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**Article type:** Review

**The shoot system architecture of *Vitis vinifera* ssp. *sativa***

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13 **Abstract**

14 Conversely to many other woody perennial crops, the *Vitis vinifera* grapevine does not display  
15 self-supporting and limited-in-space aerial architectures, but rather develops extended shoot  
16 systems relying on external mechanical supports. This behavior results from both structural  
17 factors, i.e. stem anatomy, bud and phytomer organisation, and also specificities in the  
18 modulation of primary growth and branching, i.e. phyllotaxis, apical dominance and acrotony.  
19 To mitigate the most limiting biological properties for cultivation, the grapevine domestication  
20 need a range of practices to facilitate plant management and improve agronomic performances.  
21 The structure and the functioning of the shoot system regulate not only the potential of biomass  
22 accumulation and source/sink balance and but also the canopy microclimate with effects on  
23 fruit quality and organ fungus susceptibility. This paper reviews the main biological processes  
24 and management practices that regulate grapevine shoot system architecture and development,  
25 revisiting the associated terminology.

26

27 **Keywords:** shoot primary growth, branching, winter bud, acrotony, apical dominance,  
28 prolepsis, syllepsis

29

30 **1. Introduction**

31 Woody perennial crops ensure year-to-year sustainability through several biological  
32 mechanisms (Palonen and Buszard, 1997). Among them, the lignification of supporting tissues  
33 and the development of a specialized bark are essential to protect vascular tissues and cambiums  
34 during winter. Another important process is the differentiation of winter buds that are protected  
35 by lignified scales to postpone primary meristematic activities to next crop cycles. But  
36 sustainability at plant and species level also requires an adapted strategy of propagation and  
37 reproduction, and especially a fine tuning of the assimilation and the partitioning either organic

38 (e.g. N and C derivatives) or inorganic (e.g. cations) compounds between vegetative and  
39 reproductive organs, with the management of carbon biomass playing a central role. This  
40 necessarily implies a regulation of the structure and the functioning of the shoot system  
41 development (Albani and Coupland, 2010).

42 Vegetative structure characteristics result from both primary and secondary growths through a  
43 specific spatio-temporal patterning (Costes, 2019). All stem organs result from the  
44 organogenetic activity of specific cell territories called caulinary meristems that are dedicated  
45 to cell division and morphogenesis (Greb and Lohmann, 2016). In comparison to most of  
46 perennial fruit crops, grapevine, which initially develops as a liana, presents very peculiar  
47 biological behaviors (Bugnon and Bessis, 1968). The domestication of the grapevine and  
48 especially the management of the mechanization, require specific cultivation practices to  
49 control vegetative architecture. Actually, grapevine is one of the temperate perennial fruit crops  
50 for which pruning is the most critical practice to control the quantitative and qualitative  
51 development of the vegetation and fruiting (Smart, 1995; Naor et al., 2002).

52 The structure of the shoot system results from a number of mechanisms concerning a range of  
53 plant organs, at several levels of organization, from cells to organs and from axes to branching  
54 systems (Barthelemy and Caraglio, 2007; Costes, 2019). The optimization of the shape and the  
55 functioning of the shoot system has led to a great diversity of traditional vegetative architectures  
56 (Carbonneau and Cargnello, 2003). However, canopy management systems are now rapidly  
57 evolving to facilitate the mechanisation (winter pruning, shoot positioning, chemical spraying  
58 and fruit harvest) and/or to limit pruning wounds, a source of contamination by phytophagous  
59 fungi.

60 The understanding of regulatory mechanisms of the shoot organization is essential either to  
61 optimize the use of energy resources and nutrients or to ensure some stability and sustainability  
62 of the yield, but also to decrease the dependence to phytosanitary inputs by limiting disease

63 susceptibility (Costes et al., 2013). This review presents the main biological processes that  
64 determine the vegetative architecture and its interplay with reproductive parts in grapevine,  
65 revisiting associated terminology.

66

## 67 **2. Structural and functional determinants of the shoot system structure**

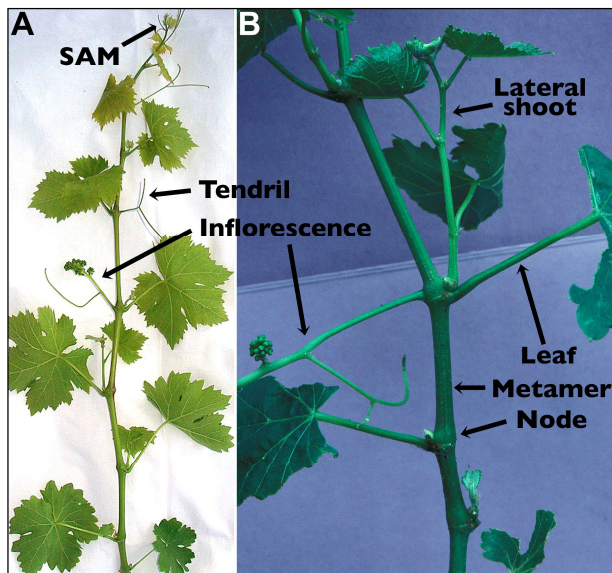
### 68 **2.1. Origin and type of vegetative meristems**

69 Except for the meristems deriving from adventive organogenesis or somatic embryogenesis  
70 (Torregrosa, 1995), all the meristems of an adult vine derive from the caulinary meristem of the  
71 zygotic embryo, called the gemmule (Bugnon and Bessis, 1968; Mullins et al., 1992). A better  
72 understanding of the complex interactions existing between hormone signals, transcriptional  
73 regulation and chromatin remodeling factors in the regulation of the activity of the vegetative  
74 meristems is progressively emerging in plants (Costes, 2019; Gaillochet and Lohmann, 2015).

75 As for other plants, grapevine zygotic caulinary meristem develops an epicotyl, which actually  
76 is the first shoot of a new genotype obtained from sexual propagation (Bernard, 1980). This  
77 first vegetative axis is composed of neformed phytomers, the minimal growth unit, that are  
78 repeated to ensure the development of the stem. In an adult plant of *V. vinifera*, a phytomer is  
79 composed of one internode (metamer) and a node (**Fig. 1**). Each node bears a leaf disposed  
80 following an alternate distichous phyllotaxis (angle of  $1/2$  at each full rotation) with the petiole  
81 base protected by two sheathing stipules. Oppositifoliated organs (tendrils or inflorescences) are  
82 distributed following a ternary frequency (see section 2.2). In *V. vinifera* ssp. *sativa*, each  
83 phytomer carries several axillary buds from which the plant will develop perennially. From this  
84 filiation, 3 essential notions arise:

85 i) The first stem meristem (gemmule), which integrates the allelic combinations from both  
86 parents, develops into diploid somatic tissues by mitosis to form all subsequent organs,  
87 including new vegetative meristems. All plants generated from axillary buds by vegetative

88 propagation (cutting or grafting) will have the same biological properties (Torregrosa et al.,  
89 2011); theoretically the lifespan of a genotype is underdeterminate;  
90 ii) Due to the structure of their caulinar meristem (Doerner, 1999; Nougarede, 2001; Torregrosa  
91 et al., 2011), higher plants vegetatively-propagated as grapevine, can accumulate different  
92 non-lethal somatic mutations in the different bud meristematic layers (L1/L2/L3 territories).  
93 If located in the initial cells of a bud meristems, this allows to establish somaclonal variants  
94 by vegetative propagation (cutting or grafting);  
95 iii) To challenge environmental fluctuations, an adult plant needs to develop a range of axillary  
96 meristems with different structures and functions.



97  
98 **Figure 1 - Structure of the *Vitis vinifera* grapevine shoot.** A) General view of a growing  
99 shoot. B) Details of the phytomer organisation.

100

101 In perennial higher plants, primary growth starts from winter buds, an organ that include  
102 protective organs and tissues to postpone growing capacities to further vegetative cycles. A  
103 bud, which is a complex structure including an apical meristem overlying several phytomer  
104 primordia is therefore considered as an embryonic shoot (van der Schoot et al., 2014). At  
105 budburst, leaf primordia expand, whereas leaves are not yet photosynthetically active and are

106 therefore dependent on the plant's reserves. In grapevine, the primary growth is not limited to  
 107 the development of preformed phytomers of the winter bud. Indeed, after budburst, shoot apical  
 108 meristems resume organogenesis adding new growing units to the preformed ones. Stem  
 109 primary growth will be determined by the resources available at plant level and the level of  
 110 competition between growing shoots. According to environmental conditions and production  
 111 targets, the practices can balance the development of the different categories of meristems to  
 112 optimize the shape and functioning of the shoot system. In the grapevine, 8 types of buds or  
 113 stem meristems can be identified, with 6 being present on an adult plant.

Meristem				Resulting
Order	Position	Function	Common name	stem name
<b>R<sub>0</sub></b>	End of the growing axe	Growth, Organogenesis, Primary anatomy	Apex, SAM (Shoot Apical Meristem)	Main shoot or cane
<b>R<sub>1</sub></b>	Axillary to R <sub>0</sub> leaf	Immediate ramification	Lateral meristem	Lateral shoot
<b>R<sub>2</sub></b>	Axillary to R <sub>1</sub> pre- leaf	Delayed ramification	Winter or latent bud	Main shoot (at the next crop cycle)
<b>R<sub>3</sub></b>	Axillary to R <sub>2</sub> scales & leaf primordia	Delayed ramification	Secondary winter or latent buds	Secondary shoots
<b>Unknown</b>	Main shoot base	Delayed ramification	Basal bud	Basal shoot
<b>Unknown</b>	Arms and Trunk	Regeneration	Old wood's bud	Sucker
<i>N/A</i>	<i>Intercotyledonary tissues</i>	<i>Growth, Organogenesis, Primary anatomy</i>	<i>Caulinary meristem</i>	<i>Epicotyl</i>
<i>N/A</i>	<i>Epidermis</i>	<i>Bud neoformation</i>	<i>Adventitious bud</i>	<i>Neoformed shoot</i>

114 R<sub>0</sub> corresponds to the primary meristem, R<sub>1</sub> axillary meristems initiated by R<sub>0</sub>, R<sub>2</sub> axillary meristems initiated by R<sub>1</sub> and R<sub>3</sub>  
 115 axillary meristems initiated by R<sub>2</sub>.

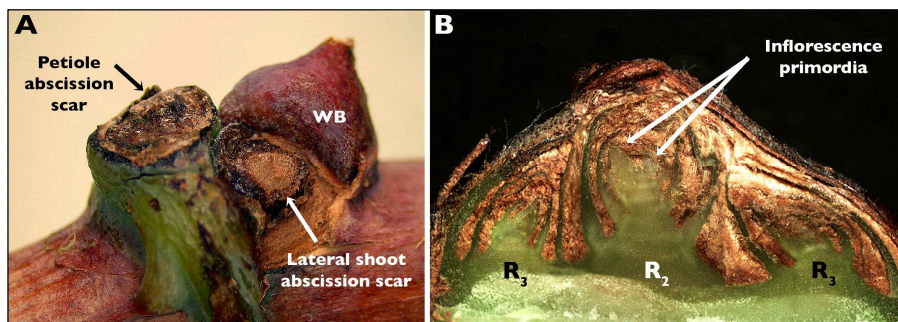
116 **Table 1 - The different types of meristems or buds of the *Vitis vinifera* grapevine.** At each  
 117 crop cycle, the ranks of the shoot apical meristem are reset to R<sub>0</sub>. In italic, caulinar meristems  
 118 that are not present on an adult plant grown in field conditions.

119

120 These meristematic structures have complementary properties to ensure the different facets of  
 121 the development of the vine and its adaptation to environmental conditions (**Table 1**):

122 **The shoot apical meristem (R<sub>0</sub>)** - This is the tip of the main growing stem. It develops all the  
123 organs of the stem including axillary meristems, and the tissues of the primary anatomy  
124 (Fournioux, 1995).

125 **The lateral shoots (R<sub>1</sub>)** - There are the first lateral meristems formed by R<sub>0</sub>, axillary to each  
126 leaf and of each node (Bugnon, 1953; Bugnon and Bessis, 1968; Deloire et al., 2020). Except  
127 in the case of excessive vigor or early shoot tipping (trimming), this axis develops only a few  
128 centimeters without lignification. At the end of the ongoing vegetative cycle, it undergoes an  
129 abscission that leaves a scar on the R<sub>0</sub> main stem (**Fig. 2A**). The phyllotaxis of R<sub>1</sub> is orthogonal  
130 to R<sub>0</sub>. In general, no attempt is made to encourage the development of lateral shoots because  
131 they degrade plant microclimate by increasing leaf density while they produce little bunches  
132 late to ripe.

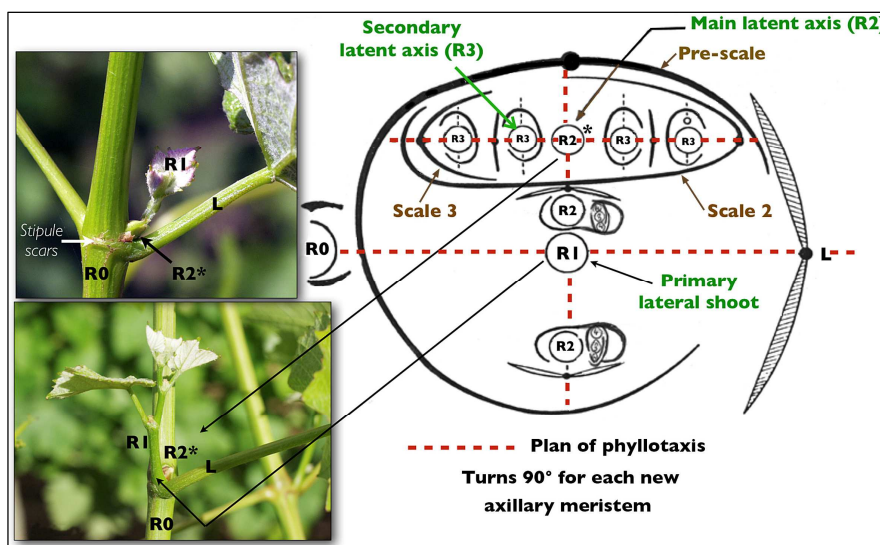


133  
134 **Figure 2 - External (A) an internal (B) views of the *Vitis vinifera* winter bud (WB).** A)  
135 Presence of the scars of the leaf petiole and of the lateral shoot at the base of the WB. B)  
136 Longitudinal section of a WB in the R<sub>2</sub> plan of phyllotaxis. At the end of the R<sub>2</sub> axis, in positions  
137 4 and 5, two primordia of inflorescences are visible; at the base of the R<sub>2</sub>, two secondary WB  
138 axes (R<sub>3</sub>) are present.

139  
140 **The winter buds (R<sub>2</sub>+R<sub>3</sub>)** - R<sub>2</sub> are the first axillary meristems formed by the lateral shoots.  
141 This meristem is initiated axillary to the first R<sub>1</sub> pre-leaf (Carolus, 1970) which form the first  
142 scale of the R<sub>2</sub> winter bud (**Fig. 2B**). This structure evolves into a complex of buds (the gemmary



143 complex). Indeed, the meristem of  $R_2$  axis will develop up to 10 preformed phytomers and also  
 144 secondary buds  $R_3$  (**Fig. 2b**). All types of vegetative (stipules, leaves, tendrils, secondary  
 145 meristems) and reproductive (inflorescences) organs can be initiated during winter bud  
 146 organogenesis but their expansion only take place at budburst when a new crop cycle starts  
 147 (Rivals, 1965). Indeed,  $R_2$  expansion and development is first inhibited by the apical dominance  
 148 of the  $R_0$  and  $R_1$  meristems, then by dormancy (see section 5). The phyllotaxis of  $R_2$  is  
 149 orthogonal to  $R_1$ , therefore parallel to  $R_0$  (**Fig. 3**).



150  
 151 **Figure 3 - Organization of the axillary meristem complex of the *Vitis vinifera* grapevine**  
 152 (adapted from Bugnon, 1953). Main shoot ( $R_0$ ), lateral shoot ( $R_1$ ), main winter bud meristem  
 153 ( $R_2$ ), secondary winter bud meristems ( $R_3$ ), leaf (L).

154  
 155 The phyllotaxis of  $R_3$  is orthogonal to  $R_2$  and  $R_0$ , allowing an easy identification at budburst by  
 156 observing the position of young leaves of the shoots arising from winter buds (Supplementary  
 157 material n°1 - **Fig. S1**). Inter-annual growth and reproductive organ production is based on the  
 158 development of successive generations of  $R_2$ . Structures  $R_3$  only develop when  $R_2$  is destroyed,  
 159 e.g. by winter or spring frost or after primary bud necrosis (Collins and Rawnsley, 2005;  
 160 Cherubino et al., 2020) or in case of excessive vigor (Champagnol, 1984).



161

162 **Supplementary material n°1 - Figure S1 - Symmetry of the phyllotaxis of the  $R_2$  and  $R_3$**   
 163 **latent axes of the winter bud of the *Vitis vinifera* grapevine.** A) The shoot from  $R_2$  develops  
 164 in the same phyllotaxis plan of the bearing axis. B) The phyllotaxis of  $R_3$  is orthogonal to the  
 165 plan of bearing axis.

166

167 **The basal buds** - They are rudimentary buds, deriving from the axillary meristems of the  $R_0$   
 168 scales, located at the junction between annual and perennial structures. These buds only develop  
 169 if the number of  $R_2$  of the main stem is too low, e.g. due to a very severe pruning, and the plant  
 170 has excess vegetative strength (see section 2.5).

171 **The old buds** - As basal buds, they are very rudimentary present beneath the bark and incapable  
 172 of fruiting. They give rise to shoots named suckers whose development cannot be controlled  
 173 nor in number or in position. Because the formation of adventitious buds has never been  
 174 observed in adult vines (Torregrosa, 1995), they are supposed to derive from previous basal  
 175 buds left after pruning, which end up being embedded in the deep tissues. whose number  
 176 decreases with the age of the vine. They have a natural regenerative potential in case of a major  
 177 vegetative accident (winter frost, mechanical trauma or pathogenes) which is used to renew the  
 178 aerial structures to limit the expansion of wood diseases.

179

## 180 **2.2. Shoot system architecture: sympod vs. monopod**

181 The fairly recent development of architectural analysis of plants (Barthelemy and Caraglio,  
182 2007) has allowed a better understanding of the endogenous processes of the shoot system  
183 organisation. The observation of the primary growth mode and its dynamics is one of the  
184 essential points to interpret aerial vegetative architecture (Vernoux et al., 2000; Barthelemy and  
185 Caraglio, 2007; Serrano-Mislata and Sablowski, 2018).

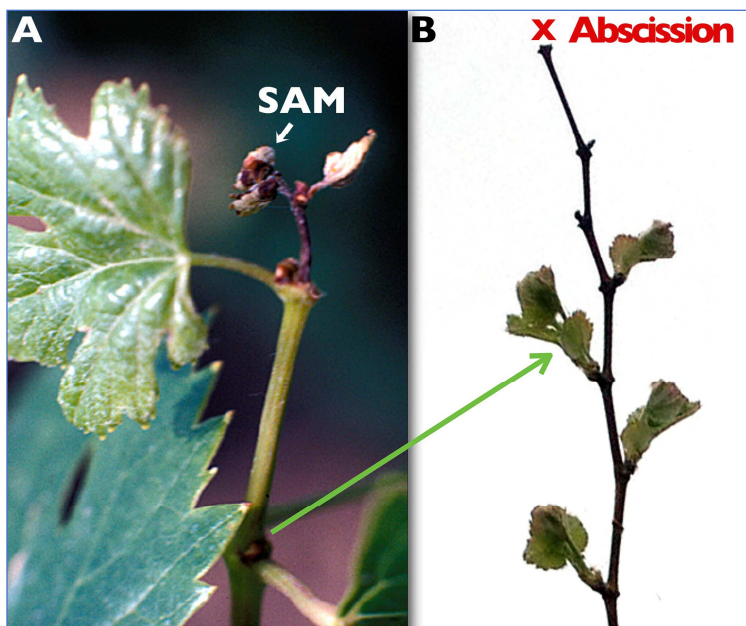
186 In higher plants, dynamics of primary growth may be continuous or rhythmic. Continuous  
187 growth is mainly observed in plants growing in tropical environments. In the absence of marked  
188 climatic variations, the main axis of some species display a continuous phyllochron  
189 (Barthelemy and Caraglio, 2007). Other models show alternating phases of extension of the  
190 main axis and growth slowing down or interruption. Whereas past growing rhythms can be  
191 visualized by the distribution of scale scars on the stems, this is not possible in grapevine due  
192 to the thickness of the secondary bark (rhytidome). In temperate climate, primary growth phases  
193 can be multiple during one season (polycyclism) or single and then corresponds to a cycle of  
194 annual growth. In some cases, the continuous growth of a species may be masked by  
195 environmental conditions that require growth to be stopped. This is the case of the grapevine,  
196 which can develop a continuous organogenesis and growth in tropical conditions, whereas, in  
197 temperate climates, growth rate is slowed down by water (summer) and/or carbon (autumn)  
198 and/or temperature (winter) deficits that eventually lead to the abscission of the portion of the  
199 axis which is not lignified.

200 On a vegetative axis continuing its development during several vegetative cycles, the position  
201 of the buds that ensure the resumption of growth defines another important descriptive element  
202 of shoot system. Indeed, in higher plants, architectural models are classified in two basic  
203 systems of organization (Bell, 1991):

204 **The sympodial model:** In this system, at the end of a growth cycle, terminal meristems of  
205 vegetative axes shift to reproductive organs or undergoes a natural abscission, interrupting the  
206 primary growth. The resumption of the growth of the main axis can only be continued by  
207 axillary buds which determine new shoot apical meristems (determinate primary growth).

208 **The monopodial model:** Here, the terminal meristem does not stop organogenesis until a  
209 terminal bud is formed at the end of a growth cycle. This terminal bud will resume the growth  
210 of the bearing axis by setting up one or more new growth units (indeterminate primary growth).

211 According to this classification, the domesticated *V. vinifera* follows the sympodial model in  
212 temperate climate. Non-hardened tips do support the maintenance of apical buds to ensure the  
213 continuity of growth from a cycle-to-cycle (**Fig. 4**). During the latent period, all buds enter in  
214 dormancy (see section 5) and the structure will remain frozen until the next growing cycle.  
215 Further development of the previous main stem  $R_0$ , will only be possible from axillary  
216 meristems. As mentioned before, as lateral branches  $R_1$  do not generally lignify,  $R_2$  winter buds  
217 of the bearing axis normally resume the growth. If  $R_2$  is damaged,  $R_3$  (and in some cases  $R_4$ )  
218 meristems can take over to establish a new  $R_0$  and continue branch development.



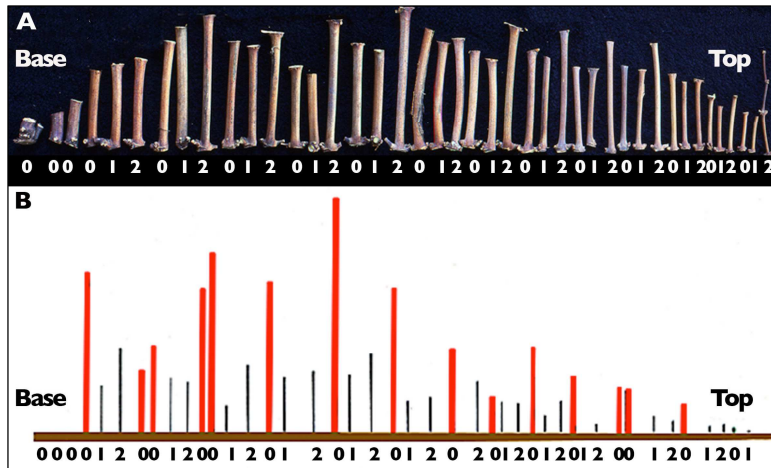
219

220 **Figure 4 - The sympodial *Vitis vinifera* grapevine model.** A) At the end of a growth cycle,  
221 phyllochron first slows down, then apex becomes necrotic and drop down. B) At the next cycle  
222 winter buds will resume the growth of the nearing axe by lateral development. SAM (Shoot  
223 Apical Meristem). X indicates the position of the abscission of the SAM when primary growth  
224 ceases.

225

### 226 **2.3. Ternary rhythm organization of the adult grapevine stem**

227 During primary growth, the length of the phytomers is not constant. After first short phytomers  
228 (Assaf, 1966), metamers increase in length before gradually shorten until shoot tip (**Fig. 5A**).  
229 The 3 to 5 first phytomers of the proximal section of the main shoot (also called proleptic shoot,  
230 see section 2.5) are composed of rudimentary phytomers with imperfect leaves and no  
231 oppositifoliated organs. Then, the morphology and structure of the phytomers follows a ternary  
232 rhythm (Zimmermann, 1954; Bouard, 1966): i.e. the repetitive succession of 3 types of  
233 phytomers. A first phytomer ( $P_0$ ), terminated by a node without oppositifoliated organs ( $N_0$ ), is  
234 followed by 2 phytomers  $P_1$  and  $P_2$ , bearing oppositifoliated organs. This structural rhythm  
235 ( $P_0/P_1/P_2$ )<sup>n</sup> also impacts on internode lengths, leaf area and lateral shoots (also called sylleptic  
236 shoots, see section 2.5) lengths (Bouard, 1966; Carbonneau, 1976; Louarn, 2005). In general,  
237 within a series of 3 successive phytomers, the length of metamer of  $P_1$  is often the shortest and  
238 that of  $P_2$  the longest (**Fig. 5A**), the lateral shots carried by the  $P_0$  nodes is regularly the longest  
239 (**Fig. 5B**). This ternary regularity of the phytomer morphology is also observed in most other  
240 *Vitis* species (Bernard, 1980).



241

242 **Figure 5 - Ternary rhythmic organization of the phytomers (P<sub>0</sub>-P<sub>1</sub>-P<sub>2</sub>) of the *Vitis vinifera***

243 **grapevine.** A) The distribution of the phytomer length from the base to the top of a stem of the

244 variety Carignan after growth arrest, showing a maximum metamer length in medial sector of

245 the vegetative axis, with locally, P<sub>2</sub> phytometer to be the longest. B) The distribution of the

246 lateral shoot length on a vigorous main stem of the variety Ugni Blanc, showing that branches

247 from P<sub>0</sub> phytomers are regularly the longest (adapted from Bouard, 1966).

248

#### 249 **2.4. Origin of the ternary rhythm and the three leaf helices**

250 At juvenile stage (seedling), the stem meristem, which does not form oppositifoliated organs

251 and has only one territory of vegetative organ differentiation, displays leaves following a single

252 helix according to an alternate spiral model of phyllotaxis (foliar angle of 2/5). In adult vines,

253 the apical meristem, which can develop oppositifoliated organs (tendrils or inflorescences), has

254 three distinct territories of vegetative organ differentiation, display leaves arranged according

255 to an alternate distichous model of phyllotaxis (foliar angle of 1/2). Oppositifoliated organs are

256 distributed along three leaf helices resulting in the previously described ternary rhythm of

257 organogenesis. However, under extreme growth intensity, in tropical climates for instance, this

258 structure is disturbed due to a position shift of the leaf and the tendril or bunch (Supplementary

259 material n<sup>o</sup>2 - **Fig. S2**), revealing the reality of the construction of the shoot architecture in 3

260 different leaf helices (Carbonneau, 2010). Within the stem secondary anatomy, vascular  
261 structures are established according to 2 orthostics dividing the stem into 2 halves that remains  
262 relatively independent (Fournioux and Bessis, 1979). This vascular organisation facilitates the  
263 conduction of the sap over long distances, which corresponds to a common botanical behavior  
264 within liana species in comparison to trees (Zimmermann and Milburn, 1982; Cruiziat et al.,  
265 2002).



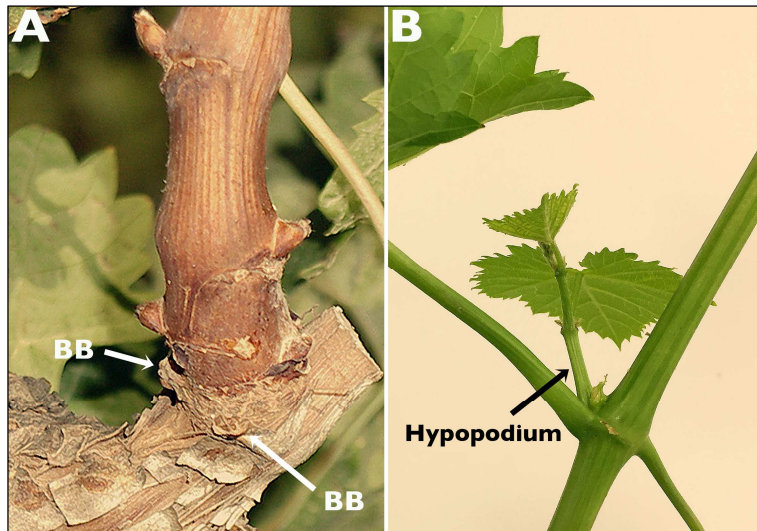
266  
267 **Supplementary material n°2 - Figure S2 - Anomalies of the ternary cycle.** Vigorous *Vitis*  
268 *vinifera* grapevine plants growing in a tropical context (Northeastern of Brazil). A shift of the  
269 position of the inflorescence which is no longer oppositifoliated on the node is observable.  
270 White arrow shows the normal position of a bunch on the main shoot, red arrow the current  
271 insertion.

272

### 273 **2.5. Nature of vegetative axes: Syllepsis vs. Prolepsis**

274 For fruit perennials, the branching along the main axis is of great importance for rapidly  
275 expanding the colonization of the environment and increasing light interception capacities. The  
276 branching is dependent on the differentiation of axillary meristems (see section 2.1). The  
277 development of secondary axes concomitantly with the main axis growth gives rise to branches  
278 called sylleptic (Hallé et al., 1978; Barthelemy and Caraglio, 2007) or immediate (Champagnat,

279 1954) shoots. In grapevine, lateral shoots initiated from  $R_1$  meristems are typical illustrations  
280 of this type of branches (**Fig. 1, Fig. 6**). However, the most frequently used branching system  
281 in cultivated grapevines is developed from axillary meristem ( $R_2$ ) of the winter buds (**Fig. 2**).  
282 These axes are known as proleptic or delayed branches because primary growth requires to be  
283 stopped before it can be developed.



284  
285 **Figure 6 - External view of proleptic and sylleptic axes' base of the *Vitis vinifera* grapevine.**

286 A) A proleptic axis displaying phyllotaxis parallel to the bearing spur with the first phytomers  
287 been very short. The base present scales scars and several rudimentary basal buds (BB). B) A  
288 sylleptic shoot displaying phyllotaxis orthogonal to the bearing stem and a long hypopodium.

289  
290 A number of morphological features differentiate sylleptic from proleptic shoots (**Table 2**). The  
291 most obvious appear at the base of the axes. In proleptic shoots, first phytomers emerging at  
292 budburst and located in the proximal section are very short (**Fig. 5a**) with rudimentary caulinary  
293 organs (Bernard, 1980). Conversely, sylleptic shoots which develop at the same time with the  
294 bearing phytomer, present a first long basal internode (hypopodium) and develop perfect  
295 caulinary organs in their proximal sections. Also, while the junction between  $R_2$  axes and  
296 previous structures shows scale scars and basal buds, the connection between  $R_1$  and  $R_0$  is clear  
297 without any basal buds and scale scars (**Fig. 6**).



Characteristics	Type of shoot	
	Proleptic	Sylleptic
<b>Common name</b>	Main shoot (R <sub>0</sub> )	Lateral shoot (R <sub>1</sub> )
<b>Bearing axe</b>	Cane or trunk	Shoot
<b>Meristematic origin</b>	R <sub>2,3,4</sub> winter buds	R <sub>1</sub> axillary meristem
<b>Pre-formed phytomers</b>	Yes (3-12)	No, only neoformation
<b>Delayed development</b>	Yes (next cycle min)	No
<b>Scale scars</b>	Yes	No
<b>Length of first internodes</b>	Shorts	Regular (long hypopodium)
<b>Status of basal organs</b>	Absent or rudimentary	Regular
<b>Phyllotaxis/bearing axe</b>	180° / previous R <sub>0</sub>	90° / previous R <sub>0</sub>
<b>Growth/bearing axe</b>	Similar	Lower (if SAM maintained)
<b>Lignification</b>	Systematic	Depending of available vigor
<b>Function</b>	Delay growth and fruit development to next cycle	Restart growth if SAM removed Increase biomass if extra resources

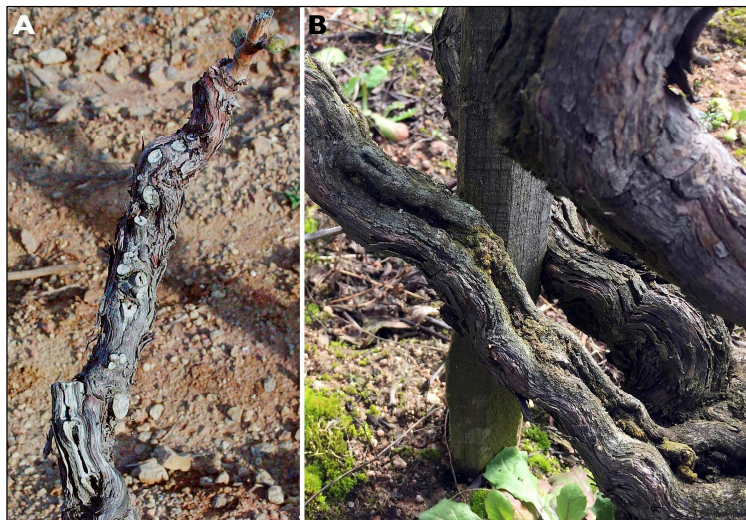
299 **Table 2** - Main morpho-functional properties of proleptic and sylleptic shoots of the *Vitis*  
300 *vinifera*.

301

302 The morphological differences between proleptic and sylleptic shoots have two main  
303 consequences in the implementation of winter pruning. The first concerns the management of  
304 basal buds. Indeed, the pruning of proleptic has to be done very close to the wheelbase to avoid  
305 a transfer of growth to basal buds which have a limited fruiting capacity and are not well  
306 vascularly connected to the plant. This induces wounding close perennial structures leading to  
307 the development of deep necrosis in the arms and the trunks, increasing the susceptibility to  
308 fungus wood diseases (Gramaje et al., 2018). In the case of a sylleptic shoots, as there are no  
309 basal buds at the junction point with previous axes, the pruning can be done at some distance  
310 from the base anywhere within the hypopodium.

311

312 The second consequence concerns the management of the vascular tissue architecture. As  
313 mentioned above, internal anatomy of the grapevine stem follow a dorsiventral symmetry  
314 (Fournioux and Bessis, 1979). Winter buds of the main axes are systematically preferred to  
315 those of sylleptic axes, as the lineage of successive R<sub>2</sub> meristems follows the same plan of  
316 phyllotaxis. This has two interests: i) to maintain optimized vascular continuity between stems  
317 of different ages limiting the complexity of the sap pathways and ii) to localize pruning wounds  
318 and resulting wood necrosis in same phyllotaxis plan (Supplementary material n°3 - **Fig. S3**).  
319 But the non-respect of this rule is not fatal as grapevine has a good capacity to bypass the sap  
320 circuits damaged by pruning wounds (Zhang and Carbonneau, 1987).



321  
322 **Supplementary material n°3 - Figure S3 - Distribution of pruning wounds on old *Vitis***  
323 ***vinifera* grapevine plants.** A) Position of the pruning wounds following the same phyllotaxis  
324 over several years. B) In very old vines, pruning wounds may coalesce to form fairly deep  
325 necrosis without preventing the dorso-ventral vascular continuity.

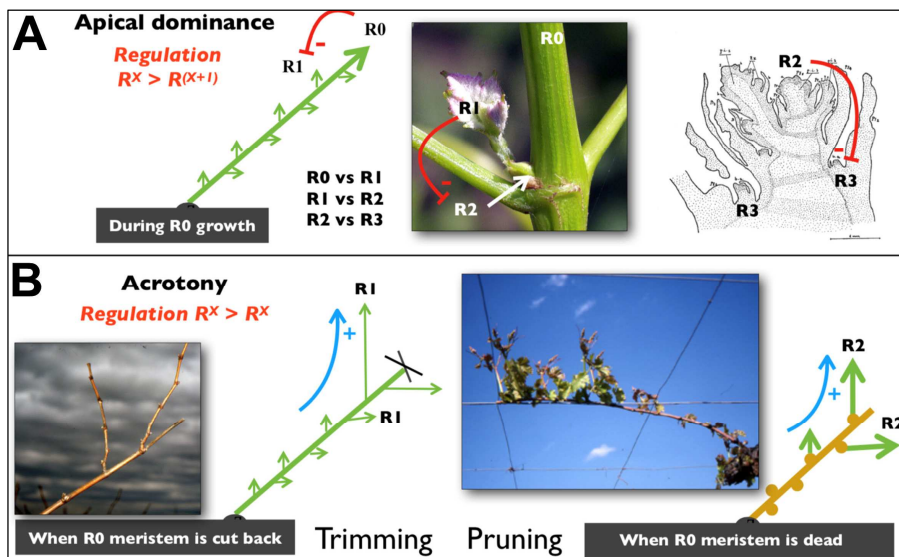
326

## 327 **2.6. Priority of shoot development: Apical dominance vs. acrotony**

328 The growth of vegetative meristems (main and lateral shoots, winter buds) are subjected to two  
329 main rules of prioritization, i.e. apical dominance and acrotony (Fournioux and Bessis, 1990;

330 Fournioux, 1995). These two mechanisms are often confused in grapevine literature as both  
 331 support axis extension vs. branching.

332 The apical dominance arbitrates the distribution of the development, during the growth,  
 333 between a shoot apical meristem (SAM) and axillary meristems it initiated (Cline, 2000). In  
 334 grapevine, apical dominance occurs at two scales: i) at stem level, the SAM ( $R_0$ ) inhibits the  
 335 development of sylleptic shoots ( $R_1$ ) which always remains shorter than the bearing axis, ii) at  
 336 phytomer level, the meristem of the lateral shoot ( $R_1$ ) inhibits the growth of winter buds  $R_2$  axes  
 337 (Fig. 7A). Thus, during stem growth, the SAM has priority over the lateral shoots, which  
 338 themselves prevent the development of winter buds. Similarly, within the winter bud, the main  
 339 axis ( $R_2$ ) has priority over the secondary latent axes ( $R_3$ ).

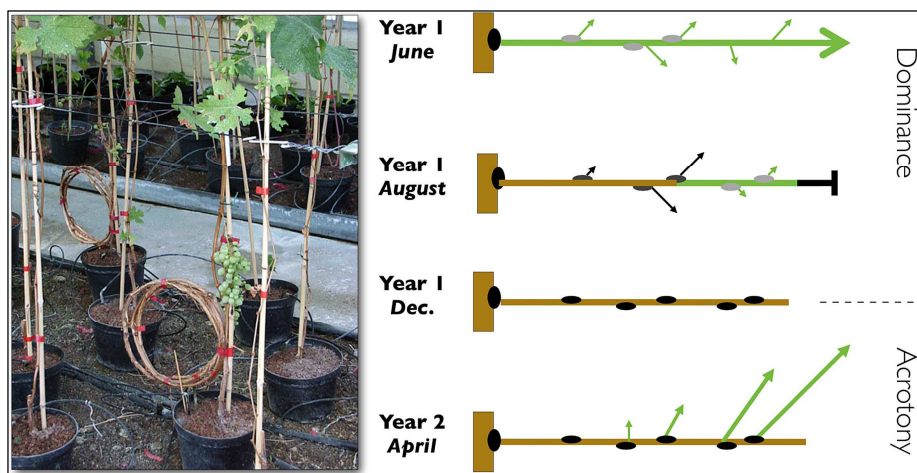


340  
 341 **Figure 7 - Diagram of the combined effects of apical dominance, acrotony and vigor on**  
 342 **vegetative development of the *Vitis vinifera* grapevine.** A) During the season, the apical  
 343 dominance prioritizes the growth according to the rank of the meristems with the gradient  
 344  $R_0 > R_1 > R_2$ . B) The acrotony and the bearing shoot vigor favour the distal meristems when  
 345 growth resumes: on the left, during the vegetation cycle for the sylleptic shoots ( $R_1$ ) after apex  
 346 ( $R_0$ ) removal; on the right, at the next vegetative cycle, after winter buds ( $R_2$ ) budburst  
 347 establishing new proleptic axes.

348

349 The acrotony determines the distribution of the branching when growth resumes. In higher  
350 plants, this rule is declined in 3 behaviors: i) Acrotony, *sensu stricto*, when the priority in  
351 branching is given to the shoot distal zone, ii) mesotony, when branching preferably merges  
352 from the shoot medial zone, and iii) basitony when the branching is more intense in the shoot  
353 proximal zone. Grapevine model exhibits a strong acrotony that acts in 2 forms (**Fig. 7B**): i)  
354 when the SAM is removed by trimming during the season, lateral shoots ( $R_1$ ) develop in priority  
355 in the distal region close to the cut end of the main shoot, ii) at bud budburst after a rest period,  
356 distal winter buds ( $R_2$ ) develop first exhibiting a higher vigor than basal winter buds.

357 In the grapevine, the combination of apical dominance and acrotony (**Fig. 8**) associated with  
358 the expression of vegetative vigor explains the general pattern of branching. During the  
359 vegetative cycle, without apex trimming, grapevine develops long shoots with short lateral  
360 sylleptic branches ( $R_1$ ). When SAM is trimmed, growth potential is immediately transferred to  
361 lateral shoots ( $R_1$ ) in the distal part of the main stem to continue the elongation. Due to apical  
362 dominance and mechanisms of nutritional competition exerted by the growing shoots (Renton  
363 et al., 2012; Mason et al., 2014), anticipated budburst of winter buds ( $R_2$ ) is inhibited (He et al.,  
364 2012; Beauvieux et al., 2018, Fadon et al., 2020). Leaves adjacent to axillary buds also have an  
365 effect on the maintenance of winter bud rest (He et al., 2012). The regulation of axillary bud  
366 dormancy (see section 5) intensity at the topological level on the main axis partly determines  
367 the intensity of acrotony expression, which varies over time. Winter buds are first maintained  
368 latent until the end of summer by correlative inhibitions.



369

370 **Figure 8** - Combination over 2 growth cycles of apical dominance, acrotony and correlative  
 371 inhibitions, that condition the primary growth and branching of the *Vitis vinifera* grapevine  
 372 stem.

373

374 Later, during the season, correlative controls are progressively replaced by unfavorable plant  
 375 growth regulators' balance. Then, growth is no longer possible, even after pruning of the main  
 376 axis or secondary shoots. During winter, the vegetative architecture stay frozen due to physical  
 377 factors (temperature, water availability) until dormancy break and environmental conditions to  
 378 become favorable to growth. At the next growing cycle, new proleptic axes are formed from  
 379 the distal winter buds of the pruned branches. Despite its general organisation as a sympodial  
 380 model, apical dominance and acrotony both cooperate to privilege primary stem elongation  
 381 avoiding excessive branching. Viticulture practices need to consider these rules to control the  
 382 vegetative architecture and avoid excessive vegetative developments (Supplementary material  
 383 n°4 - **Fig. S4**). In winter, the reduction of the length of bearing axes by pruning and the  
 384 modification of correlative inhibitions between winter buds by cane arching, are both practices  
 385 to limit acrotony effects (**Fig. 9**). During the season, shoot positioning which is implemented to  
 386 delay SAM trimming aim prolonging apical dominance to inhibit lateral branching.



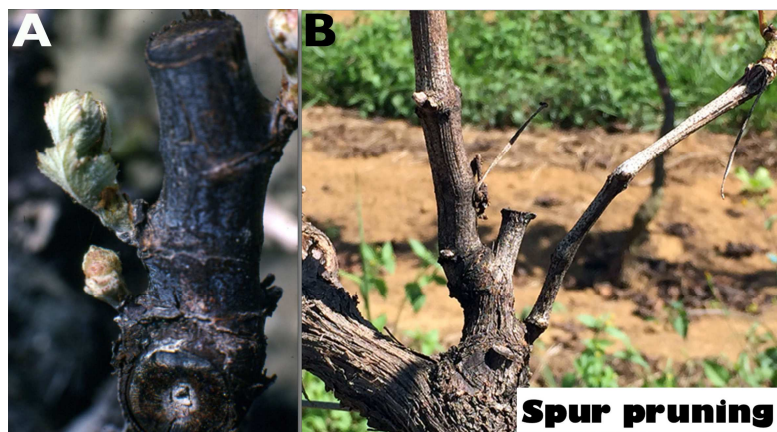
387

388 **Supplementary material n°4 - Figure S4 - Trunk extension of a very old *Vitis vinifera***

389 **grapevine plant managed through spur pruning in the South of France.** Despite a constant

390 control of the acrotony by spur pruning the perennial structures elongate.

391



392

393 **Figure 9 - Effect of acrotony on axes spur-pruned of the *Vitis vinifera* grapevine.** A) In a

394 temperate climate (Montpellier, France), shoots from winter buds ranked 2 and 3 are more early

395 in bursting than the winter bud from the base. B) In a sub-tropical altitude climate (Pocos de

396 Caldas, Minas Gerais, Brazil), at the end of the vegetative cycle, the proleptic axis from winter

397 bud ranked 2 is more developed than the one developed from rank 1.

398

## 399 **2.7. Other parameters impacting the vegetative structure**

### 400 **2.7.1. Morphological factors**

401 Several morphological factors modulate the shoot system shape: the length and the diameter of  
402 the metamers, the proportion of secondary tissues and the precocity and intensity of the  
403 lignification. The primary anatomical structure (Bernard, 1980) which doesn't include strong  
404 supporting tissues, includes massive collenchyma bundles in the cortex and small pericyclic  
405 fiber patches in the central cylinder. This anatomical arrangement (Swanepoel et al., 1984)  
406 allows a great flexibility of the apices, whose direction of growth is very plastic. As for other  
407 liana species, grapevine SAM directional growth is strongly dependent on gravitropism with  
408 interactions with thigmotropism (mechanosensory movement responses) and phototropism  
409 (Trevisan-Scorlas and Dornelas, 2011).

410 As other perennial plants, the grapevine develops secondary tissues by successively  
411 differentiating vascular (VC) and subero-pellodermic (SPC) cambiums, the last been also called  
412 phellogen or cork cambium (Bernard, 1980). Located in the deepest layers of the cortex and  
413 developing poorly lignified cells (Pratt, 1974), the grapevine SPC plays a modest role in shoot  
414 architecture. On the other hand, VC, totally reconfigures the internal anatomy of the grapevine.  
415 VC produce several kinds of secondary tissues, in particular secondary xylem which will  
416 progressively become the main tissue of the stem (Fournioux, 1995). While the stem primary  
417 anatomy is rich in water and has little mechanical resistance to lateral deformations, secondary  
418 tissues gradually becomes rigid due to lignification (Bouard, 1966). In grapevine, there is some  
419 diversity in the length of the phytomers (Huglin, 1958) and in diameter of the metamers (Galet,  
420 1990). Variability has also been mentioned for the ratio between supporting tissues and vascular  
421 and filling parenchyma, especially the balance between the pith and secondary xylem, which  
422 potentially influences the rigidity of the vegetative axes. Combined, all these factors play on

423 the shape of the shoots of scion and rootstock varieties, which varies from erect to curved forms  
424 (Galet, 1990).

### 425 **2.7.2. Environmental factors**

426 The amount of resources available for each vegetative point strongly influences the architecture  
427 of the stems. This is due to 2 main effects: the variation of the length of the main axes and the  
428 intensity of the branching.

429 As the final number of phytomers is not pre-determined in winter buds, after budburst, an  
430 indefinite number of neo-formed growing units can be added by the R<sub>2</sub> SAM to proleptic axes.  
431 Under temperate climates, the number of pre-formed and neoformed are generally balanced  
432 (Bernard, 1975) with a maximum of metamer length in the medial zone of the stem (Assaf,  
433 1966). However, in vigorous situations, the number and size of phytometers can increase  
434 dramatically. The simple variation in the number of buds maintained after pruning (bud load)  
435 can modulates stem fresh biomasses by a factor of 5 (Freeman et al., 1979) with consequences  
436 on the mechanical constraints that apply to vegetative axes. Thus, a variety known to display  
437 regular upright-bearing shoots may present a lying down vegetation shape in highly vigorous  
438 situations.

439 Sylleptic branching is first related to the influence of apical dominance on the development of  
440 lateral shoots (R<sub>1</sub>). In the absence of SAM trimming, in non-vigorous situations, the greatest  
441 intensity for sylleptic branching is found in the medial sector of the bearing axis. This region is  
442 also the one where metamer growth is more intense, as observed in various perennial plants  
443 (Assaf, 1966; Génard et al., 1994; Costes et al., 2006). In grapevine, lateral shoots which are  
444 poorly developed (<20cm) generally do not lignify. However, if extra resources are available  
445 and/or the apical dominance is early suppressed, lateral shoots can develop to display same  
446 types of caulinary organs as proleptic axes, including reproductive structures (see section 4),  
447 and finally lignify becoming perennial (**Fig. 10**).





448

449 **Figure 10 - Intensity of sylleptic branching of the *Vitis vinifera* grapevine.** A) In the absence  
 450 of SAM tipping and in non-vigorous situation, a moderate development of sylleptic shoots in  
 451 the medial zone of the bearing axis. B) Lignification and fructification of the lateral shoots in a  
 452 vigorous situation.

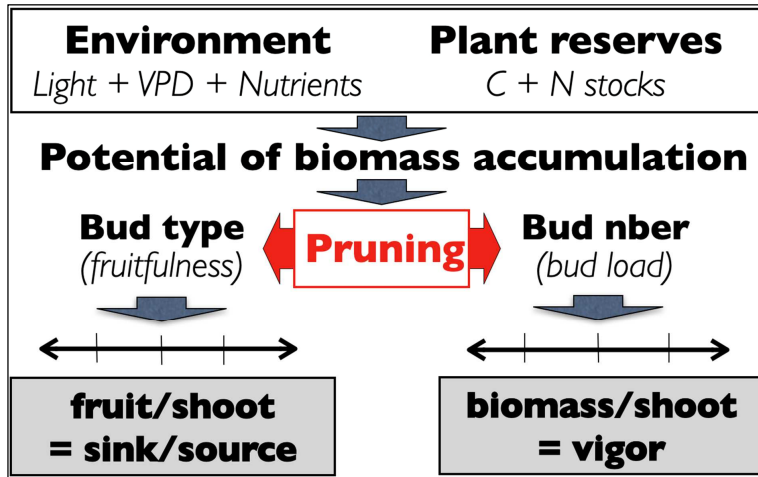
453

454 Moreover, intra-shoot trophic competition can modify lateral shoot development (Pallas et al.  
 455 2008). While, phytomer production on the primary axis and the probability and timing of  
 456 proleptic axes is not affected by trophic competition, the development duration and phyllochron  
 457 of sylleptic shoots are locally reduced by the presence of bunches on fertile phytomers.  
 458 Environmental factors, such as climatic accidents, can also modify the vegetative architecture:  
 459 e.g. destroying  $R_2$  within winter buds winter frosts can increase bushing, causing a range of  
 460 mechanical trauma, hail or lightning can dramatically modify the initial organizational pattern  
 461 of the vegetative architecture (Branas, 1974).

### 462 **2.7.3. Cultivation practices: plant biomass strength vs. shoot vigor**

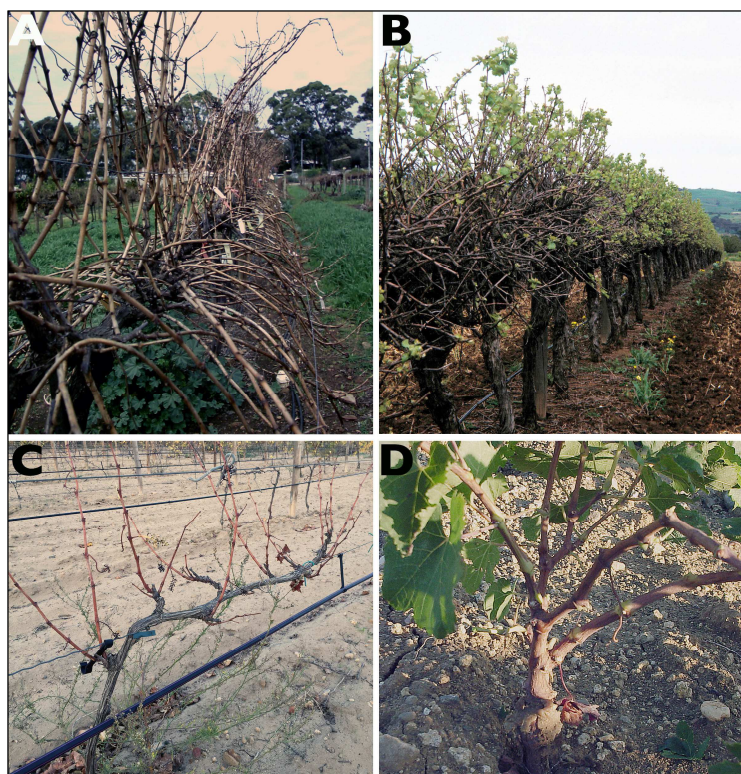
463 All practices influencing the potential of biomass accumulation can modify the vegetative  
 464 architecture of the *V. vinifera* grapevine (Branas, 1975; Champagnol, 1984; Keller M, 2020;  
 465 Carbonneau et al., 2020). Nevertheless, winter pruning is probably the most powerful tool to  
 466 modify the vigor of grapevine vegetative axes, in particular as a result of effect on plant  
 467 source/sink balance. Indeed, bud load directly regulate the level of the trophic competition  
 468 between proleptic axes: vigor is an inverse function of the number of bud maintained at pruning  
 469 (Freeman et al., 1979). Another important aspect is in relation to the type of buds selected

470 (Huglin, 1958). As the potential of fruitfulness of winter buds varies with their position along  
 471 bearing axes (see section 4.1), the quantity of fruit per vegetative axis is dependent of the type  
 472 of buds maintained at pruning (**Fig. 11**).



473  
 474 **Figure 11 - Main factors to regulate plant biomass strength and shoot vigor of the *Vitis***  
 475 ***vinifera* grapevine.**

476  
 477 Plant biomass strength and shoot vigor are two quantifiable important parameters used for  
 478 grapevine growing management. Dry matter content of lignified shoots is rather constant, i.e.  
 479 50% (Pouget, 1963; Bouard, 1966) and variations between annual and perennial compartments  
 480 are well correlated in a specific condition (Hunter, 1998). Then the plant biomass strength can  
 481 be estimated from the annual biomass accumulated in pruning wood and in the harvest. In  
 482 viticulture, it is common to estimate the source/sink balance using the Ravaz's index (1903) that  
 483 corresponds to fresh pruning wood/yield ratio, both expressed in kg per plant (Carbonneau and  
 484 Deloire, 2020). The vigor of a shoot vigor can be assessed by measuring primary growth rate  
 485 or lateral shoot branching during the season and also by dimensional parameters at the end of  
 486 the cycle (lignified stem fresh or dry weight and length, metamer diameter). Plant biomass  
 487 strength and shoot vigor are parameters that can be modulated independently, leading to 4  
 488 possible extreme configurations in grapevine (**Fig. 12**).



489

490 **Figure 12 - The 4 extreme cases of the ratio plant biomass strength/shoot vigor of the *Vitis***

491 ***vinifera* grapevine:** A) A powerful vine managed by hand pruning, displaying vigorous shoots.

492 B) A powerful vine managed through minimal pruning with little vigorous shoots. C) A weak

493 hand pruned vine with weak shoots. D) A young vine, with a low total biomass strength

494 displaying very vigorous shoots.

495

#### 496 **2.7.4. Biotic factors**

497 In a vineyard, various types of organisms can modulate the plant biomass strength and/or shoot

498 vigor through direct or indirect effects. For example, the presence of weeds or cover grass

499 impact on nutrient and water supply (Celette and Gary, 2013) with significant effects on

500 development of the vines (Carbonneau et al., 2020; Morlat et al., 1993). The same with a range

501 of pests and diseases that influence the assimilation of carbon or mineral resources. For

502 example, leaf fungal diseases (e.g. downy or powdery mildew) reduce the quantity of the

503 biomass assimilated by limiting the performance of carbon assimilation. Soil-borne rots also

504 can reduce growth of the vines until a significant decline by affecting the development or the  
505 functioning of the root system (Branas, 1974; Galet, 1977; Wilcox et al., 2006).  
506 Many pathogens have direct non-specific effects on the vegetative architecture of the grapevine.  
507 For example, fungi such as anthracnosis (*Gleosporium ampelophagum*) or phomopsis  
508 (*Phomopsis viticola*) or bacterial diseases such as *Agrobacterium* sp. or *Xylophilus ampelinus*  
509 can cause local shoot necrosis with some impact on the vegetative architecture. Some pathogens  
510 cause very specific modification of the shoot morphology: e.g. the Grapevine Fanleaf Virus  
511 (GFIV) which shortens internodes and deregulates apical dominance, Eutypiosis which  
512 miniaturizes all caulinary organs, Yellows (Phytoplasma) or Pierce's disease (*Xylella*  
513 *fastidiosa*) which limit the lignification of the stem accentuating shoot curving (Galet, 1977;  
514 Wilcox et al., 2006).

515

### 516 **3. Inter-annual plant development**

#### 517 **3.1. In the wild context**

518 The non-domesticated *Vitis vinifera* spp. *silvestris* covers the perimeters of the Mediterranean  
519 basin and the Middle East, occupying large forest areas (Zohary and Spiegel-Roy, 1975). The  
520 domestication of the *V. vinifera* grapevine is thought to have taken place in Transcaucasia, at  
521 the intersection of the Lesser Caucasus region and the northern curve of the fertile crescent. It  
522 can be hypothesized that, after picking grapes from wild grapevines, humans started to cultivate  
523 vines, initially without modifying the vegetative architecture. During this period, grapevine  
524 plants were probably present in 'Neolithic gardens' comparable to the Indian orchards  
525 discovered in North America (Carbonneau, 1997). The first step of viticulture was probably  
526 based on the selection of the best fruit-bearing individuals from spontaneous crossbreeding:  
527 selection of hermaphroditic, fertile vines with larger bunches and berries. Thus, the wild vine  
528 evolved from a state of liana (Supplementary material n°5 - **Fig. S5**) where the reproductive

529 apparatus is present only as a help for the survival of the species (dioecious vine with a large  
530 predominance of males) to a domesticated liana where the fruits became an increasing  
531 physiological sink. Another important step of the domestication was the pruning which was  
532 implemented to get bigger grapes and to stabilize the yield. This viticultural know-how remains  
533 in perpetual evolution (Carbonneau, 2002), the most recent technical improvement being a  
534 return to the wild form with "minimal pruning" or "no pruning" approaches (Carbonneau et al.,  
535 2003).



536

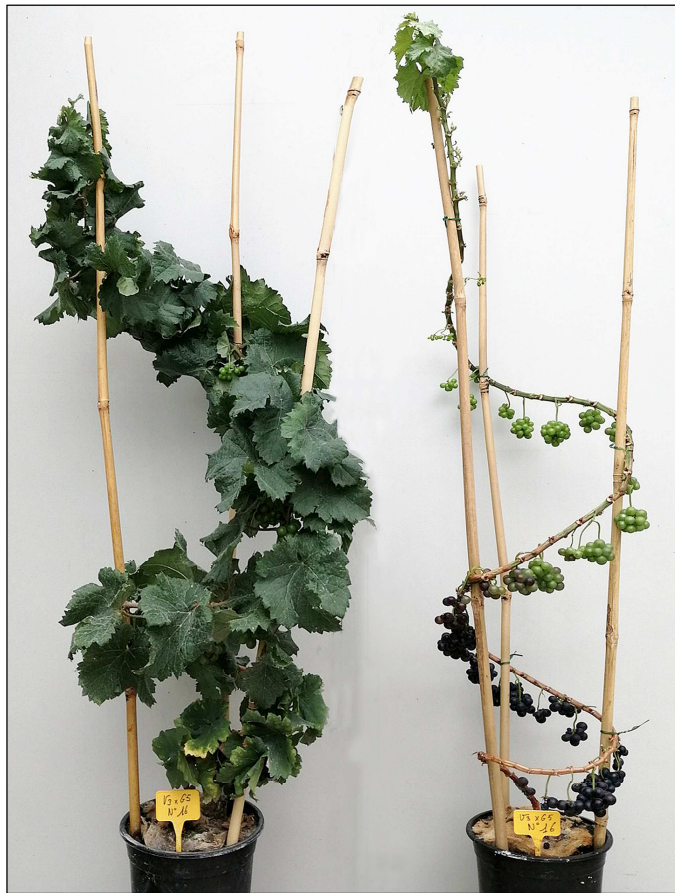
537 **Supplementary material n°5 - Figure S5 - Monumental wild *Vitis vinifera* ssp. *sylvestris***  
538 **grapevine plant near the ancient Lycian site of Kaunos** (near Antalya on the south coast of  
539 Turkey). In the creek, the vegetation covers various shrubs and multiple trunks climb to a pine  
540 tree. With a minimum of 400 m of perennial structure, the biomass strength of this vine is  
541 exceptional.

542

543 **3.2. In cultivated systems**

544 Grapevine is one of the perennial fruit crop for which the "reformatting" operation of pruning  
545 is the more critical. Indeed, winter pruning will decrease bud load to 10-20 buds per plant,  
546 whereas a grapevine use to develop more than 100 new winter buds a year in standard  
547 conditions. Pruning is performed manually or mechanically (i.e. precision and minimal  
548 pruning) to limit the effects of acrotony and to balance the growing potential between winter  
549 buds. Winter pruning is often complemented with green operations with some of which (shoot  
550 positioning, SAM trimming) that modulate apical dominance to reduce the intensity of  
551 secondary branching (Smart and Robinson, 1991; Wolf et al., 1986; Poni et al., 2014). Winter  
552 pruning and green operations generally rely on a mechanical supporting system (trellising) to  
553 manage vegetative growth (Carbonneau and Cargnello, 2003) and facilitate the mechanization.  
554 The recent development of the minimal pruning training system highlighted the capacity of  
555 self-regulation of the grapevine (Carbonneau et al., 2020). The vine develops naturally as a  
556 bush hanging from tree branches or from the ground, with branches of increasingly higher order  
557 with age. When pruned in minimal pruning, vines respond to the bud overload by adjusting  
558 throughout the vegetative cycle at the level of the whole plant, vegetative growth and yield to  
559 available resources. This phenomenon is called self-regulation, as opposed to the situation of  
560 the pruned vine where farmers tends to impose a specific balance between vegetative and  
561 reproductive organs. Self-regulation consists, in chronological order of: i) reducing budburst  
562 rate by reinforcing acrotony, decreasing shoot vigor then winter bud fertility, ii) reducing fruit  
563 set and size, and finally iii) delaying ripening period (Zheng et al., 2016). Despite the limitation  
564 of individual shoot fruitfulness, grapevines managed in minimal pruning tend to be more  
565 productive (around + 30%) because of the increased number of developing shoots. This relative  
566 overproduction is not detrimental in the face of a risk of exhaustion because vine regulates itself  
567 to ensure its sustainability. Finally, it should be noted that unpruned vines present less wood

568 diseases (Travadon et al., 2016) in relation to the limitation of the wounds caused to perennial  
569 vegetative structures.



570  
571 **Figure 13 - Plants of the *Vitis vinifera* microvine line V3xG5, carrying the *Vvgai1* mutation**  
572 **(Torregrosa et al., 2019) and the *MrRpv1/Run1* (Feecham et al., 2013) loci both being at**  
573 **heterozygous status.** The plant on the right was manually defoliated to facilitate the  
574 visualization of the distribution of the reproductive organs.

575

#### 576 **4. Number and position of the fruits**

577 Most of the reports about grapevine fruiting wrongly specify that the reproductive cycle  
578 requires two successive vegetative cycles to be completed. This assertion is not true as, during  
579 a single of growing cycle, lateral shoots, which are strictly neoformed sylleptic structures, are  
580 fully able to display inflorescences and fruits (Olivain and Bessis, 1987). Moreover, somaclonal  
581 variants of *V. vinifera* carrying the *Vvgai1* mutation and their derivatives (**Fig. 13**) which

582 produce a non-functional form of the DELLA GAI1 protein (Torregrosa et al., 2019), display a  
583 dwarf phenotype with a continuous conversion of the tendrils into inflorescences (Boss and  
584 Thomas, 2001; Chaib et al., 2010; Pellegrino et al., 2019). Finally, it was shown that the  
585 application of CCC (Chloroformequat Chloride) allows the conversion of newly formed tendrils  
586 into inflorescences (Coombe, 1967). Therefore, the assertion that the grapevine reproductive  
587 cycle lasts 2 years only applies to proleptic axes developed under temperate climates.

#### 588 **4.1. Fructification of proleptic axes**

589 The dynamics of inflorescence primordia differentiation in winter buds have been described  
590 many times in detail (Pratt, 1971, Srinivasan & Mullins, 1981; Cheema et al. 1996, Li-Mallet,  
591 2016). The position of inflorescences on the main axis is directly determined by the ontogeny  
592 of winter buds during their development. In general, bunches are carried on the 4-6<sup>th</sup> phytomers  
593 from the stem base, i.e. in the pre-formed section of proleptic shoots (Carolus, 1970, Cheema  
594 et al., 1996). The pattern of inflorescences disposition corresponds to a complete cycle of  
595 oppositifoliated organs (Bouard, 1971; 1987). The number and the size of the clusters are also  
596 dependant on environmental conditions at bud burst up to flowering time (Pouget, 1981;  
597 Guilpart et al., 2014).

598 During the primary growth of the main shoot, once a tendril has been formed, no more  
599 reproductive organs can be differentiated by higher ranked phytomers. This is true for the wild  
600 and domesticated genotypes, except for *Vvgail* mutants (microvines and derivatives) which  
601 display a continuous flowering behavior regardless of the position and type of axes (Pellegrino  
602 et al., 2019).

603 In the non-dwarf genotypes, the potential of fruitfulness, i.e. the number and size of  
604 inflorescences primordia, of proleptic axes vary according to their position along bearing axes.  
605 In the *V. vinifera* grapevine, under temperate climate, the number of bunches per R<sub>2</sub> proleptic  
606 varies from 1 to 3, exceptionally 4. The maximum fruitfulness is observed for the proleptic axes



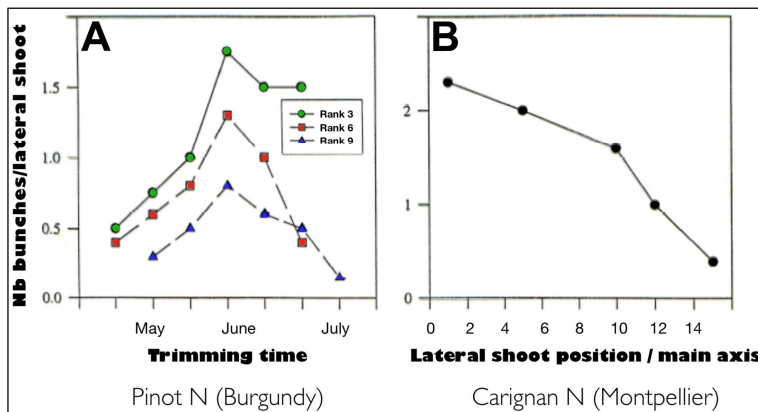
607 developed in the medial zone of the bearing stem, i.e. for 5-15<sup>th</sup> phytomers from the stem base  
608 (Huglin and Schneider, 1998). The fruitfulness of R<sub>3</sub> proleptic axes is 5-10 times lower than  
609 that R<sub>2</sub> stems but the distribution of clusters is not modified. Proleptic shoots developed from  
610 old wood buds are infertile the first year, but they develop a new generation of winter buds  
611 which display the same fruitfulness as the shoot arising from regular winter buds (Huglin and  
612 Schneider, 1998).

613 At plant and stem levels (Lavee et al., 1981), the fruitfulness of the winter buds is positively  
614 impacted by any conditions (severe pruning, water and nutrient supplies) increasing biomass  
615 plant strength and shoot vigor (Huglin, 1958; Sanchez and Dokoozlian 2005; Guilpart et al.,  
616 2014). Another important aspect is the distribution of the buds maintained at pruning which to  
617 determine the position of the grapes inside the vegetative architecture. At pruning, a careful  
618 selection of the distribution of the bud load can determine the fructification zone to help in  
619 mechanical harvesting and to regulate the microclimate of the fruits.

#### 620 **4.2. Fructification of sylleptic axes**

621 As proleptic axes, the reproductive organs of sylleptic are the first oppositifoliated organs.  
622 Fruiting intensity of the lateral shoots is dependent on both, the resources available at axis level  
623 and the correlative inhibitions undergone by R<sub>1</sub> meristem at local level (Olivain and Bessis,  
624 1987). In low or moderate conditions of vigor, in the absence of early SAM trimming, lateral  
625 shoots remain weak (<20cm) and exhibit a low fruitfulness (Olivain and Bessis, 1987). Olivain  
626 and Bessis (1988a, b) showed that the suppression of apical dominance can modify both the  
627 distribution and intensity of lateral shoot fruiting. Indeed, the potential of fruitfulness is  
628 decreasing with the insertion rank, which corresponds to a distribution of the potential fertility  
629 very different from that observed in non-trimmed vegetative axes. These observations firstly  
630 reported with the variety Pinot Noir in Burgundy by Olivain and Bessis (**Fig. 14A**), were

631 confirmed with the variety Carignan in Montpellier by Prof. D. Boubals (personal  
632 communication) (**Fig. 14B**).



633  
634 **Figure 14 - Effect of the date and level (first proximal position=0) of apex trimming on**  
635 **syllaptic shoots' fruitfulness in the *Vitis vinifera* grapevine** (redraw from Olivain and Bessis,  
636 1988a,b and Boubals D., personal communication).

637  
638 Another interesting observation (Olivain and Bessis, 1988a, b), to control the intensity of the  
639 lateral shoot fruitfulness is on the effect of the date of SAM trimming. Indeed, whatever the  
640 severity (position of the section along the main axis) of the trimming, the period around  
641 flowering is the most prone to boost the development and the fruiting of lateral shoots. This  
642 period, which corresponds to the maximum primary growth rate in temperate climate (Bernard,  
643 1980), is thus a critical phase to control the architecture of the annual shoot and the development  
644 and the fruiting of sylleptic axes.

645  
646 **5. Seasonal effects: dormancy**

647 In temperate climates, the grapevine primary growth is rhythmic and synchronized by cycles of  
648 favorable and unfavorable phases. Towards the end of a growth cycle, when the annual stem  
649 develops a primary bark, winter buds progressively lose their growing capacities due to  
650 dormancy effects (Pouget, 1963). The dormancy is a generic term that breaks down into 3

651 successive stages (Fadon et al., 2020): i) **The pre-dormancy (para-dormancy)**, during which  
652 the development of the winter buds is prevented by correlative inhibitions (apical dominance  
653 of R<sub>0</sub> and R<sub>1</sub>) and external physiological factors (limitation of the resources to growth at plant  
654 level, competition with reproductive organs during fruit maturation). During this period, an  
655 anticipated R<sub>2</sub> winter bud development can only be obtained after R<sub>0</sub> SAM trimming and all  
656 lateral shoot (R<sub>1</sub>) removing (Gu et al., 2012; Pou et al. 2019); ii) **Dormancy or endo-**  
657 **dormancy**, which is mainly regulated by bud internal physiological factors (plant growth  
658 regulator balance). The release of endo-dormancy progresses gradually under the influence of  
659 cold temperatures (Nigond, 1966) or other abiotic stresses; iii) **Eco-dormancy**, which is only  
660 dependent of environmental factors, particularly to temperature regime (Camargo et al., 2017).  
661 After budburst, proleptic axis growth rate is determined by temperature and nutrient resources  
662 (plant biomass strength and vigor).

### 663 **5.1. Temperate climates (with a winter and temperatures below +10°C)**

664 Under temperate climate, grapevine performs a single cycle of vegetative and reproductive  
665 development per year. Pruning is performed during the vegetative resting phase to regulate the  
666 number, the position and the average fruitfulness potential of the winter buds for the next crop  
667 cycle (Champagnol, 1984). If performed during eco-dormancy, the date of pruning impact little  
668 the timing of winter bud budburst. *V. vinifera* grapevine plants follows the phases of dormancy  
669 as detailed above, with low temperatures breaking the endo-dormancy. In grapevine, cold  
670 requirements are low compared to other perennial fruit species from temperate regions, such as  
671 apple (Williams et al., 1979). An exposition to a few days of temperatures below +10°C is  
672 enough to alleviate dormancy (Pouget, 1963; Nigond, 1961, 1966, 1967). Since the end of the  
673 dormancy and the rate of budburst are dependent on the sum of positive temperatures,  
674 phenological models make possible to predict the date of budburst with a precision of a few  
675 days (Pouget, 1988; Camargo et al., 2017). After budburst, the organogenesis of proleptic

676 shoots is thermal-time dependent (Lebon et al., 2004). Late pruning after budburst induces  
677 significant phenological shifts of shoot development until the flowering. This can be useful to  
678 escape to spring frost period, but unfortunately has limited impact on the timing of grape  
679 ripening (Ravaz, 1912; Gatti et al., 2016).

## 680 **5.2. Subtropical climates (with a winter and temperatures above +10°C)**

681 It is generally possible to perform 2 vegetative cycles per year but two issues complicate the  
682 cropping with *V. vinifera* varieties. The first one concerns the insufficiency of low temperatures  
683 to get a complete breaking of the bud dormancy. Hopefully, as bud dormancy in *V. vinifera* is  
684 not very deep, dormancy is generally broken by a combination of abiotic stresses that naturally  
685 occur or can be implemented at the end of a a crop cycle: water deficit, high temperature, leaf  
686 removal and the use of plant growth regulators (e.g. ethylene, cyanamid-derivatives).  
687 Nevertheless, these effects are difficult to regulate and a residual dormancy can remain, with  
688 consequences in the distribution of the vegetative growth and fruiting.

689 The second issue is related to the adequacy of subtropical climate with the requirements of the  
690 proleptic shoot fruiting which last onto 2 vegetative cycles. Indeed, the differentiation of  
691 inflorescence primordia in winter buds which requires specific light and temperature conditions  
692 (Sanchez and Dokoozlian, 2005), that are not always suitable during one of the two possible  
693 vegetative cycle. Another aspect is in relation to the susceptibility of *V. vinifera* grapes to a  
694 range of fungi, which require a massive and costly use of pesticides to get healthy grapes if the  
695 summer cycle is humid. Moreover, to produce qualitative red wine grapes require cool night, i.e.  
696 with temperatures below +15/20°C conditions (Tonietto and Carbonneau, 2004), conditions  
697 that are not frequent during sub-tropical summers.

698 To challenge this issues, by controlling the date of pruning, a first production cycle is positioned  
699 during the (dry) winter, which is suitable to grape quality but not to the development of fruitful  
700 winter buds (Cherubino-Ribeiro et al., 2020). After harvest, the vines are pruned again for a

701 second vegetative cycle during summer to develop fertile winter buds for the next cycle (de  
702 Almeida et al., 2019). During this second growing cycle, inflorescences are removed because  
703 it will be too challenging to get qualitative table, juice or wine grapes. Then, 2 vegetative cycles  
704 a year are performed but only one is useful to get fruits (Ahmed et al., 2019).

### 705 **5.3. Tropical climates (no winter and temperature rarely below 20°C)**

706 Two or even 3 vegetative cycles can be performed because a complete vegetative cycle from  
707 budburst to ripe fruits is around 120 days (+/- 20 days depending on the variety and the level of  
708 sugar targeted at harvest). However, the cultivation of *V. vinifera* varieties, which is a temperate  
709 species, is complicated due to problems of dormancy break management and/or fungal pressure  
710 during the wet period. In most tropical climates (Brazil, India, Thailand), vine growing is  
711 preferably established with interspecific hybrids (Galet, 1990; Yamada and Sato, 2016).  
712 However, the cultivation of *V. vinifera* is often possible by practicing two vegetative cycles for  
713 one production cycle which will be positioned during the driest season if a humid season has to  
714 be avoided. Even if theoretically 3 cycles could be obtained, only 2 cycles per plot are  
715 implemented to allow the vines to accumulate carbon reserves in the perennial organs. Actually,  
716 after a harvest, vinegrowers maintain the vegetation for 45 days before pruning again and  
717 starting a new production cycle. If the overall climate is dry over year and in absence of  
718 radiative deficit, such as in the north of Brazil (e.g. Petrolina in the Pernambuco state), the two-  
719 yearly cycles of production per plot can be staggered to spread the production of grapes  
720 throughout the year.

721 With *V. vinifera* varieties, the main problem is the absence of dormancy breaking due to  
722 insufficient low temperatures (Sudawan et al., 2016). The regulation of the vegetative  
723 architecture and the fruiting cannot be naturally established. A range of practices can be  
724 implemented to reduce bud endo-dormancy: severe water stress, defoliation with contact  
725 herbicides, or sprayings of urea, ethephon or garlic extracts (Kubota et al., 2000). More recently

726 Chervin and Fennel (2019) proposed to applying low concentration of ethanol. However, these  
727 measures are difficult to monitor or to implement and are of variable effectiveness in field  
728 conditions. To date, the most effective treatment to force bud dormancy break (Shulman et al.,  
729 1983; Or et al., 1999) and synchronize proleptic shoots' development is the spraying of calcium  
730 ( $\text{CH}_2\text{Ca}$ ) or hydrogen ( $\text{CH}_2\text{N}_2$ ) cyanamide. This treatment that is done just after pruning induces  
731 a complete bud burst within a period of 2-4 weeks. Nevertheless, these molecules are dangerous  
732 for applicators (Inamdar et al., 2015) and the environment as well and alternatives are still  
733 studied, as tropical viticulture is expanding, especially for table grape and grape juice  
734 production.

735

## 736 **6. Consideration of shoot architectural features for improvement**

737 The shoot architecture is a major determinant of the potential of production (Carbonneau et al.,  
738 2020), the level of light interception (Louarn et al., 2008) and the whole-canopy gas exchanges  
739 (Prieto et al., 2020). Understanding the biological and environmental factors that modulate  
740 shoot and its interactions with reproductive organs is essential to optimize not only the  
741 regulation of the carbon allocation between vegetative and reproductive organs but also the  
742 microclimate of the canopy. However, modelling shoot system architecture is a complex matter  
743 as many factors interact at local, shoot and plant level (Lebon et al., 2004; 2006). An approach  
744 integrating sink strength variation and the local effects of sink proximity was proposed to  
745 complement current models based on organogenesis mechanistic and thermal time (Pallas et  
746 al., 2008).

747 Because of the diversity for stem architecture (Louarn et al., 2007), it is important to identify  
748 the genetic traits controlling primary growth, branching and shoot system shape. In higher  
749 plants, several studies have demonstrated the implication of genetic determinants in the control  
750 of plant vegetative architecture. Based on the analysis of tropical tree structures, Hallé and co-

751 authors (Hallé and Oldeman, 1970; Hallé et al., 1978) proposed architectural models combining  
752 traits of primary and secondary growth and flowering distribution. When architecture was  
753 broken down into elementary processes, many of them were found genetically controlled in  
754 apple trees (Segura et al., 2008). In the grapevine, QTLs of vegetative development traits have  
755 already been identified: metamer length and phyllochron (Houel et al. 2015), leaf area (Coupel-  
756 Ledru et al., 2014), primary growth rate (Bert et al., 2013; Coupel-Ledru et al., 2016) or above-  
757 ground biomass (Tandonnet et al., 2018). Moreover, functional studies identified genes  
758 regulating organogenesis mechanisms, such a winter bud para-dormancy (He et al., 2012) or  
759 tendril differentiation (Diaz-Riquelme et al., 2014; Arro et al., 2017). Nevertheless, we are still  
760 far to have a clear picture of the genetic determinants of shoot system organization and data are  
761 still too fragmentary for marker-assisted selection.

762 The only criterion that is considered in grapevine breeding is shoot bearing with two options:  
763 i) erected shoots to facilitate the trellising of the vegetation, or ii) curved down shoots to manage  
764 descending vegetation and minimal pruning. However, in the absence of a comprehensive  
765 understanding of the G and GxE factors that determine shoot architecture traits, the assessment  
766 of phenotypic values of elite genotypes can only be performed through empirical approaches.  
767 Within *V. vinifera* and more generally the genus *Vitis*, which is the current botanical perimeter  
768 for grapevine breeding, studies are thus needed to characterize the genotypic and phenotypic  
769 diversity and plasticity existing for shoot architecture traits. These advances are a prerequisite  
770 to implement efficient selections of either scion or rootstock genotypes not only more easy to  
771 manage, but also better adapted to abiotic and biotic stresses than current varieties.

772

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779

## 780 **References**

781 Ahmed S, Roberto SR, Shahab M, Colombo RC, Silvestre JP, Koyama R, de Souza RT (2019).  
782 Proposal of double-cropping system for 'BRS Isis' seedless grape grown in subtropical area.  
783 *Scientia Horticulturae* 251: 118-126. <https://doi.org/10.1016/j.scienta.2019.03.022>

784 Albani MC, Coupland G. 2010. Comparative analysis of flowering in annual and perennial  
785 plants. *Current Topics in Developmental Biology* 91: 323-348.  
786 [https://doi.org/10.1016/S0070-2153\(10\)91011-9](https://doi.org/10.1016/S0070-2153(10)91011-9).

787 Arro J, Cuenca J, Ynag Y, Liang Z, Cousins P, Zhong GY. 2017. A transcriptome analysis of  
788 two grapevine populations segregating for tendril phyllotaxy. *Horticulture Research* 4:  
789 17032. doi: 10.1038/hortres.2017.32.

790 Assaf R. 1966. Modalité de croissance de quelques rameaux de vigne et d'arbres fruitiers.  
791 *Journal d'Agriculture Traditionnelle et de Botanique Appliquée* 13: 147-182.  
792 <https://doi.org/10.3406/jatba.1966.2878>.

793 Almeida Junior O, de Souza CR, Alcântara Novelli Dias F, de Paula Fernandes F et al. 2019.  
794 Effect of pruning strategy on 'Syrah' bud necrosis and fruitfulness in Brazilian subtropical  
795 Southeast. *Vitis* 58: 87-94. doi: 10.5073/vitis.2019.58.87-94.

796 Barthelemy D, Caraglio Y. 2007. Plant architecture: a dynamic, multilevel and comprehensive  
797 approach to plant form, structure and ontogeny. *Annals of Botany* 99: 375-407.  
798 doi:10.1093/aob/mcl260.



799 Beauvieux R, Wenden B, Dirlwanger E. 2012. Bud dormancy in perennial fruit tree species:  
800 a pivotal role for oxidative cues. *Frontiers in Plant Science* 16.  
801 <https://doi.org/10.3389/fpls.2018.00657>.

802 Bell AD. 1991. *Plant form: an illustrated guide to flowering plant morphology*. Oxford  
803 University Press, England.

804 Bernard AC. 1975. Sur la croissance de la vigne. *La France Viticole* 1-2: 1-15.

805 Bernard AC. 1980. *Contribution à l'étude de la biologie et des méristèmes des Vitacées*. PhD  
806 of Montpellier University, France.

807 Bert PF., Bordenave L, Donnart M, Hévin C, Ollat N, Decroocq S. 2013. Mapping genetic loci  
808 for tolerance to lime-induced iron deficiency chlorosis in grapevine rootstocks (*Vitis* sp.).  
809 *Theoretical and Applied Genetics* 126: 451–473. doi.10.1007/s00122-012-1993-5.

810 Booker J. 2003. Auxin acts in xylem-associated or medullary cells to mediate apical dominance.  
811 *The Plant Cell* 15: 495-507.

812 Boss PK., Thomas MR. 2002. Association of dwarfism and floral induction with a grape 'green  
813 revolution' mutation. *Nature* 416: 847-850.

814 Bouard J. 1966. *Recherches physiologiques sur la vigne et en particulier sur l'aoûtement des*  
815 *sarments*. PhD of Bordeaux University, France.

816 Bouard J. 1971. *Tissus et organes de la vigne. Traité d'ampélogie. Sciences et Techniques de*  
817 *la Vigne*, Dunod Ed., Paris, France.

818 Bouard J. 1987. La disposition des grappes sur les rameaux principaux de *Vitis vinifera* L. *Proc.*  
819 *III<sup>th</sup> Symposium International de la Physiologie de la Vigne*, Bordeaux, 24-27 juin 1986,  
820 OIV Ed, Paris 9-15.

821 Branas J. 1974. *Viticulture*. Dehan Ed., Montpellier, France.

822 Bugnon F. 1953. *Recherches sur la ramification des Ampélidacées*. PhD of Dijon University,  
823 France.

824 Bugnon F, Bessis R. 1968. *Biologie de la vigne: acquisitions récentes et problèmes actuels*.  
825 Masson et Cie Ed., Paris, France.

826 Camargo HA, Salazar MR, Zapata DM, Hoogenboom G. 2017. Predicting the dormancy and  
827 bud break dates for grapevines. *Acta Horticulturae* 1182: 153-160.  
828 <https://doi.org/10.17660/ActaHortic.2017.1182.18>.

829 Carbonneau A. 1976. Analyse de la croissance des feuilles du sarment de vigne estimation de  
830 sa surface foliaire par échantillonnage. *Connaissance de Vigne et du Vin* 10: 141-159.

831 Carbonneau A. 1997. Le *Vitis vinifera silvestris* européen. *Proc XXII<sup>th</sup> Congrès Mondial de la*  
832 *Vigne et du Vin OIV*, Buenos Aires, 1-8 Dec, Argentina.

833 Carbonneau A. 2002. Genèse et évolution des systèmes de conduite de la vigne. *C.R. Acad.*  
834 *Suisse du Vin* 40: 72-81.

835 Carbonneau A, Cargnello G. 2003. *Architectures de la vigne et systèmes de conduite*. Dunod  
836 Ed., Paris, France.

837 Carbonneau A, Deloire A, Garrier G. 2003. *Eléments historiques de l'évolution des*  
838 *architectures de vigne*. In *Vignobles du Sud XVI<sup>ème</sup> – XIX<sup>ème</sup> siècle*, Université Montpellier  
839 III – Paul Valéry Ed., 459-466.

840 Carbonneau A. 2010. Tropical viticulture: specificities and challenges for a quality Viticulture.  
841 Comm. *Proc 2<sup>th</sup> International Symposium on Tropical Wines*, Petrolina – Pernambuco, Brazil,  
842 26-28 May 2010, EMBRAPA publications, Brazil.

843 Carbonneau A, Deloire A. 2020. *Raisonnement du terroir viticole*. In “*Traité de la vigne*”, 3<sup>th</sup>  
844 Ed., Dunod Ed. Paris, France, ISBN 978-2-10-079857-5.

845 Carbonneau A, Metay A, Torregrosa L et al. 2020. *Raisonnement des techniques culturales*. In  
846 “*Traité de la vigne*”, 3<sup>th</sup> Ed. Dunod Ed., Paris, France, ISBN 978-2-10-079857-5.

847 Celette F, Gary C. 2013. Dynamics of water and nitrogen stress along the grapevine cycle as  
848 affected by cover cropping. *European Journal of Agronomy* 45: 142-152. doi:  
849 10.1016/J.EJA.2012.10.001.

850 Champagnat P. 1954. Recherches sur les rameaux anticipés des végétaux ligneux. *Revue de*  
851 *Cytologie et de Biologie Végétales* 15: 1-51.

852 Chaib J, Torregrosa L, Mackenzie D, Corena P, Bouquet A, Thomas MR. 2010. The microvine  
853 - a model system for rapid forward and reverse genetics of grapevines. *The Plant Journal*  
854 61: 1083-1092.

855 Champagnol F. 1984. *Éléments de physiologie de la vigne et de viticulture générale*. Dehan  
856 Ed., Montpellier, France.

857 Chervin C, Fennell A. 2019. Ethanol sprays to release grapevine bud dormancy: a potential  
858 alternative to cyanamides. *OenoOne* 53. doi.org/10.20870/oeno-one.2019.53.4.249.

859 Cherubino-Ribeiro TT, Fernandes-Brum CN, Rita de Souza C et al. 2020. Transcriptome  
860 analyses suggest that changes in fungal endophyte lifestyle could be involved in grapevine  
861 bud necrosis. *Nature Scientific Reports* 10: 9514. doi.org/10.1038/s41598-020-66500-0.

862 Cline MG. 2000. Execution of the auxin replacement apical dominance experiment in temperate  
863 woody species. *American Journal of Botany* 87: 182-190.

864 Collins C., Rawnsley B. 2005. Factors influencing primary bud necrosis (PBN) in Australian  
865 vineyards. *Acta Horticulturae* 689: 81-86. DOI: 10.17660/ActaHortic.2005.689.5.

866 Coombe BG. 1967. Effects of growth retardants on *Vitis vinifera* L. *Vitis* 6: 278-287.

867 Costes E, Lauri PE, Regnard JL. 2006. Analyzing fruit tree architecture: implications for tree  
868 management and fruit production. *Horticultural Reviews* 32, J. Janick (Ed.), ISBN 0-471-  
869 73216-8.

870 Costes E, Lauri PE, Simon S, Andrieu B. 2013. Plant architecture, its diversity and manipulation  
871 in agronomic conditions, in relation with pest and pathogen attacks. *European Journal of*  
872 *Plant Pathology* 135: 455-470.

873 Costes E. 2019. Physiology and genetics of plant architecture. *Annual Plant Reviews* 2: 1031-  
874 1068. <https://doi.org/10.1002/9781119312994.apr0658>.

875 Coupel-Ledru A, Lebon E, Christophe A et al. 2014. Genetic variation in a grapevine progeny  
876 (*Vitis vinifera* L. cvs Grenache×Syrah) reveals inconsistencies between maintenance of  
877 daytime leaf water potential and response of transpiration rate under drought. *Journal of*  
878 *Experimental Botany* 65: 6205-6218. doi: 10.1093/jxb/eru228.

879 Coupel-Ledru A, Lebon E, Christophe A et al. 2016. Reduced nighttime transpiration is a  
880 relevant breeding target for high water-use efficiency in grapevine. *Proceedings of the*  
881 *National Academy of Science* 113: 8963-8968. <https://doi.org/10.1073/pnas.1600826113>.

882 Cruiziat P, Cochard H, Ameglio T. 2002. Hydraulic architecture of trees: main concepts and  
883 results. *Annals of Forest Science*, Springer Verlag/EDP Sciences 59: 723-752,  
884 doi.10.1051/forest:2002060.

885 Deloire A, L. Torregrosa L, Carbonneau A. 2020. *Structures et Developpements*. In “*Traité de*  
886 *la vigne*”, 3<sup>th</sup> Ed., Dunod Ed., Paris, France, ISBN 978-2-10-079857-5.

887 Diaz-Riquelme JD, Martinez-Zapater JM, Carmona MJ. 2014. Transcriptional analysis of  
888 tendril and inflorescence development in grapevine (*Vitis vinifera* L.). *PLoS One* 17: e92339.  
889 doi: 10.1371/journal.pone.0092339.

890 Doerner P. 1999. Shoot meristems: Intercellular signals keep the balance. *Current Biology* 9:  
891 377-380. [https://doi.org/10.1016/S0960-9822\(99\)80232-2](https://doi.org/10.1016/S0960-9822(99)80232-2).

892 Carolus M. 1970. *Recherches sur l'organogenèse et l'évolution morphologique du bourgeon*  
893 *latent de la vigne (Vitis vinifera L. var. Merlot)*. PhD of Bordeaux University, France.

894 Cheema SS, Torregrosa L, Domergue P, Carbonneau A. 1996. Evolution de la différenciation  
895 inflorescentielle durant l'organogenèse des bourgeons latents de *Vitis vinifera* L. cv. Syrah.  
896 *Le Progrès Agricole et Viticole* 113: 257-262 and 279-285.

897 Fadon E, Fernandez E, Behn H, Luedeling E. 2020. A conceptual framework for winter  
898 dormancy in deciduous trees. *Agronomy* 10, 241: doi:10.3390/agronomy10020241.

899 Feechan A, Anderson C, Torregrosa L et al. 2013 Genetic dissection of a TIR-NB-LRR locus  
900 from the wild North American grapevine species *Muscadinia rotundifolia* identifies  
901 paralogous genes conferring resistance to major fungal and oomycete pathogens in cultivated  
902 grapevine. *The Plant Journal* 76: 661-674.

903 Freeman BM, Lee TH, Turkington CR. 1979. Interaction of irrigation and pruning level on  
904 growth and yield of shiraz vines. *American Journal of Enology and Viticulture* 30: 218-223.

905 Fournioux JC, Bessis R. 1979. Etude des relations criblo-vasculaires entre les différents organes  
906 de la tige de la vigne (*Vitis vinifera* L.). *Connaissance de la Vigne et du Vin* 13: 91-114.

907 Fournioux JC. 1995. *Facteurs de l'édification de la tige de Vitis vinifera L. dans différentes*  
908 *conditions de culture*. PhD of Dijon University, France

909 Fournioux JC, Bessis R. 1990. Eléments du contrôle de la morphogenèse de la vigne *in vitro*:  
910 sympodisation. *Canadian Journal of Botany* 68, 841-851.

911 Gailloch C, Lohmann JU. 2015. The never-ending story: from pluripotency to plant  
912 developmental plasticity. *Development* 142: 2237-2249.

913 Galet P. 1977. *Maladies et parasites de la vigne*. Dehan Ed., Montpellier, France.

914 Galet P. 1990. *Cépages et Vignobles de France: Les vignes américaines*, Masson Ed., Paris,  
915 France.

916 Gatti M, Pirez FJ, Chiari G et al. 2016. Phenology, canopy aging and seasonal carbon balance  
917 as related to delayed winter pruning of *Vitis vinifera* L. cv. Sangiovese grapevines. *Frontiers*  
918 *in Plant Science* 7. [https://doi: 10.3389/fpls.2016.00659](https://doi.org/10.3389/fpls.2016.00659).

919 Génard M, Pagès L, Kervella J. 1994. Relationship between sylleptic branching and  
920 components of parent shoot development in the peach tree. *Annals of Botany* 74: 465-470.

921 Gramaje D, Úrbez-Torres JR, Sosnowski MR. 2018. *Managing grapevine trunk diseases with*  
922 *respect to etiology and epidemiology: Current strategies and future prospects*. In Plant  
923 diseases. Karasev AV (Ed.), The American Phytopathological Society.  
924 <https://doi.org/10.1094/PDIS-04-17-0512-FE>.

925 Greb T, Lohmann JU. 2016. Plant stem cells. *Current Biology* 26: 816-821.

926 Gu S, Jacobs S, McCarthy B, Gohil H. 2012. Forcing vine regrowth and shifting fruit ripening  
927 in a warm region to enhance fruit quality in 'Cabernet Sauvignon' grapevine (*Vitis vinifera*  
928 L.). *Journal of Horticultural Science and Biotechnology* 87: 287-292.

929 Guilpart N, Metay A, Gary C. 2014. Grapevine bud fertility and number of berries per bunch  
930 are determined by water and nitrogen stress around flowering in the previous year. *European*  
931 *Journal of Agronomy* 54: 9-20.

932 Hallé F, Oldeman RA. 1970. *Essai sur l'architecture et la dynamique de croissance des arbres*  
933 *tropicaux*. Masson et Cie Ed. Paris, France.

934 Hallé F, Oldeman RA., Tomlinson PB. 1978. *Tropical Trees and Forests*. Springer Verlag Rd.,  
935 Berlin, Germany.

936 He D, Mathiason K, Fennell A. 2012. Auxin and cytokinin related gene expression during active  
937 shoot growth and latent bud paradormancy in *Vitis riparia* grapevine. *Journal of Plant*  
938 *Physiology* 169: 643-648. doi: 10.1016/j.jplph.2012.01.001.

939 Houel C, Chatbanyong R, Doligez A et al. 2015. Identification of stable QTLs for vegetative  
940 and reproductive traits in the microvine (*Vitis vinifera* L.) using the 18K Infinium chip. *BMC*  
941 *Plant Biology* 15: 205. doi.10.1186/s12870-015-0588-0.

942 Huglin P. 1958. Recherches sur les bourgeons de la vigne initiation florale et développement  
943 végétatif. *Annales de l'Amélioration des Plantes* 18: 113-272.

- 944 Huglin P, Schneider C. 1998. *Biologie et écologie de la vigne*. Lavoisier Ed., Paris, France.
- 945 Hunter J. 1998. Plant spacing implications for grafted grapevine I. Soil characteristics, root  
946 growth, dry matter partitioning, dry matter composition and soil utilization. *South African*  
947 *Journal of Enology and Viticulture* 19: 25-34.
- 948 Inamdar SZ, Chandrhas J, Srinath C, Kulkarni RV. 2015. Hydrogen cyanamide induced  
949 cutaneous reactions: occupational pesticide poisoning and need for surveillance. *Indian*  
950 *Journal of Pharmacy Practice* 8: 84–86.
- 951 Keller M. 2020. *The Science of Grapevines*. 3<sup>rd</sup> Edition. Academic Press, USA. eBook ISBN:  
952 9780128167021.
- 953 Kubota N, Matthews MA, Takahagi T, Kliewer WM. 2000. Effects of garlic preparations and  
954 of calcium and hydrogen cyanamides on budbreak of grapevines grown in greenhouses.  
955 *American Journal of Enology and Viticulture* 51: 409-414.
- 956 Lavee S, Melamud H, Ziv M, Bernstein Z. 1981. Necrosis in grapevine buds of *V. vinifera* cv.  
957 Queen of Vineyard. I. Relation to vegetative vigor. *Vitis* 20: 8-14
- 958 Lebon E, Pellegrino A, Tardieu F, Lecoœur J. 2004 Shoot development in grapevine (*Vitis*  
959 *vinifera*) is affected by the modular branching pattern of the stem and intra- and inter-shoot  
960 trophic competition. *Annals of Botany* 93: 263-274. <http://dx.doi.org/10.1093/aob/mch038>.
- 961 Lebon E, Pellegrino A, Louarn G, Lecoœur J. 2006. Branch development controls leaf area  
962 dynamics in grapevine (*Vitis vinifera*) growing in drying soil. *Annals of Botany* 98: 175-185.  
963 doi:10.1093/aob/mcl085.
- 964 Li-Mallet A, Rabot A, Geny L. 2016 Factors controlling inflorescence primordia formation of  
965 grapevine: their role in latent bud fruitfulness? A review. *Botany* 94: 147-163. doi.  
966 org/10.1139/cjb-2015-0108.
- 967 Louarn G. 2005. *Analyse et modélisation de l'organogénèse et de l'architecture du rameau de*  
968 *vigne (Vitis vinifera L.)*. PhD of Institut Agro of Montpellier, Montpellier, France.

969 Louarn G, Guedon Y, Lecoeur J, Lebon E. 2007. Quantitative analysis of the phenotypic  
970 variability of shoot architecture in two grapevine (*Vitis vinifera*) cultivars. *Annals of Botany*  
971 99: 425-437. doi: 10.1093/aob/mcl276.

972 Louarn G, Lecoeur J, Lebon E. 2008. A Three-dimensional statistical reconstruction model of  
973 grapevine (*Vitis vinifera*) simulating canopy structure variability within and between  
974 cultivar/training system pairs. *Annals of Botany* 101: 1167-1184. doi:10.1093/aob/mcm170.

975 Mason MG, Ross JJ, Babst BA, Weinclaw BN, Beveridge CA. 2014. Sugar demand, not auxin,  
976 is the initial regulator of apical dominance. *Proceedings of the National Academy of Science*  
977 111: 6092-6097.

978 Morlat R, Jacquet A, Asselin C. 1993. Principaux effets de l'enherbement permanent contrôlé  
979 du sol, dans un essai de longue durée en Anjou. *Le Progrès Agricole et Viticole* 110: 406-  
980 410.

981 Mullins MG, Bouquet A, Williams LE. 1992. *Biology of the grapevine*. Cambridge University  
982 Press, Cambridge, UK.

983 Naor A, Gai Y, Bravdo B. 2002. Shoot and cluster thinning influence vegetative growth, fruit  
984 yield, and wine quality of 'Sauvignon blanc' grapevines. *Journal of the American Society for*  
985 *Horticultural Science* 127: 628-634. <https://doi.org/10.21273/JASHS.127.4.628>.

986 Nigond J. 1961. Etude de la dormance de la vigne sous le climat Languedocien. *Bulletin de la*  
987 *Société Française de Physiologie Végétale* 7: 78-81.

988 Nigond J. 1966. Quelques aspects de la dormance des bourgeons de la vigne sous le climat du  
989 Languedoc. *Bulletin de la Société de Botanique de France* 113: 85-99. doi:  
990 10.1080/00378941.1966.10838457.

991 Nigond J. 1967. *Contribution à l'étude de la dormance de la vigne sous le climat du Languedoc*.  
992 PhD of Paris University, Paris, France.



- 993 Nougarede A. 2001. Le méristème caulinaire des angiospermes: nouveaux outils, nouvelles  
994 interprétations. *Acta Botanica Gallica* 148: 3-77.
- 995 Olivain C, Bessis R. 1987. L'organogenèse inflorescentielle dans les bourgeons anticipés de  
996 vigne (*Vitis vinifera* L. cépage Pinot). *Vitis* 26: 98-106.
- 997 Olivain C, Bessis R. 1988a. Fertilité des rameaux anticipés de vigne (*Vitis vinifera* L.): I -  
998 expression au vignoble. *Agronomie* 8: 133-138.
- 999 Olivain C, Bessis R. 1988b. Fertilité des rameaux anticipés de vigne (*Vitis vinifera* L.): II -  
1000 Influence de la fertilité potentielle et de la vitesse de croissance. *Agronomie* 8: 187-192.
- 1001 Or E, Nir G, Vilozny I. 1999. Timing of hydrogen cyanamide application to grapevine buds.  
1002 *Vitis* 38: 1-6.
- 1003 Palonen P, Buszard D. 1997. Current state of cold hardiness research on fruit crops. *Canadian*  
1004 *Journal of Plant Sciences* 77: 399-420.
- 1005 Pallas B, Louarn G, Christophe A, Lebon E, Lecoer J. 2008. Influence of intra-shoot trophic  
1006 competition on shoot development in two grapevine cultivars (*Vitis vinifera*). *Physiologia*  
1007 *Plantarum* 134: 49-63. doi: 10.1111/j.1399-3054.2008.01100.x.
- 1008 Pellegrino A, Romieu C, Rienth M, Torregrosa L. 2019. *The microvine, a versatile plant*  
1009 *model to boost grapevine studies in physiology and genetics*. In: "Advances in grape and  
1010 wine biotechnologies" (Morata A. Ed.), IntechOpen, London, UK. ISBN 978-1-78984-  
1011 613-3.
- 1012 Poni S, Zamboni M, Vercesi A, Garavani A, Gatti M. 2014. Effects of early shoot trimming of  
1013 varying severity on single high-wire trellised Pinot noir grapevines. *American Journal of*  
1014 *Enology and Viticulture* 65: 493-498.
- 1015 Pou A, Balda P, Albacete A, Martínez de Toda F. 2019. Forcing vine regrowth to delay ripening  
1016 and its association to changes in the hormonal balance. *Vitis* 58: 95-101. doi:  
1017 10.5073/vitis.2019.58.special-issue.95-101.

- 1018 Pouget R. 1963. Recherches physiologiques sur le repos végétatif de la Vigne (*Vitis vinifera* L.)  
1019 la dormance des bourgeons et le mécanisme de la disparition. *Annales de l'Amélioration des*  
1020 *Plantes* 13 1-247.
- 1021 Pouget R. 1981. Action de la température sur la différenciation des inflorescences et des fleurs  
1022 durant les phases de pré-débourrement et de post-débourrement des bourgeons latents de la  
1023 vigne. *Journal International des Sciences de la Vigne et du Vin* 15.  
1024 <https://doi.org/10.20870/oeno-one.1981.15.2.1791>.
- 1025 Pouget R. 1988. Le débourrement des bourgeons de la vigne: méthode de prévision et principes  
1026 d'établissement d'une échelle de précocité de débourrement. *Connaissance de la Vigne et*  
1027 *du Vin* 22: 105-123.
- 1028 Pratt C. 1971. Reproductive anatomy of grapes - A review. *American Journal of Enology and*  
1029 *Viticulture* 22: 92-109.
- 1030 Pratt C. 1974. Vegetative anatomy of cultivated grapes - A review. *American Journal of*  
1031 *Enology and Viticulture* 25: 131-50.
- 1032 Prieto J, Louarn G, Pena JP, Ojeda H, Simonneau T, Lebon E. 2020. A functional–structural  
1033 plant model that simulates whole-canopy gas exchange of grapevine plants (*Vitis vinifera*  
1034 L.) under different training systems. *Annals of Botany* 126: 647-660.  
1035 <https://doi.org/10.1093/aob/mcz203>.
- 1036 Ravaz L. 1903. Sur la brunissure de la vigne. *Compte Rendu à l'Académie des Science de Paris*  
1037 136: 1276-1278.
- 1038 Ravaz L. 1912. *Taille précoce ou taille tardive*. Goulet & Fils (Ed), Libraires de l'Ecole  
1039 Nationale d'Agriculture, Montpellier, France.
- 1040 Renton M, Hanan J, Ferguson BJ, Beveridge CA. 2012. Models of long-distance transport: how  
1041 is carrier-dependent auxin transport regulated in the stem? *New Phytologist* 194: 704-715.

1042 Rivals P. 1965. Essai sur la croissance des arbres et sur leurs systèmes de floraison (application  
1043 aux espèces fruitières). *Journal d'Agriculture Tropicale et de Botanique Appliquée* 12: 655-  
1044 686.

1045 Sanchez L., Dokoozlian N. 2005. Bud microclimate and fruitfulness in *Vitis vinifera* L.  
1046 *American Journal of Enology and Viticulture* 56: 4.

1047 van der Schoot C, Paul LK, Rinne PLH. 2014. The embryonic shoot: a lifeline through winter.  
1048 *Journal of Experimental Botany* 65: 1699-1712.

1049 Trevisan-Scorza LC, Dornelas MC. 2011. Plants on the move: towards common mechanisms  
1050 governing mechanically-induced plant movements. *Plant Signal Behavior* 6: 1979-1986,  
1051 doi: 10.4161/psb.6.12.18192.

1052 Shulman Y, Nir G, Fanberstein L, Lavee S (1983) The effect of cyanamide on the release from  
1053 dormancy of grapevine buds. *Scientia Horticulturae* 19: 97–104.

1054 Smart RE, Robinson M. 1991. *Sunlight into wine: A handbook for winegrape canopy*  
1055 *management*. Winetitles, Adelaide, Australia.

1056 Smart RE. 1995. Principles of grapevine canopy microclimate manipulation with implication  
1057 for yield and quality. A review. *American Journal of Enology and Viticulture* 36: 230-239.

1058 Sudawan B, Chang CS, Chao HF, Ku MS, Yen YF. 2016. Hydrogen cyanamide breaks  
1059 grapevine bud dormancy in the summer through transient activation of gene expression and  
1060 accumulation of reactive oxygen and nitrogen species. *BMC Plant Biology* 16, 202.

1061 Swanepoel JJ, de la Harpe AC, Orffer CJ. 1984. A comparative study of the grapevine shoot  
1062 and cane: Periderm and secondary phloem. *South African Journal of Enology and Viticulture*  
1063 5: 59-63.

1064 Tandonnet JP, Marguerit E, Cookson SJ, Ollat N. 2018. Genetic architecture of aerial and root  
1065 traits in field-grown grafted grapevines is largely independent. *Theoretical and Applied*  
1066 *Genetics* 131: 903-915. doi.10.1007/s00122-017-3046-6.

1067 Tonietto J, Carbonneau A. 2004. A multicriteria climatic classification system for grape-  
1068 growing regions worldwide. *Agriculture and Forest Meteorology* 124: 81-97.

1069 Torregrosa L. 1995. Grapevine biotechnologies: plant regeneration through adventitious  
1070 organogenesis and somatic embryogenesis. *Le Progrès Agricole et Viticole* 112: 479-489  
1071 and 510-515.

1072 Torregrosa L, Fernandez L, Bouquet A. et al. 2011. *Origins and Consequences of Somatic*  
1073 *Variation in Grapevine*. In “*Genetics, genomics and Breeding of Grapes*” (C. Kole Ed.),  
1074 Science publishers, Enfield, New Hampshire, USA. [https://www.doi: 10.1201/b10948-4](https://www.doi.org/10.1201/b10948-4).

1075 Torregrosa L, Rienth M, Romieu C, Pellegrino A. 2019. The microvigne, a model for grapevine  
1076 physiology studies and genetics. *OenoOne* 53. [https://doi.org/10.20870/oeno-](https://doi.org/10.20870/oeno-one.2019.53.3.2409)  
1077 [one.2019.53.3.2409](https://doi.org/10.20870/oeno-one.2019.53.3.2409).

1078 Travadon R, Lecomte P, Diarra B et al. 2016. Grapevine pruning systems and cultivars  
1079 influence the diversity of wood-colonizing fungi. *Fungal Ecology* 24: 82e93.  
1080 <https://doi.org/10.1016/j.funeco.2016.09.003>.

1081 Segura V, Cilas C, Costes, E. 2008. Dissecting apple tree architecture into genetic, ontogenetic  
1082 and environmental effects: mixed linear modelling of repeated spatial and temporal  
1083 measures. *New Phytologist* 178: 302-314.

1084 Serrano-Mislata A, Sablowski R. 2018. The pillars of land plants: new insights into stem  
1085 development. *Current Opinion in Plant Biology* 45: 11-17.

1086 Srinivasan C, Mullins MG. 1981. Physiology of flowering in the grapevine - a review. *American*  
1087 *Journal of Enology and Viticulture* 32: 47-63.

1088 Vernoux T, Autran D, Traas, J. 2000. *Developmental control of cell division patterns in the*  
1089 *shoot apex*. In: *The Plant Cell Cycle* (Inzé D. Ed.), 25-37. Dordrecht: Springer, The  
1090 Netherlands.

- 1091 Williams RR, Edwards GR, Coombe BG. 1979. Determination of the pattern of winter  
1092 dormancy in lateral buds of apples. *Annals of Botany* 44: 575-581.
- 1093 Wilcox WF, Gubler WD, Uyemoto JK. 2006. *Compendium of grapevine diseases, disorders*  
1094 *and pests.* American Phytopathological Society Ed.,  
1095 <https://doi.org/10.1094/9780890544815>, ISBN:978-0-89054-481-5.
- 1096 Wolf T, Pool R, Mattick L. 1986 Responses of young Chardonnay grapevines to shoot tipping,  
1097 ethephon, and basal leaf removal. *American Journal of Enology and Viticulture* 37: 263-268.
- 1098 Yamada M, Sato A. 2016. Advances in table grape breeding in Japan. *Breeding Science* 66:  
1099 34–45. doi: 10.1270/jsbbs.66.34.
- 1100 Zhang DP, Carbonneau A. 1987. Etude du trajet de la sève brute en fonction de la longueur du  
1101 tronc chez la vigne. *Proc. III<sup>th</sup> Symp. Int. Physiologie Vigne*, Bordeaux, 24-27 Juin, OIV,  
1102 Paris, France.
- 1103 Zheng W, del Galdo V, García J, Balda P, Martínez de Toda F. 2016. Minimal pruning as a tool  
1104 to delay fruit maturity and to improve berry composition under climate change. *American*  
1105 *Journal of Enology and Viticulture* 68: 136-140. doi: 10.5344/ajev.2016.16038.
- 1106 Zimmermann J. 1954. Sprosshistologie und Holzreife bei Rebe. *Mitt. Klosterneuburg* 4: 101-  
1107 109.
- 1108 Zimmermann MH, Milburn JA. 1982. *Transport and storage of water.* In: Lange O.L., Nobel  
1109 P.S., Osmond C.B., Ziegler H. (Eds), *Physiological Plant Ecology II. Encyclopedia of Plant*  
1110 *Physiology (New Series)*, Springer, Berlin, Germany. [https://doi.org/10.1007/978-3-642-](https://doi.org/10.1007/978-3-642-68150-9_6)  
1111 [68150-9\\_6](https://doi.org/10.1007/978-3-642-68150-9_6).
- 1112 Zohary D, Spiegel-Roy P. 1975. Beginnings of fruit growing in the old world. *Science* 187:  
1113 319-27. doi: 10.1126/science.187.4174.319.