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# How plant allometry influences bud phenology and fruit yield in two *Vaccinium* species

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• **Background and Aims** 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 yield for two shrub species, *Vaccinium angustifolium* and *Vaccinium myrtilloides*, to test the hypothesis that phenology is linked to the plants' allometric traits, which are predictors of fruit production.
• **Methods** We measured leaf and flower phenology and the above-ground biomass of both *Vaccinium* species in a commercial wild lowbush blueberry field (Quebec, Canada) over a 2-year crop cycle; 1 year of pruning followed by 1 year of harvest. Leaf and flower phenology were measured, and the allometric traits of shoots and buds were monitored over the crop cycle. We hand-collected the fruits of each plant to determine fruit attributes and biomass.
• **Key Results** During the harvesting year, the leafing and flowering of *V. angustifolium* occurred earlier than that of *V. myrtilloides*. This difference was related to the allometric characteristics of the buds due to differences in carbon partitioning by the plants during the pruning year. Through structural equation modelling, we identified that the earlier leafing in *V. angustifolium* was related to a lower leaf bud number, while earlier flowering was linked to a lower number of flowers per bud. Despite differences in reproductive allometric traits, vegetative biomass still determined reproductive biomass in a log–log scale model.
• **Conclusions** Growing buds are competing sinks for non-structural carbohydrates. Their differences 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 between the two *Vaccinium* species. For similar above-ground biomass, both *Vaccinium* species had similar reproductive outputs in terms of fruit biomass, despite differences in reproductive traits such as fruit size and number.

**Key words:** Carbon allocation, plant allometry, phenology, plant architecture, fruit production, plant biomass, *Vaccinium angustifolium*, *Vaccinium myrtilloides.*

## INTRODUCTION

How a plant allocates carbon for reproduction is fundamental to 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 life strategies of plants and are species-specific. Carbohydrates produced via photosynthesis are allocated to metabolism, growth of above- or below-ground structures, formation of reserves, and reproduction (Körner, 2003; Park *et al.*, 2009; Hartmann and Trumbore, 2016); thus, plants partition carbon among different growing structures. Reproductive biomass – fruit yield in commercial species – matches plant biomass (Weiner *et al.*, 2009) and 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, 2012).

In commercial wild blueberry fields, crop management consists of a 2-year crop cycle. The cycle begins with mechanical pruning in late autumn, about 2 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, 1996). 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 fruit characteristics (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 flowering buds, alters patterns of carbon allocation and partitioning (Lacointe, 2000; Marcelis and Heuvelink, 2007).

Earlier phenology is precarious in northern regions for the two *Vaccinium* species studied here because of the possibility of spring frosts, the main factor reducing wild blueberry fruit yield (Olson and Eaton, 2001; Strik and Yarborough, 2005; Ministère de l'Agriculture, 2016). Although some commercial blueberries, such as *Vaccinium angustifolium* and *Vaccinium myrtilloides*, 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.

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 hypotheses that (1) 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.

## MATERIALS AND METHODS

### *Experimental design*

We conducted our study from spring 2017 to autumn 2018 at the Bleuetière d'Enseignement et de Recherche (BER) in Normandin Quebec, Canada (48°49′35″N, 72°39′35″W). We established an experimental design that included two adjacent sites composed of two fields at each site and four blocks of 12 experimental units (EUs) in each field arranged in a split-plot design (Supplementary Data Fig. S1). Each site contained 96 EUs, each 15 × 22 m (330 $m^2$), separated by 3-m buffer zones. All EUs received one of 12 different treatments. These treatments were combinations of mechanical or mechanical and thermal pruning, with or without fungicide application, and mineral, organic or without fertilization (Table S1, Fig. S1). However, the effects of these various treatments are not presented in this paper, but see Fournier (2020). Site 1 was pruned thermally in autumn 2016 and mechanically in spring 2017. Site 1 was harvested in 2018. Site 2 was pruned mechanically and thermally in autumn 2017. Site 2 was in a pruning year in 2018 and a harvesting year in 2019 (after completion of this study). In addition, 52 beehives were used in spring 2018 to ensure sufficient flower pollination during the harvesting year (Table S1).

### *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 Data Figs S2 and S3). The same eight shoots in each EU were then monitored periodically throughout the growing season, for phenological measurements. We noted the species *Vaccinium angustifolium* Aiton (VA) or *Vaccinium myrtilloides* Michx (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 3–4 d (Table S1) following a six-stage leaf development protocol (Figs S3 and S4). Floral and fruit bud phenology were also recorded for Site 1 (every 3–4 d) during the harvesting year using an 11-stage development protocol (Figs S5 and S6).

We recorded several allometric traits of the blueberry shoots (Supplementary Data Fig. S2). 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)] (Fig. S2). 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 above-ground plant BM (g DM), excluding fruits (Fig. S2). Leaf area ($cm^2$) was measured with a planimeter (Li-3100, Li-Cor, Lincoln, NE, USA). Based on these collected

data, above-ground 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 (Tables SM1–2 and Fig. SM1). We calculated specific leaf area (SLA) as:

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

*Meteorological data*

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

*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:

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

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

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

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 its frequency of observation for each sampling day (DOY). In the model, species, year and the date at which the $E_i$ 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 probability $P(E_i)$, 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:

$$E_{st} = -(b_{E_i} + b_s + b_y)$$

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 from:

$$P(b_{E_i}) = \frac{b_{E_i}}{b_{DOY}}$$

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

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

We used structural equation modelling (SEM) to assess the direct and indirect effects of bud allometric traits on phenology and fruit number and biomass for both *V. angustifolium* and *V. myrtilloides*. The model structure was established based on our hypothesis, according to which the number of units (leaf and flower bud elements) influence bud phenology (Fig. 1). Plant productivity is thus influenced by both the number of units and

TABLE 1. *Mean monthly minimum, mean and maximum temperature and total monthly rainfall (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 |

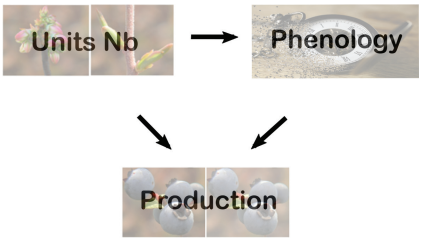


FIG. 1. Conceptual model of the relationship between the number of units of leaves and flower buds, their phenology, and fruit production.

bud phenology. Only *P*(*50*), representing the DOY for passing from Stage 5 to Stage 6, was included in the SEM because it represents the DOY at which the phenology was completed for both leaf and flower buds. The degree of multicollinearity between variables was assessed by variance inflation factors (VIFs), retaining all variables having a VIF value <5 (Zuur *et al.*, 2010). SEM analysis was run using the *lavaan* package in R (Rosseel, 2012), with 1000 bootstrap resampling (Beaujean, 2014). The model was accepted when $P_{\chi 2} > 0.05$, and goodness of fit was assessed using the fitting index combination of a comparative fit index (CFI) of >0.95 and a standardized root mean square residual (SRMR) of <0.09 (Hooper *et al.*, 2008).

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 Data Fig. S2 (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. angustifolium* and *V. myrtilloides*, using reproductive biomass (R or fruit BM) as the dependent variable and vegetative biomass (V or above-ground plant BM) as the independent variable. The two variables were $\log_{10}$-transformed 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 non-significant ($P > 0.05$) factors were removed from the models. The normality of the residual predicted values was verified. All linear mixed models and mixed-effect models were developed using SAS 9.2 (SAS Institute, Cary, NC, USA).

## RESULTS

### *Phenological differences between species*

The leaf, flower, and fruit phenology of *V. angustifolium* and *V. myrtilloides* were monitored in 2017 and 2018 (Supplementary Data Figs S3–S6). During the pruning year, *V. angustifolium* and *V. myrtilloides* showed no differences in leaf phenology (Tables 2 and 3; Fig. 2A, B): the timing of the phenological phases ($P_{(50)}$) of the leaves between species differed by only 1–2 d, a non-significant difference (Table 3; Fig. 2A, B). 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 d compared to 2018 (Tables 2 and 3; Fig. 2A, B).

TABLE 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)*. The 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 | $9610.803_{1,\ 10402}$ (**$P < 0.001$**) |

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 d earlier, respectively (Fig. 2D, E; Tables 2 and 3). We observed significant phenological differences between species in the harvesting year for leaf bud and flower bud (Table 2). Flowering occurred later than leaf bud burst even though we observed increases in the size and swelling of the flower buds earlier than those for the leaf buds (Stage 1 for both leaf and flower buds). Leaf buds opened 5 d prior to flower buds in *V. angustifolium* and 2 d before flower buds in *V. myrtilloides* (Table 3; Fig. 2D, E). We modelled a difference of 8 d between the two species for the probability of open flowers (Stage 6, Supplementary Data Fig. S5); we observed open flowers on DOY 171 for *V. angustifolium* and DOY 179 for *V. myrtilloides* (Table 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, Fig. S5; Table 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 developmental stages (Fig. 2C); however, the date at which we observed the first mature fruit was similar between the species (Fig. 2C): 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*.

### *Species effect on allometric characteristics*

The two blueberry species differed in most of their plant allometric characteristics, particularly during the harvesting year (Fig. 3; Table 4). During the pruning years, both species had similar plant heights (Fig. 3A), ramification numbers, plant BM (Fig. 3D), and SLA (Fig. 3J; Table 4). In the pruning years, however, we observed significantly higher leaf numbers for *V. myrtilloides* than for *V. angustifolium* (Fig. 3H; Table 4). Furthermore, we also observed a significant difference

TABLE 3. *Day of the year (DOY) corresponding to the 50 % probability ($P_{(50)}$) of reaching the following stage for leaf (L) or flower (F) buds of* Vaccinium 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 |

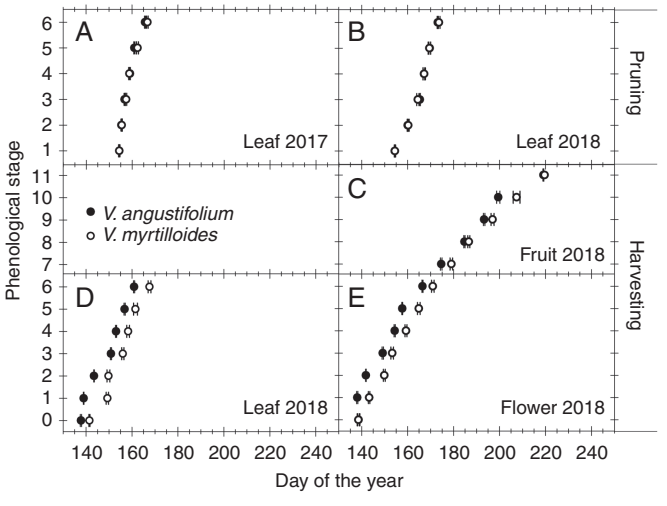


FIG. 2. Mean timing of the phenological stages of *Vaccinium angustifolium* and *V. myrtilloides* leaf buds in the vegetative years and the mean timing of the leaf, flower and fruit buds in the pruning and harvesting years. Error bars represent the standard error of the mean.

between years for leaf number (Table 4) and SLA (Table 4) in the pruning years, with both traits lower in 2018. We observed no significant year and species interactions (Table 4).

During the harvesting year, plant BM (Fig. 3E), branch length (Fig. 3C), ramification numbers, SLA (Fig. 3J) and fruit BM (Fig. 3O) did not differ between the two species (Table 4). All other characteristics differed significantly between the two blueberry species; for example, *V. angustifolium* had a greater flower bud number (Fig. 3K) and BM per fruit (Fig. 3R) than *V. myrtilloides*. All other allometric traits had higher values for *V. myrtilloides* (Table 4), including plant height (Fig. 3B) and the number of leaf buds (Fig. 3F), leaves (Fig. 3I), branches (Fig. 3E), apical flowers (Fig. 3M), total flowers (Fig. 3L), flowers by bud (Fig. 3N), apical fruits (Fig. 3Q) and total fruits (Fig. 3P). Branch growth slowed around DOY 185, as fruits began to develop.

### *Links between species, phenology and allometric characteristics in the harvesting year*

The SEM suitably fit our hypothesis ($P_{\chi 2}$ = 0.35, CFI = 1, SRMR = 0.003), underlining the direct and indirect relationships between the units' number, phenology and fruit production. The SEM explained 70 % and 50 % of the variance in fruit biomass and total fruit number, respectively. All significant coefficients are represented in Fig. 4, while a complete list of all obtained coefficients is shown in Supplementary Data Table S2. Fruit biomass was linked positively and directly to total fruit number (0.78) and negatively, but directly, to flower *P*(*50*) (–0.08, Fig. 4). Total fruit number was affected positively by total flower number (0.7) and leaf *P*(*50*) (0.10, Fig. 4). Leaf *P*(*50*) ($R^2$ = 0.04) covaried strongly with flower *P*(*50*) (0.67), but it was also linked directly to the number of flowers per bud (0.15) and leaf bud number (0.13, Fig. 4). Flower *P*(*50*) ($R^2$ = 0.07) was affected positively by leaf bud number (0.19) and the number of flowers per bud (0.16, Fig. 4) but was affected negatively by total flower number (–0.26).

Vegetative BM significantly determined reproductive BM on a log–log R–V mixed-effect model (Table 5; Fig. 5). Species and the interaction between species and vegetative BM were not significant and were thus removed from the model (Table 5). The predicted log of reproductive BM increased with the log of vegetative BM (Table 5) 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 Data Fig. S2).

## 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 (leaf and flower phenology are linked to the plants' allometric traits and species). 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 above-ground biomass determined fruit biomass

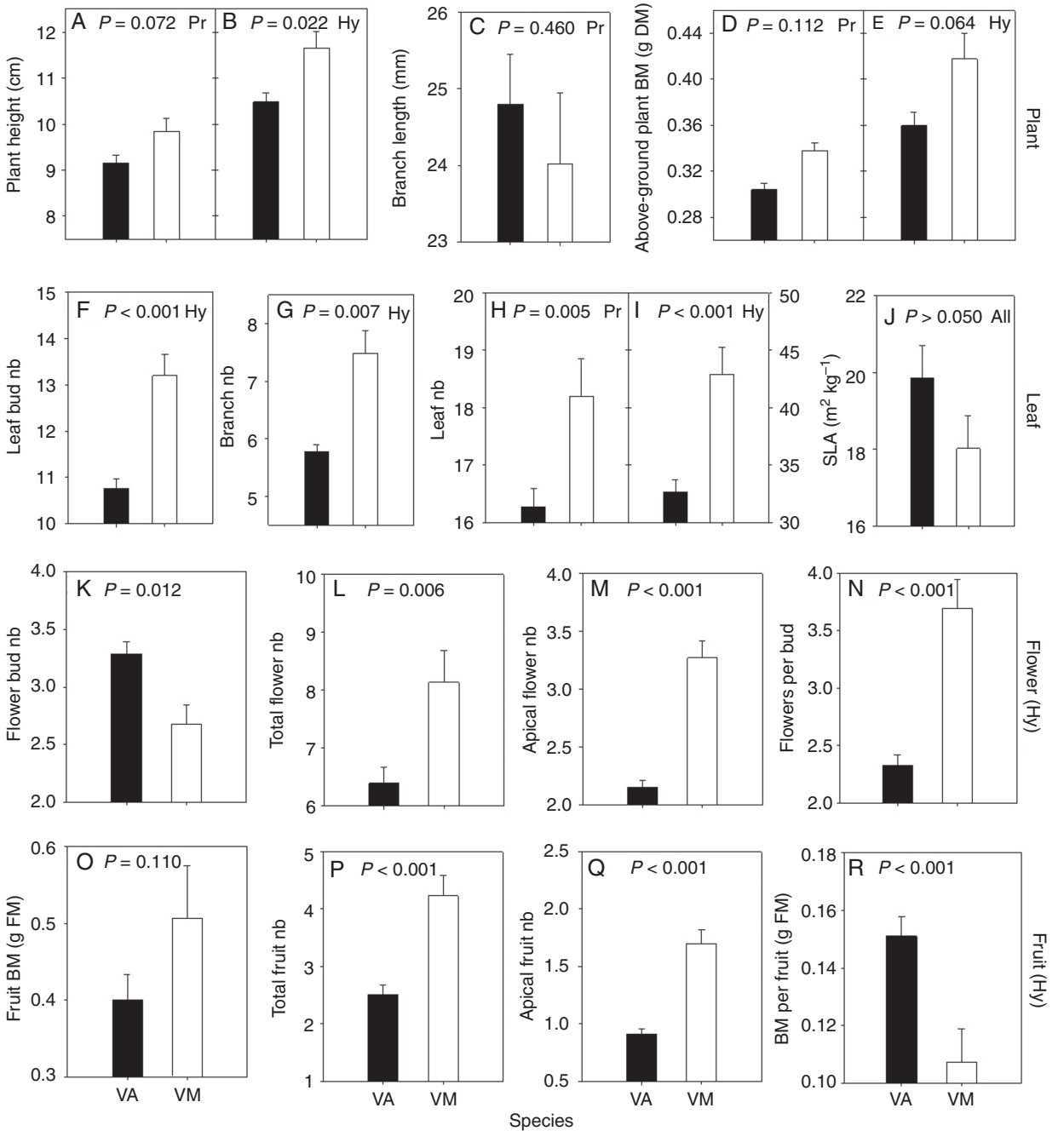


FIG. 3. Mean of the allometric traits per plant of the two *Vaccinium* species. Traits are presented for the different organs: plant, leaf, flower and fruit. Data were collected in the pruning year (Pr), harvesting year (Hy) or both (All). Error bars represent the standard error of the mean. VA = *V. angustifolium*, VM = *V. myrtilloides*, nb = number, BM = biomass, DM = dry BM, and FM = fresh BM.

(Weiner *et al.*, 2009; Wenk and Falster, 2015); therefore, we only partially accept our second hypothesis (both phenology and plant allometry are predictors of fruit production). Delayed phenology can increase reproductive biomass indirectly by protecting flower buds from spring frost and favour 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*.

### *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 1).

TABLE 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; values in bold are significant in the main model. Probability (*P*) is not significant (n.s.) 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. = above-ground.*

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

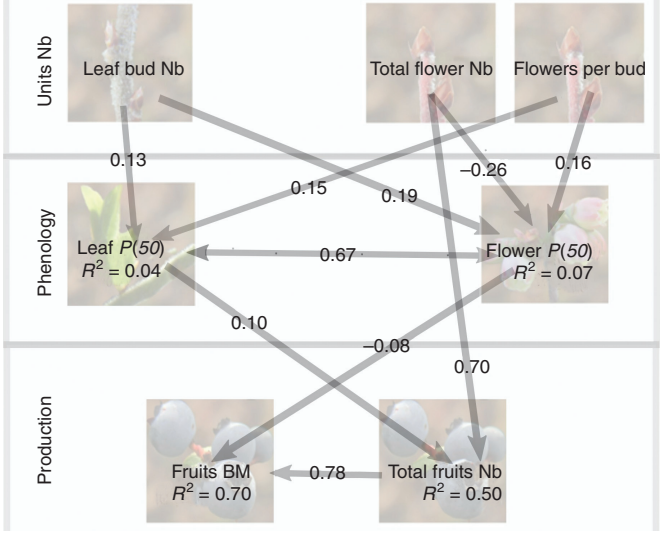


FIG. 4. Structural equation model fit for both *Vaccinium myrtilloides* and *V. angustifolium* with significant standardized coefficients.

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). Although our SEM represented only a small part of the variability in the leaf and flower *P*(*50*) – bud phenology depends on several other internal and external factors (Badeck *et al.*, 2004; Bell, 2009; Anna and Rufus, 2012) – the number of meristems partially influenced the phenological timing of the two species and their representative fruit production (see the following section).

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 it 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 greater branch production during the harvesting year.

TABLE 5. *Complete and simplified mixed-effect model built for reproductive biomass (fruit BM). The results include estimation, standard error (s.e.), and test of effects with* t*-statistics, degrees of freedom (df), and* P*-value (*$t_{df}$*(*P*-value)). The significance of the* P*-value is based on* $\alpha = 0.05$*; values in bold are significant in the main model. BM = biomass, VA =* V. angustifolium*, VM =* V. myrtilloides*.*

| Model | Effet | Species | Estimation (s.e.) | 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)** |

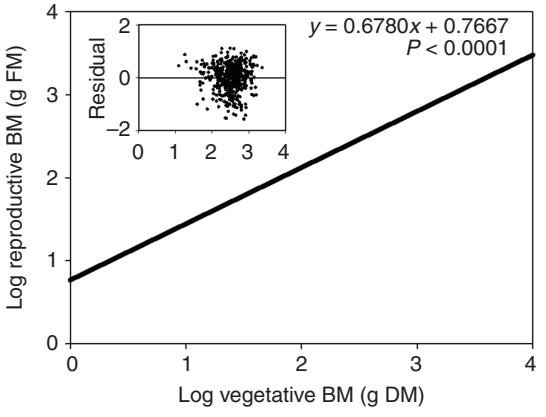


FIG. 5. Change in the log of reproductive biomass (g fresh weight), i.e. fruit BM - R, predicted by the R–V mixed-effect model according to log of vegetative BM (g dry weight), i.e. above-ground plant BM - V. BM: biomass, FM: fresh BM, DM: dry BM.

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*) (Mason *et al.*, 2014) and roses (*Rosa hybrida*) (Barbier *et al.*, 2015), respectively, decapitation of the apex leads to rapid auxiliary bud release because of a reduced sink competition between the apex and the lower dormant buds that receive more sucrose after excision. Moreover, at high levels of sucrose, auxiliary rosebuds open more rapidly, whereas low levels of sucrose result in a 3-d 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 below-ground 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 non-structural carbon partitioning in the buds of *V. angustifolium* and *V. myrtilloides* differed, in part, because of their above-ground allometry. *Vaccinium 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, i.e. a lower number of vegetative meristems anticipate leaf *P*(*50*), for *V. angustifolium* compared to *V. myrtilloides*. However, unlike leaf buds, flower phenology was not related to flower bud number (not significant, Supplementary Data Table S2). Rather, the number of flowers per bud influenced both flower *P*(*50*) and leaf *P*(*50*), i.e. a lower number of flower units per bud anticipated for both *P*(*50*). This result thus corresponds to the delayed phenology in *V. myrtilloides* (Smith, 1969), a species having more flowers per bud.

Although the total flower number and number of flowers per bud were highly correlated ($\rho = 0.70$, data not shown), these traits had opposite effects on flower *P*(*50*). The effect of total flower number (standardized coefficient of –0.26, anticipating effect) was stronger and opposite to that of the number of flowers per bud (0.16, delaying effect). These opposite effects run counter to our hypothesis but could be explained by flower bud allometry: (1) several single flowers would require fewer resources and so earlier phenology compared to a grouped unit of flowers needing a greater amount of resources to develop, thereby increasing sink competition (Baïram *et al.*, 2019); and (2) a flower bud having more units could require a higher degree of vascularization, which may require more time to develop compared to a flower bud having fewer flower units (Baïram *et al.*, 2019).

Due to resource partitioning between reproductive and vegetative meristems, a higher leaf bud number tends to delay flower *P*(*50*). This positive link between leaf bud and flower *P*(*50*) is explained by the ability to quickly grow green leaves that assimilate $CO_2$ and speed up the entire growth process when more leaves are produced. This latter phenomenon also explains the strong covariance between flower *P*(*50*) and leaf *P*(*50*). During the harvesting year, the first phases of flower phenology occurred earlier than leaf phenology; in both species, however, leaf bud burst (Stage 6, leaf completely open, Supplementary Data Fig. S4) occurred prior to the first flower opening (Stage 6, Fig. S5) (Shipley, 2002; Weraduwage *et al.*, 2015). During the harvesting year, however, 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).

### *How plant allometry and phenology determine fruit production*

Our SEM results show that the 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, fruit biomass decreased slightly under a delayed flower *P*(*50*). Earlier flower phenology thus seems to increase the time required for fruit development, thereby increasing a fruit's biomass. Nonetheless, flower phenology had a much greater direct influence on fruit biomass during 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. As fruit size is closely correlated with seed number (Aalders and Hall, 1961; Jackson *et al.*, 1972; Myra *et al.*, 2004), a delayed flower phenology can limit fruit biomass. Moreover, 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). Other than the time for development reflected by phenology, insect pollinators, such as bees, are critical for seed production success and fruit biomass.

While the total number of produced fruits was higher in *V. myrtilloides*, the fruits were smaller than those of *V. angustifolium*. Both carbon allocation and pollination success can explain this difference. Plant allometry is linked directly to plant allocation, and this is essentially size-dependent (Weiner *et al.*, 2009; Wenk and Falster, 2015). In shrubs such as *Vaccinium* sp., above-ground vegetative biomass is represented mainly by the photosynthetic biomass (i.e. leaves), while shoots and twigs are less important contributors. However, below-ground biomass represents >90 % of the total plant biomass (Marty *et al.*, 2019) and contributes to the carbon requirements, especially at the time of shoot growth. The below-ground reserves are shared between the different developing shoots, thus limiting the effect on a single shoot (Morin, 2008). Reproductive biomass increases with above-ground biomass in a log–log allocation model, the R–V model (Weiner *et al.*, 2009). When plant biomass increases, potential reproduction output also increases; however, 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, 2018). In our R–V mixed-effect model, this pattern was represented by a slope <1 (Weiner *et al.*, 2009; Wenk and Falster, 2015) with no minimum size for reproduction (negative *x*-intercept). This balance between the source–sink carbon ratio was also represented in the SEM results by the direct and positive link between leaf *P*(*50*) and total fruit number (standardized coefficient of 0.10). An earlier leaf development limits the total fruit number by allocating more resources to the vegetative structures than productive structures. Therefore, to attain greater fruit production, the maximum plant biomass must be reached within a short time interval to avoid allocation overlap between the vegetative and reproductive structures. For a similar above-ground biomass, both *Vaccinium* species had similar reproductive outputs in terms of fruit biomass, despite differences in fruit size and number. Nonetheless, a large reproductive allocation was observed for a given vegetative biomass (i.e. a large point distribution around the regression lines, Supplementary Data Fig. S2). According to Bonser and Aarssen (2009), reproductive output also integrates developmental, genotypic and environmental factors, creating a large reproductive allometry, represented here by fruit biomass. Marked reproductive output at a given size could also be related to other factors, such as pollination. Indeed, reduced pollination success could explain the lower biomass per fruit in *V. myrtilloides* (Jackson *et al.*, 1972). As mentioned above, fruit size is closely correlated with seed number, resulting from successful ovule fertilization by pollen vectors (Aalders and Hall, 1961; Jackson *et al.*, 1972; Myra *et al.*, 2004). Reduced pollination success is therefore related to smaller fruits as the smaller fruit of *V. myrtilloides* may hold fewer seeds (Aalders and Hall, 1961; Jackson *et al.*, 1972). This limited pollination could be related to the reduced bee presence during the late phenology of *V. myrtilloides* (as discussed above) but also to the lower number of individuals of *V. myrtilloides* in our study fields. Moreover, because there is only 3 d of overlap in flower phenology between the two 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 (Fig. S7), i.e. very low reproductive biomass relative to above-ground 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).

## CONCLUSIONS

We have 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. *Vaccinium 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 vegetative biomass and plant architecture.

## SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Table S1. Crop management calendar, treatment information and date of data collection for each studied site. Table S2. Structural equation model regression parameters. Figure S1. Schematic diagrams of the experimental design. Figure S2. Development of allometric traits of blueberry plants in time. Figure S3. Phenological stage of *Vaccinium* sp. – leaf in pruning year. Figure S4. Phenological stage of *Vaccinium* sp. – leaf in harvesting year. Figure S5. Phenological stage of *Vaccinium* sp. – flower in harvesting year. Figure S6. Phenological stage of *Vaccinium* sp. – fruit in harvesting year. Figure S7. R–V mixed effect model showing the relationship between the log reproductive BM (i.e. fruit BM – R), and the log vegetative BM (i.e. above-ground plant BM) with data for each species. Table SM1. Shapiro–Wilk test of normality with *P* values and result of each variable used. Table SM2. Result of linear regression for each variable estimate: equation, $R^2$ and analysis of the variance of the linear fit. Figure SM1. The three regressions of the estimation produced.

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**Table S1.** Crop management calendar, treatment informations 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 $P_2O_5$ $ha^{-1}$ as super triple phosphate, 15 kg of $K_2O$ $ha^{-1}$ potassium sulfate and 0.7 kg of B $ha^{-1}$ borate<br>**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** :<br>135 : May 15$^{th}$, 140 : May 20$^{th}$,<br>145 : May 20$^{th}$, 150 : May 30$^{th}$,<br>155 : June 4$^{th}$, 160 : June 9$^{th}$,<br>165 : June 14$^{th}$, 170 : June 19$^{th}$,<br>175 : June 24$^{th}$, 180 : June 29$^{th}$<br>185 : July 4$^{th}$, 190 : July 9$^{th}$,<br>195 : July 14$^{th}$, 200 : July 19$^{th}$,<br>220 : August 8$^{th}$. |
| **Data collection in harvesting year** | **Phenology :** 135, 137, 142, 145, 149, 152, 156, 158, 164, 171, 178, 185, 192, 220.<br>**Allometry :** 220. | | |

**Table S2. Structural equation model (**SEM) regression's parameters. Bold standardized coefficients were used to build SEM model (Figure 4). nb = number.

| Variables | | | Estimate | Standard error | z-value | P(>\|z\|) | Standardized coefficient |
|---|---|---|---|---|---|---|---|
| **Regressions** | BM fruits | Flower bud nb | 0.013 | 0.017 | 0.790 | 0.430 | 0.039 |
| | | Total flower nb | 0.006 | 0.010 | 0.585 | 0.558 | 0.047 |
| | | **Flower P50** | **-0.011** | **0.004** | **-2.655** | **0.008** | **-0.081** |
| | | Flowers per bud | -0.016 | 0.015 | -1.065 | 0.287 | -0.047 |
| | | Leaf bud nb | 0.006 | 0.006 | 1.014 | 0.311 | 0.036 |
| | | Leaf P50 | -0.007 | 0.005 | -1.492 | 0.136 | -0.050 |
| | | **Total fruit nb** | **0.153** | **0.011** | **13.305** | **0.000** | **0.785** |
| | Total fruit nb | Flower P50 | -0.035 | 0.027 | -1.283 | 0.199 | -0.051 |
| | | **Leaf P50** | **0.073** | **0.028** | **2.597** | **0.009** | **0.101** |
| | | **Total flower nb** | **0.451** | **0.033** | **13.560** | **0.000** | **0.706** |
| | | Leaf bud nb | 0.031 | 0.030 | 1.013 | 0.311 | 0.035 |
| | | Flower bud nb | 0.017 | 0.088 | 0.197 | 0.844 | 0.010 |
| | | Flowers per bud | -0.035 | 0.027 | -1.283 | 0.199 | -0.051 |
| | Flower P50 | Flower bud nb | -0.042 | 0.140 | -0.302 | 0.763 | -0.016 |
| | | **Total flower nb** | **-0.240** | **0.055** | **-4.355** | **0.000** | **-0.257** |
| | | **Flowers per bud** | **0.418** | **0.144** | **2.901** | **0.004** | **0.161** |
| | | **Leaf bud nb** | **0.248** | **0.049** | **5.066** | **0.000** | **0.192** |
| | Leaf P50 | Total flower nb | -0.012 | 0.065 | -0.180 | 0.857 | -0.013 |
| | | **Flowers per bud** | **0.383** | **0.190** | **2.018** | **0.044** | **0.155** |
| | | **Leaf bud nb** | **0.158** | **0.049** | **3.248** | **0.001** | **0.129** |
| | | Flower bud nb | -0.196 | 0.157 | -1.245 | 0.213 | -0.080 |
| **Covariances** | Flower P50 | **Leaf P50** | **25.371** | **1.936** | **13.102** | **0.000** | **0.671** |

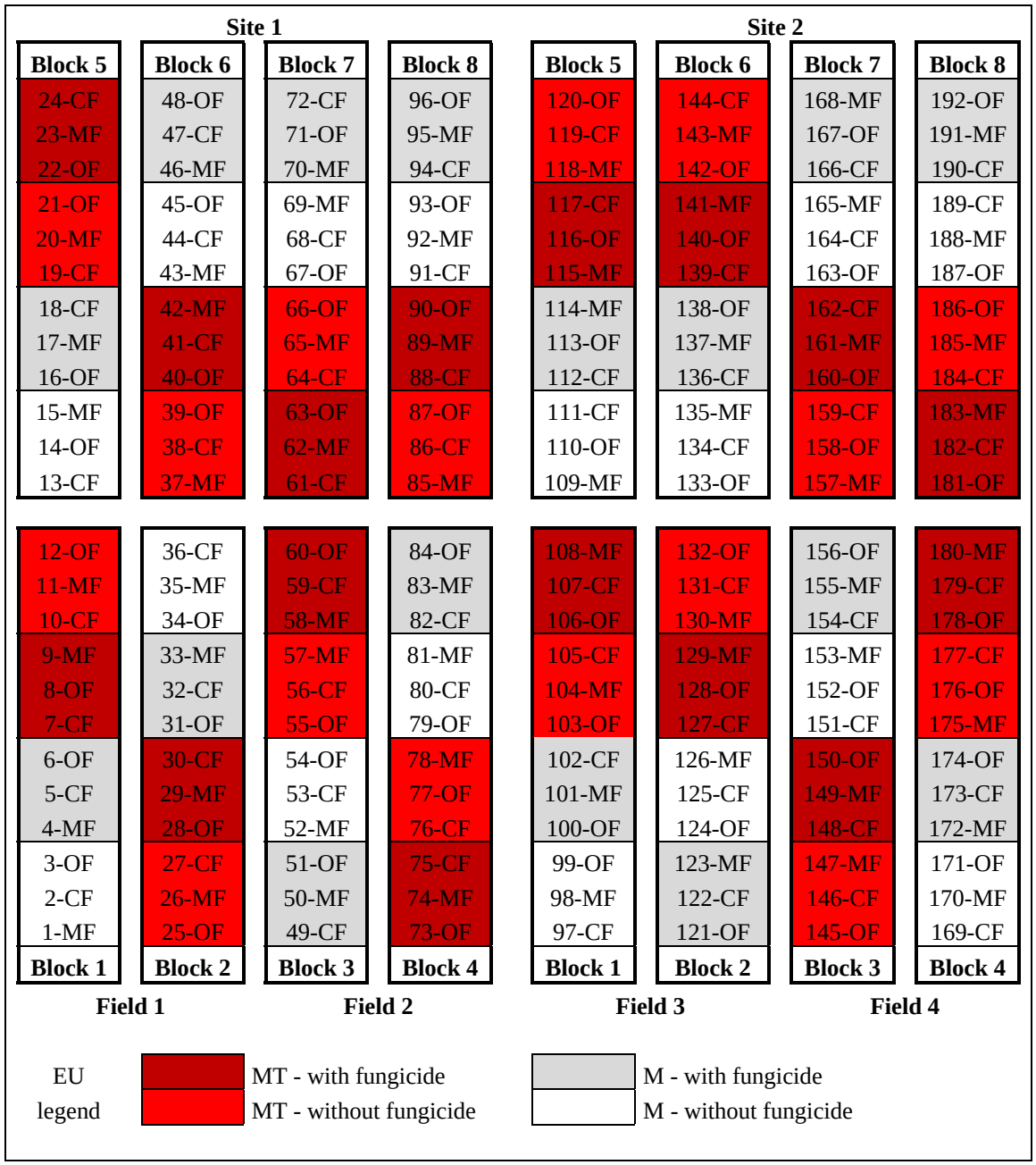



**Figure S1**. Schematic diagrams of the experimental design. Each site contained 96 experimental units (EU) of 15 × 22 m (330 $m^2$) separated by a 3-m buffer zone, for a total of 192 EU. M, mechanical pruning; MT, mechanical and thermal pruning; MF, mineral fertilizer; OF, organic fertilizer (poultry manure); CF, without fertilizer (see Table S1 for details).

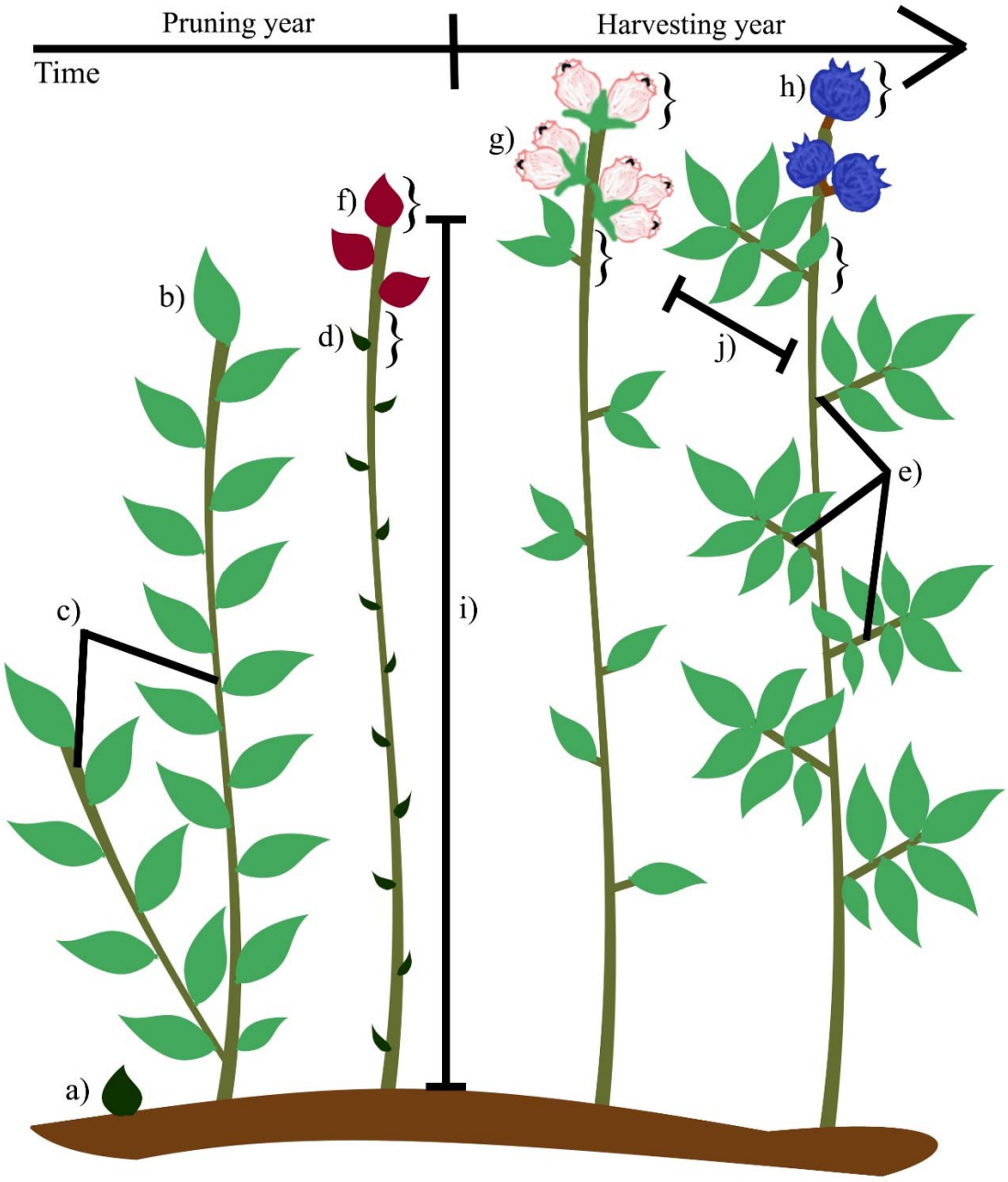



**Figure S2.** Development of allometric traits of blueberry plant in time. Apical traits were illustrated with a brace (}), and total traits are all structures present on a plant. For each part represent by a letter, measured data were include in parenthesis (BM for biomass, nb for number, nb/1 for 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 (nb, g DM, $cm^2$), c) ramifications (nb), d) leaf buds (apical phenology, nb), e) branches (nb) and its j) apical length (mm), f) flower buds (apical phenology, nb), g) apical and total flowers (nb, nb/1), h) apical and total blueberries (nb, nb/1, g FM), aboveground plant i) height (cm) and BM (g DM)

**Foliar budding chart of *Vaccinium sp.* in cropping year**

| Stage | *Vaccinium sp.* | Indentification |
|---|---|---|
| 1 |  | Bud is a little pink button |
| 2 |  | Bud elongates and become pointed |
| 3 |  | Bud increases in width, becomes round and translucide |
| 4 |  | Bud doubles in size and turns green |
| 5 |  | Leaves are distinct |
| 6 |  | Leaves are completely open |

**Figure S3.** Phenological stage of *Vaccinium* sp. – leaf in pruning year.

**Foliar budding chart of *Vaccinium sp.* in production year**

| Stage | *V. angustifolium* | *V. myrtilloides* | Indentification |
|---|---|---|---|
| 0 |  |  | Brown bud without other color and close |
| 1 |  |  | Pink scales spread and are distinct, size increase |
| 2 |  |  | Bud switches from pink to green, becomes pointed, translucent, and double size |
| 3 |  |  | Leaves are discovered and bud grows longer |
| 4 |  |  | Leaves are distinct and is twice as big as stage 3 |
| 5 |  |  | Leaves separate but still curled on themselves |
| 6 |  |  | Leaves are completely open |

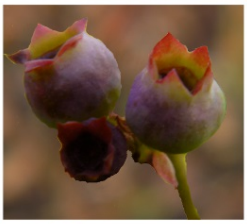
**Figure S4.** Phenological stage of Vaccinium sp. – leaf in harvesting year.

**Floral budding chart of *Vaccinium sp.* in production year**

| Stage | *V. angustifolium* | *V. myrtilloides* | Indentification |
|---|---|---|---|
| 0 |  |  | Brown bud, small, without other colors and close |
| 1 |  |  | Pink coloration appers with distinction between scales and start to swell |
| 2 |  |  | Colored scales, size a third larger that stage 1 |
| 3 |  |  | Bud starts to open, increase in size |
| 4 |  |  | Bud completely open |
| 5 |  |  | Distinction between sepals and petals of flowers |
| 6 |  |  | First flower open |

**Figure S5.** Phenological stage of Vaccinium sp. – flower in harvesting year.

**Fruit budding chart of *Vaccinium sp.* in production year**

| Stage | *Vaccinium sp.* | Indentification |
|---|---|---|
| 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 exceed the width of the calix but the fruit stays green |
| 10 |  | Fruit is coloured from pink to purple or not completely blue |
| 11 |  | Fruit is blue and ripe |

**Development stages of fruit follow development stages of flower.*

**Figure S6.** Phenological stage of Vaccinium sp. – fruit in harvesting year.

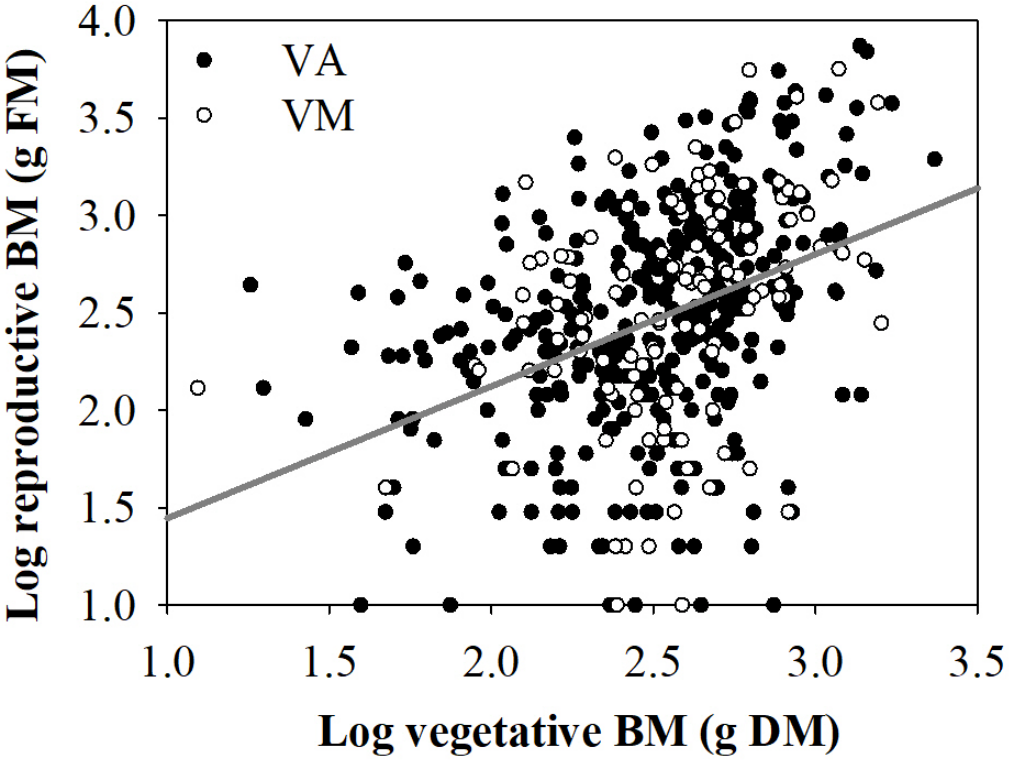



**Figure S7.** R-V mixed effect model (grey line) showing the relationship between the log reproductive BM, i.e., fruit BM - R, and the log vegetative BM, i.e. aboveground plant BM with data of each specie. VA: *V. angustifolium*, VM: *V. myrtilloides*, BM: biomass, FM: fresh BM, DM: dry BM.

## Supplementary Analysis

To have normality of the all data, each variable was transformed with natural logarithm of the variable + 1 (such as LN(variable + 1)). The Table SM1 present the result of the Shapiro-Wilk test of normality and the P value of each variable (JMP, Analysis – Distribution procedure).

**Table SM1.** Shapiro-Wilk test of normality with P value and result of each variable used.

| 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 aera + 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 the aboveground plant BM was calculated with the 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 the Table SM2. All regression analysis were performed with JMP 14 Pro (SAS Institute Inc. (2018), Cary, NC, USA)

**Table SM2.** Result of linear regression for each variable estimate: equation, $R^2$ and the analysis of the variance of the linear fit.

| **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) | Model | 1 | 82.411 | 82.411 | 434.264 |
| | Error | 187 | 35.487 | 0.190 | **Prob > F** |
| $R^2$ = 0.699 | 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 nb) | Model | 1 | 84.671 | 84.671 | 1864.533 |
| | Error | 187 | 8.492 | 0.045 | **Prob. > F** |
| $R^2$ = 0.909 | 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) | Model | 1 | 119.114 | 119.114 | 1900.438 |
| | Error | 187 | 11.721 | 0.063 | **Prob. > F** |
| $R^2$ = 0.910 | C. total | 188 | 130.835 | | **<0.001** |

The Figure SM1 showed the three regression of estimation produced.

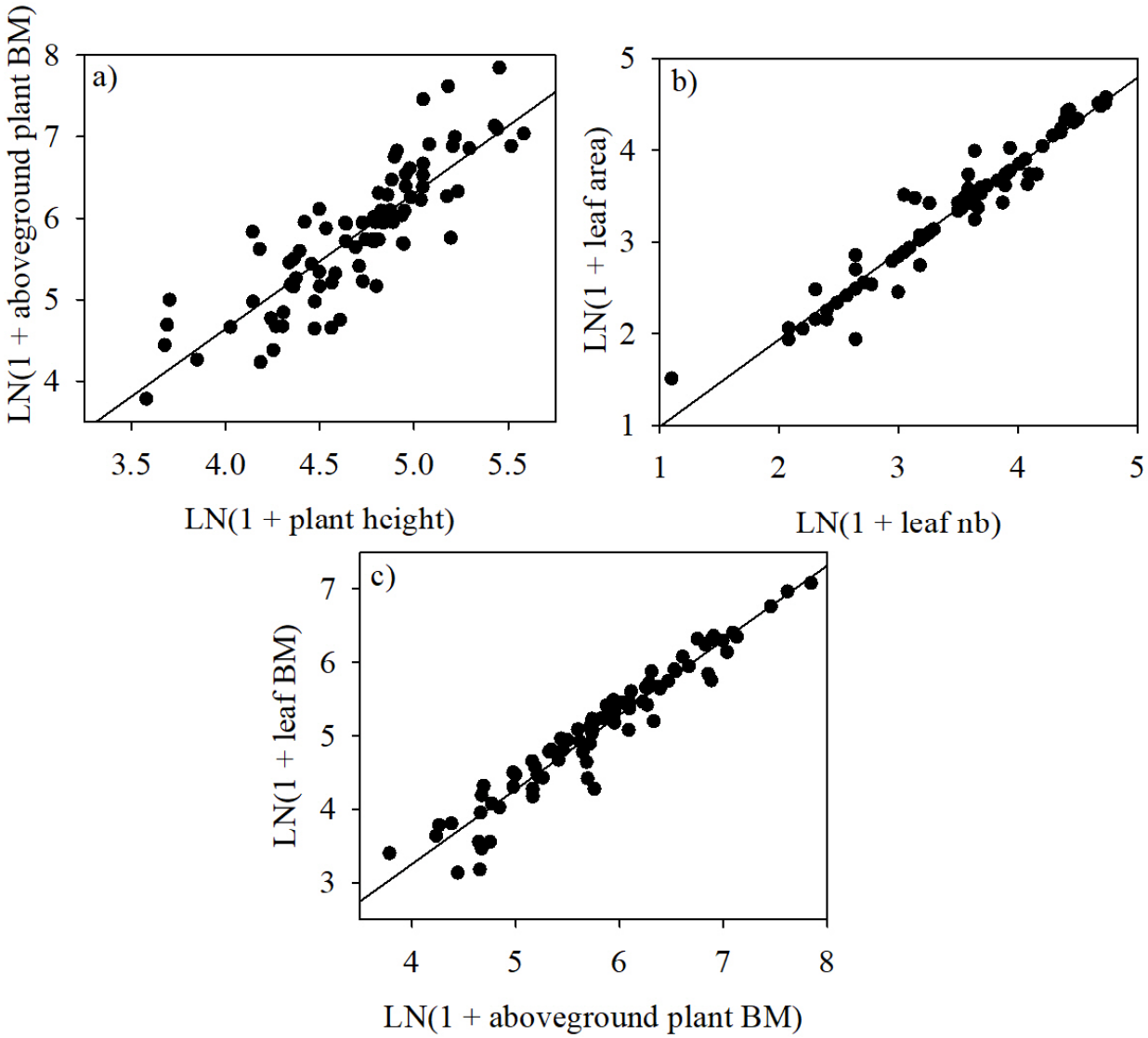



**Figure SM1.** Regression the natural logarithm of 1 + variable a) abovegroung plant BM depends on plant height, b) leaf area depends on leaf number and c) leaf BM depends on abovegroung plant BM.