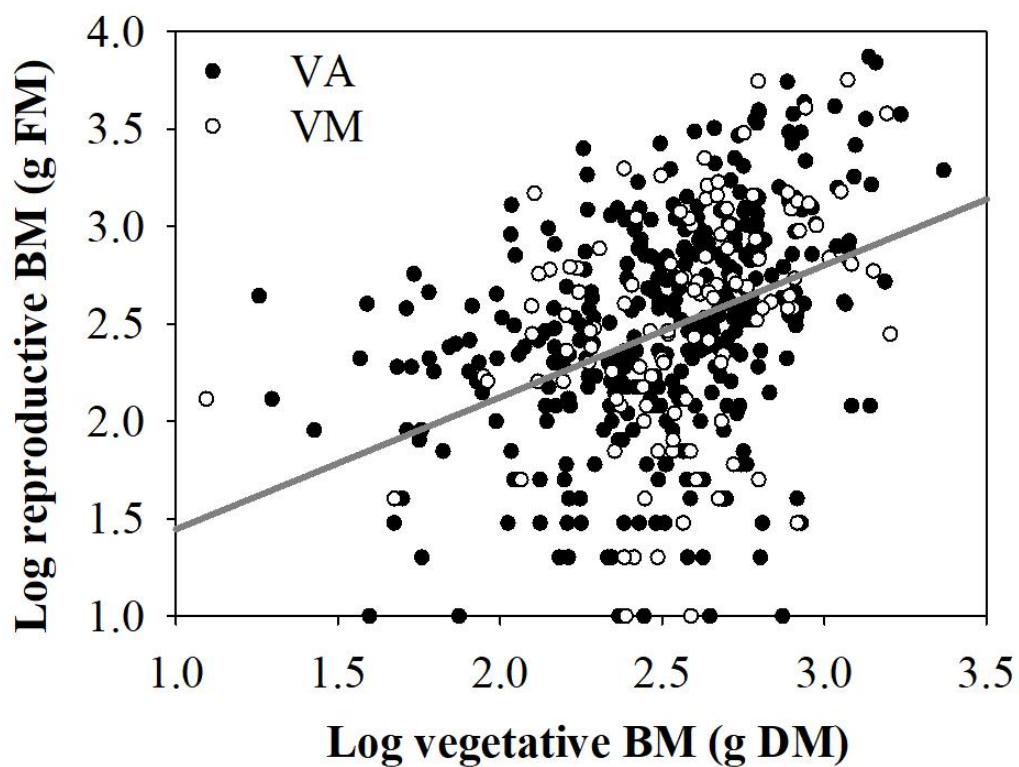
Figure SM.3. R-V mixed effect model (grey line) showing the relationship between the log reproductive BM, i.e., fruit BM - R, and the log vegetative BM, i.e. aboveground plant BM with data of each specie. VA: *V. angustifolium*, VM: *V. myrtilloides*, BM: biomass, FM: fresh BM, DM: dry BM.

Foliar budding chart of *Vaccinium sp.* in a pruning year

Stage	*Vaccinium sp.*	Identification
1		Bud is a small, pink button
2		Bud elongates and becomes pointed
3		Bud increases in width, becomes round and translucent
4		Bud doubles in size and turns green
5		Leaves are distinct
6		Leaves are completely open

Figure SM.4. Phenological stages of *Vaccinium* sp. – leaf in a pruning year.

Figure SM.5. Phenological stages of *Vaccinium* sp. – leaf in a harvesting year.

Floral budding chart of *Vaccinium sp.* in a harvesting year

	V. angustifolium	V. myrtilloides	Identification
0			Small brown bud and closed
1			Pink coloration appears, scales become distinct, bud begins to swell
2			Colored scales, three times larger than Stage 1 buds
3			Bud begins to open, increases in size
4			Bud completely open
5			Distinction between sepal and petal of flowers
6			First flower open

Figure SM.6. Phenological stages of *Vaccinium* sp. – flower in a harvesting year.

Fruit budding chart of *Vaccinium sp.* in a harvesting year

Stage	*Vaccinium sp.*	Identification
7*		Petals of flowers have fallen, the underside of the sepals stays round and not swollen
8		The underside of the sepals swells but does not exceed the width of the calix
9		The underside of the sepals exceeds the width of the calix but the fruit stays green
10		Fruit is colored pink to purple, but not entirely blue
11		Fruit is blue and ripe

*Developmental stages of fruit follow
the developmental stages of flower.*

Figure SM.7. Phenological stages of *Vaccinium* sp. – fruit in a harvesting year.
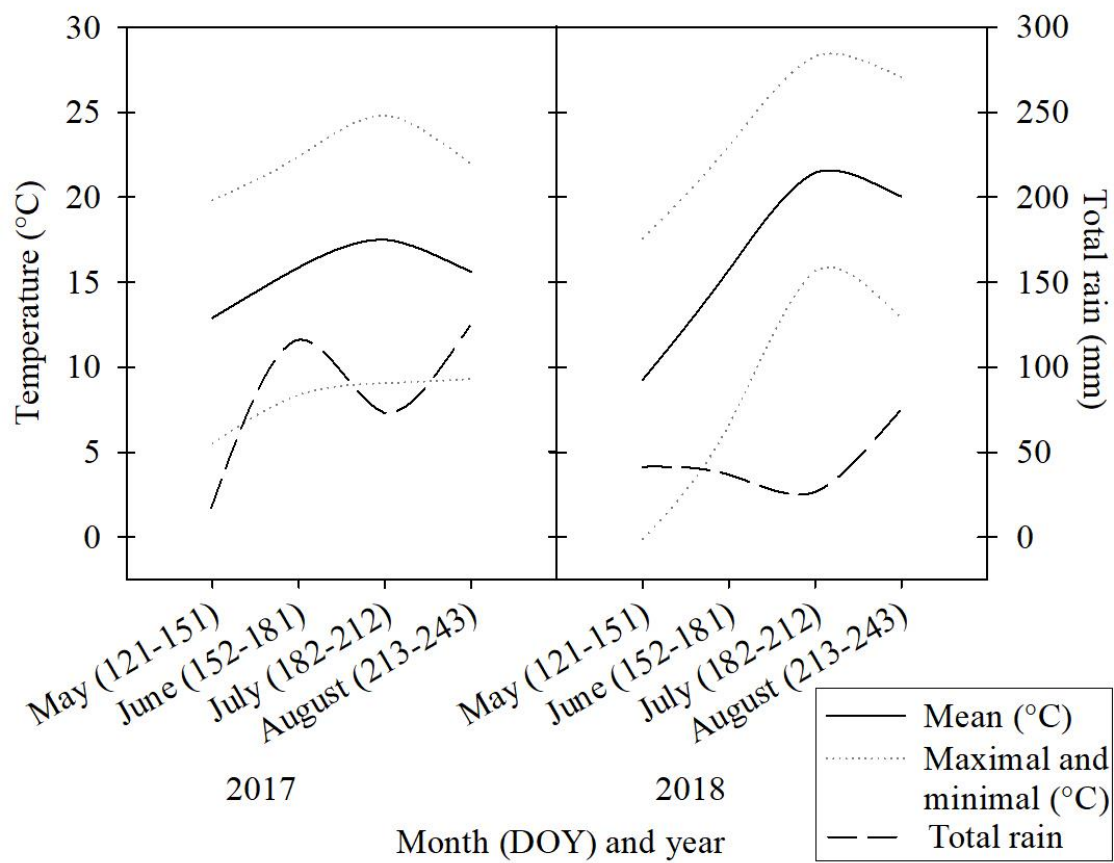
Figure SM.8. Minimal, mean and maximal temperature (°C) and total rain (mm) for May to August in 2017 and 2018.

Annexe 2. Supplementary material – regression

To have normality of all the data, each variable was transformed with natural logarithm of the variable + 1 (such as LN(variable + 1)). Table SMR.4 presents the result of the Shapiro-Wilk test of normality and the P value of each variable (JMP, Analysis – Distribution procedure).

Table SMR.4. Shapiro-Wilk test of normality with *P*-value and result of each variable.

Variable	W	*P*-value	Result
LN(plant height + 1)	0.988819	0.1443	Normal
LN(aboveground plant BM + 1)	0.991436	0.3266	Normal
LN(leaf area + 1)	0.986129	0.0599	Normal
LN(leaf nb + 1)	0.986594	0.0698	Normal
LN(leaf BM + 1)	0.991706	0.3535	Normal

The estimation of aboveground plant BM was calculated with plant height, the estimation of leaf area by leaf number and leaf BM by aboveground plant BM (JMP, Analysis – Fit Y by X procedure). The result of the analysis is reproduced in Table SMR.5. All regression analyses were performed with JMP 14 Pro (SAS Institute Inc. (2018), Cary, NC, USA).

Table SMR.5. Result of linear regression for each variable estimate: equation, R2 and analysis of variance of the linear fit. N: number, BM: biomass.

Variable and equation	Analysis of variance				
Aboveground plant BM	**Source**	**DF**	**Sum of squares**	**Mean squares**	**F ratio**
LN(1+ aboveground plant BM) = -2.162594 + 1.7022067*LN(1+ plant height) $R^2 = 0.699$	Model	1	82.411	82.411	434.264
	Error	187	35.487	0.190	**Prob > F**
	C. total	188	117.898		**<0.001**
Leaf area	**Source**	**DF**	**Sum of squares**	**Mean squares**	**F ratio**
LN(1+leaf area) = - 0.095515 + 0.978233*LN(1+leaf N) $R^2 = 0.909$	Model	1	84.671	84.671	1864.533
	Error	187	8.492	0.045	**Prob. > F**
	C. total	188	93.163		**<0.001**
Leaf BM	**Source**	**DF**	**Sum of squares**	**Mean squares**	**F ratio**
LN(1+ leaf BM) = -0.759857 + 1.0051439 *LN(1+ aboveground plant BM) $R^2 = 0.910$	Model	1	119.114	119.114	1900.438
	Error	187	11.721	0.063	**Prob. > F**
	C. total	188	130.835		**<0.001**

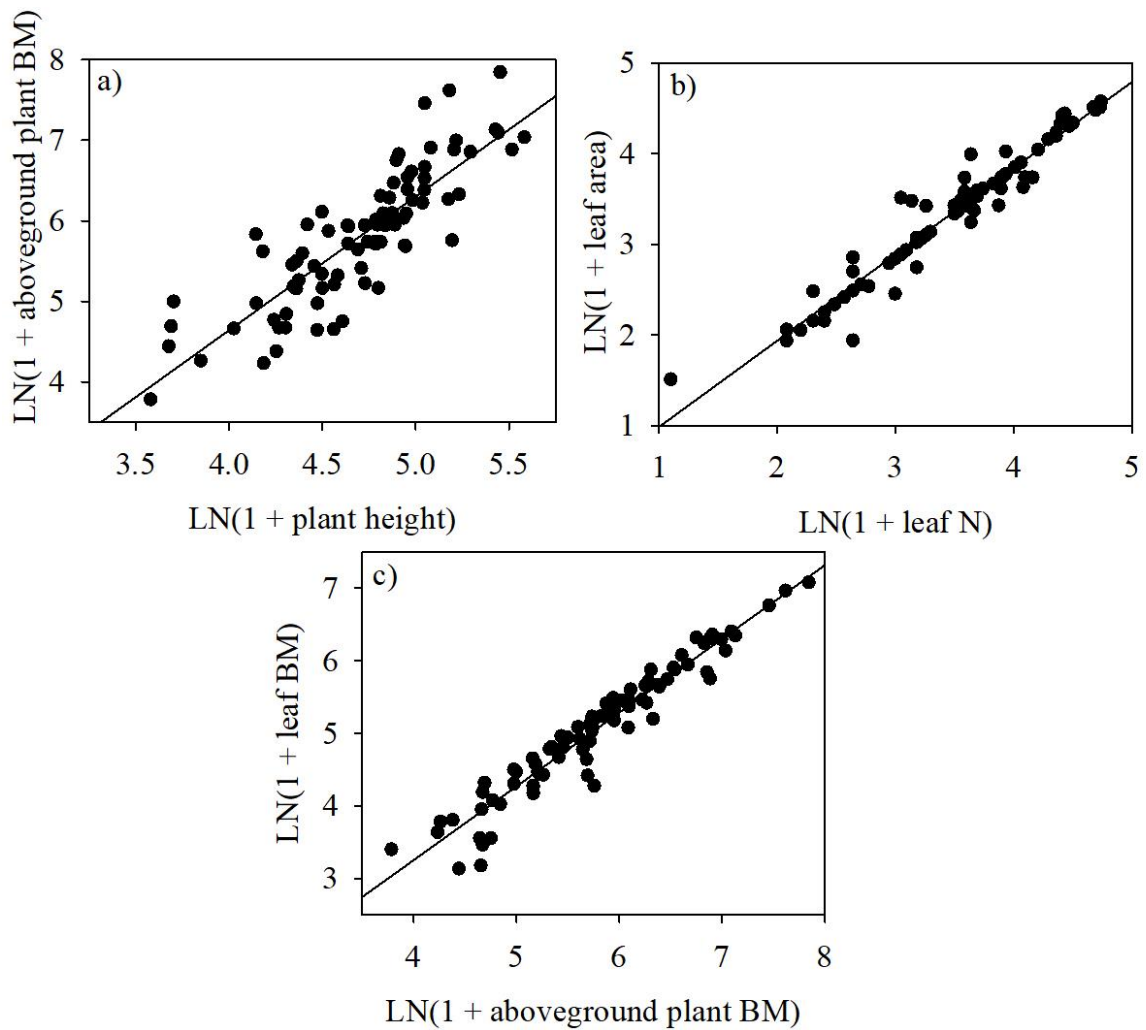Figure SMR.9 shows the three regressions of estimation produced.

Figure SMR.9. Regression the natural logarithm of 1 + variable a) aboveground plant BM depends on plant height, b) leaf area depends on leaf number (N) and c) leaf BM depends on aboveground plant BM.