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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**

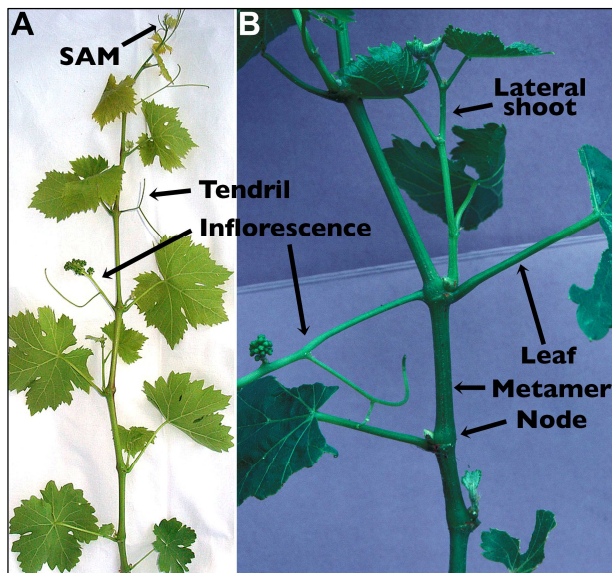
68 **2.1. Origin and type of vegetative meristems**

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 neoformed 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 |
| R₀ | End of the growing axe | Growth, Organogenesis, Primary anatomy | Apex, SAM (Shoot Apical Meristem) | Main shoot or cane |
| R₁ | Axillary to R ₀ leaf | Immediate ramification | Lateral meristem | Lateral shoot |
| R₂ | Axillary to R ₁ pre- leaf | Delayed ramification | Winter or latent bud | Main shoot (at the next crop cycle) |
| R₃ | Axillary to R ₂ scales & leaf primordia | Delayed ramification | Secondary winter or latent buds | Secondary shoots |
| Unknown | Main shoot base | Delayed ramification | Basal bud | Basal shoot |
| Unknown | 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 R₀ corresponds to the primary meristem, R₁ axillary meristems initiated by R₀, R₂ axillary meristems initiated by R₁ and R₃
 115 axillary meristems initiated by R₂.

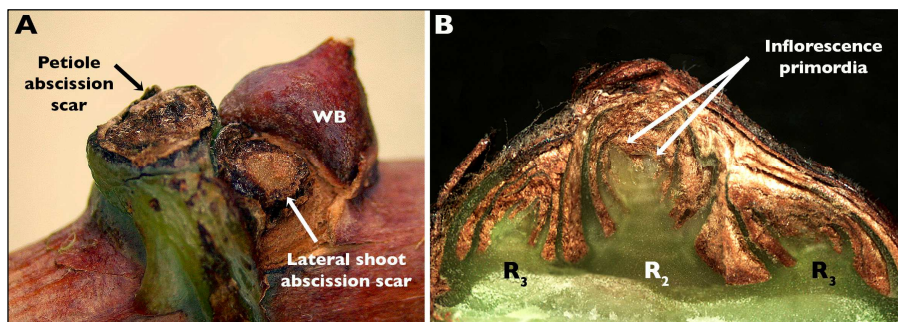
116 **Table 1 - The different types of meristems or buds of the *Vitis vinifera* grapevine.** At each
 117 crop cycle, the ranks of the shoot apical meristem are reset to R₀. In italic, caulinar meristems
 118 that are not present on an adult plant grown in field conditions.

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 (R₀)** - 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).

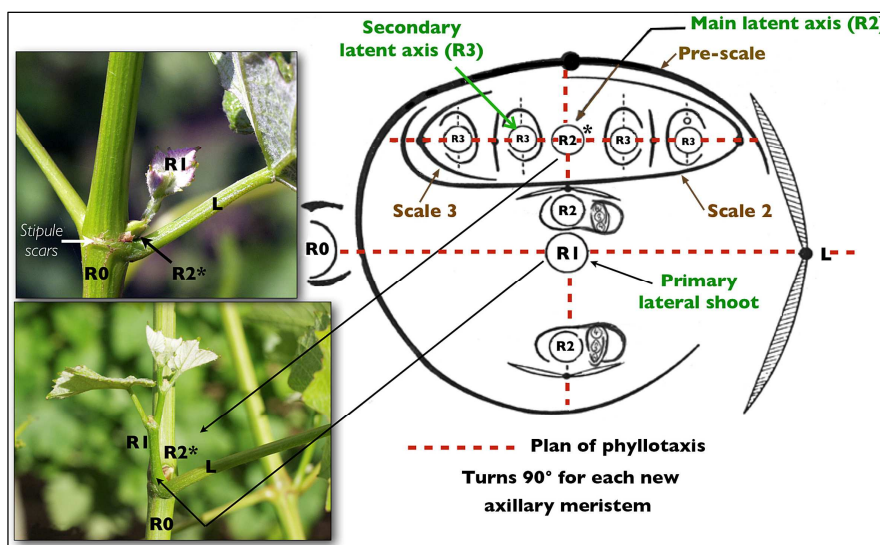
125 **The lateral shoots (R₁)** - There are the first lateral meristems formed by R₀, axillary to each
126 leaf and of each node (Bugnon, 1953; Bugnon and Bessis, 1968; Deloire et al., 2020). Except
127 in the case of excessive vigor or early shoot tipping (trimming), this axis develops only a few
128 centimeters without lignification. At the end of the ongoing vegetative cycle, it undergoes an
129 abscission that leaves a scar on the R₀ main stem (**Fig. 2A**). The phyllotaxis of R₁ is orthogonal
130 to R₀. 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 R₂ plan of phyllotaxis. At the end of the R₂ axis, in positions
137 4 and 5, two primordia of inflorescences are visible; at the base of the R₂, two secondary WB
138 axes (R₃) are present.

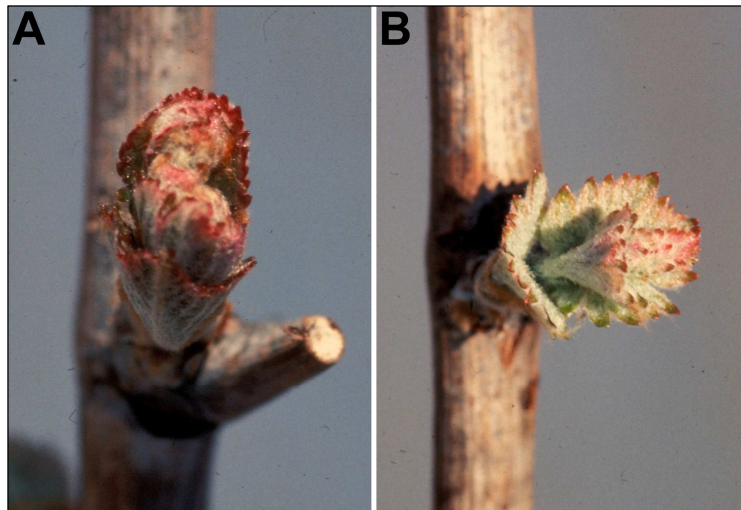
139
140 **The winter buds (R₂+R₃)** - R₂ are the first axillary meristems formed by the lateral shoots.
141 This meristem is initiated axillary to the first R₁ pre-leaf (Carolus, 1970) which form the first
142 scale of the R₂ winter bud (**Fig. 2B**). This structure evolves into a complex of buds (the 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

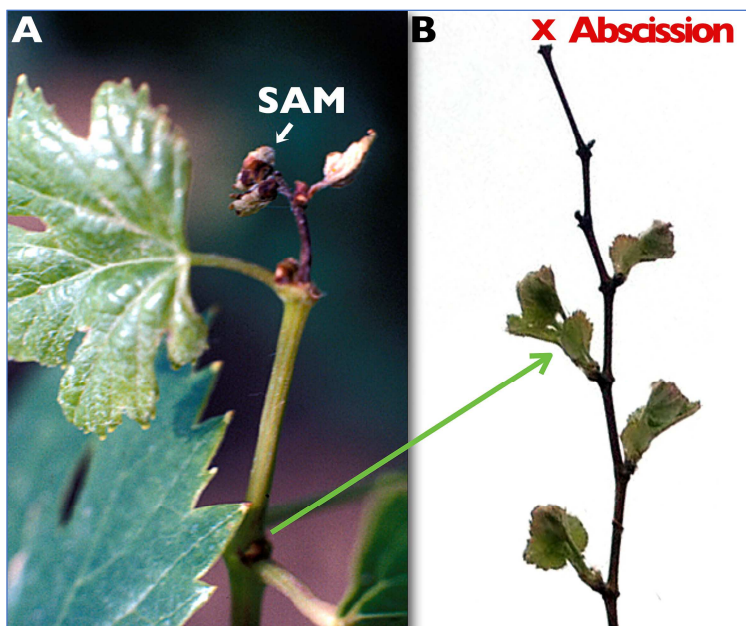
180 **2.2. Shoot system architecture: sympod vs. monopod**

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.



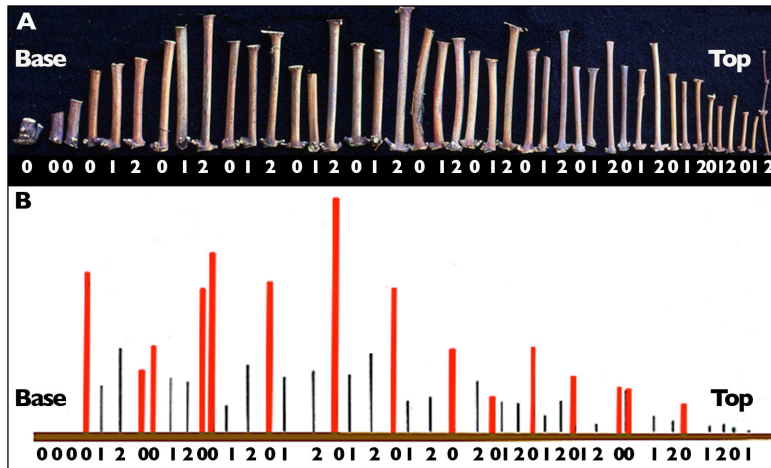
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220 **Figure 4 - The sympodial *Vitis vinifera* grapevine model.** A) At the end of a growth cycle,
221 phyllochron first slows down, then apex becomes necrotic and drop down. B) At the next cycle
222 winter buds will resume the growth of the nearing 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 ($P_0/P_1/P_2$)ⁿ 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 (P₀-P₁-P₂) 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, P₂ 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 P₀ 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^o2 - **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).



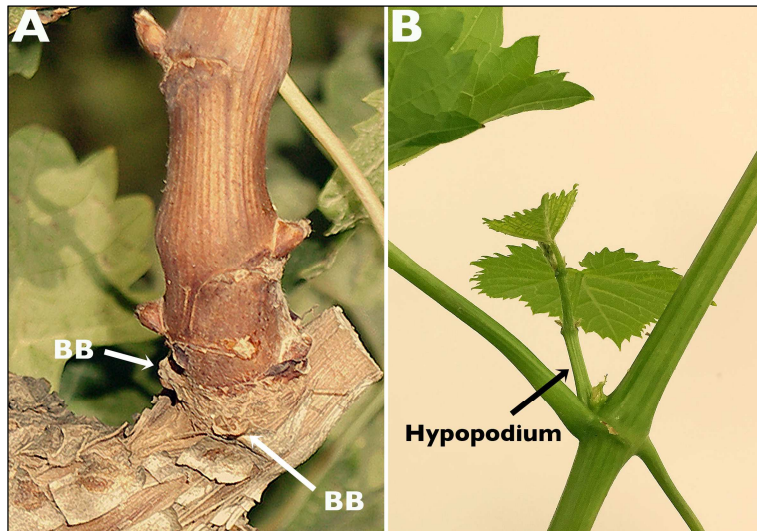
266
267 **Supplementary material n°2 - Figure S2 - Anomalies of the ternary cycle.** Vigorous *Vitis*
268 *vinifera* grapevine plants growing in a tropical context (Northeastern of Brazil). A shift of the
269 position of the inflorescence which is no longer oppositifoliated on the node is observable.
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 |
| Common name | Main shoot (R ₀) | Lateral shoot (R ₁) |
| Bearing axe | Cane or trunk | Shoot |
| Meristematic origin | R _{2,3,4} winter buds | R ₁ axillary meristem |
| Pre-formed phytomers | Yes (3-12) | No, only neoformation |
| Delayed development | Yes (next cycle min) | No |
| Scale scars | Yes | No |
| Length of first internodes | Shorts | Regular (long hypopodium) |
| Status of basal organs | Absent or rudimentary | Regular |
| Phyllotaxis/bearing axe | 180° / previous R ₀ | 90° / previous R ₀ |
| Growth/bearing axe | Similar | Lower (if SAM maintained) |
| Lignification | Systematic | Depending of available vigor |
| Function | Delay growth and fruit development to next cycle | Restart growth if SAM removed Increase biomass if extra resources |

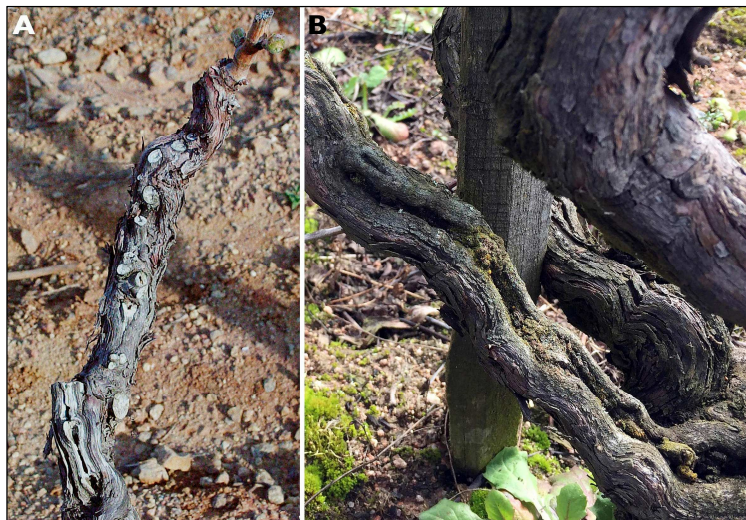
299 **Table 2** - Main morpho-functional properties of proleptic and sylleptic shoots of the *Vitis*
300 *vinifera*.

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 R₂ 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.

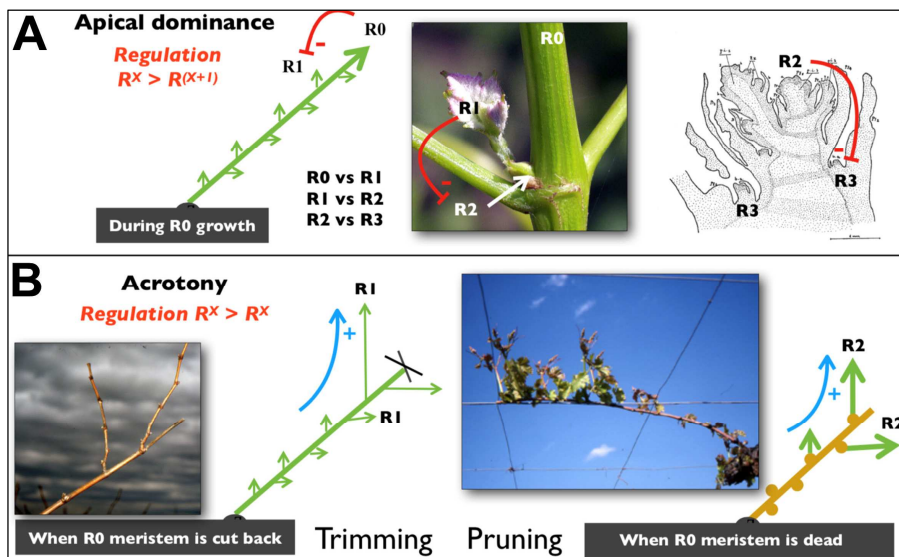
326

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).

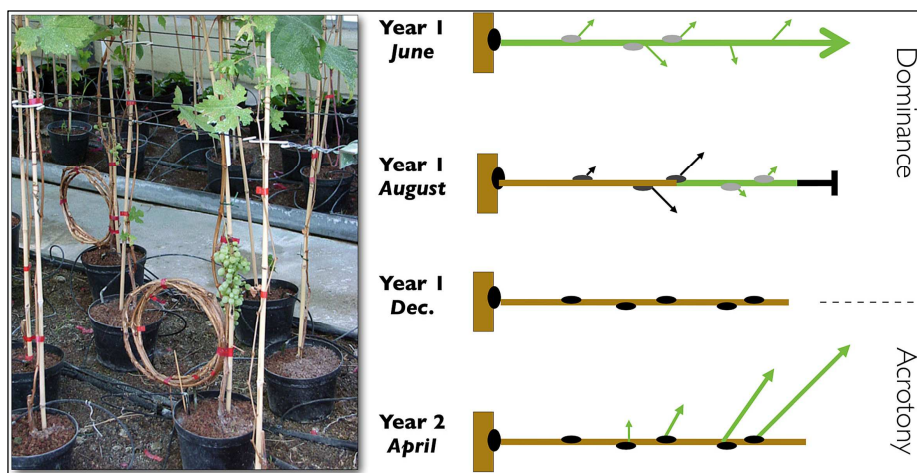


340
 341 **Figure 7 - Diagram of the combined effects of apical dominance, acrotony and vigor on**
 342 **vegetative development of the *Vitis vinifera* grapevine.** A) During the season, the apical
 343 dominance prioritizes the growth according to the rank of the meristems with the gradient
 344 $R_0 > R_1 > R_2$. 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.



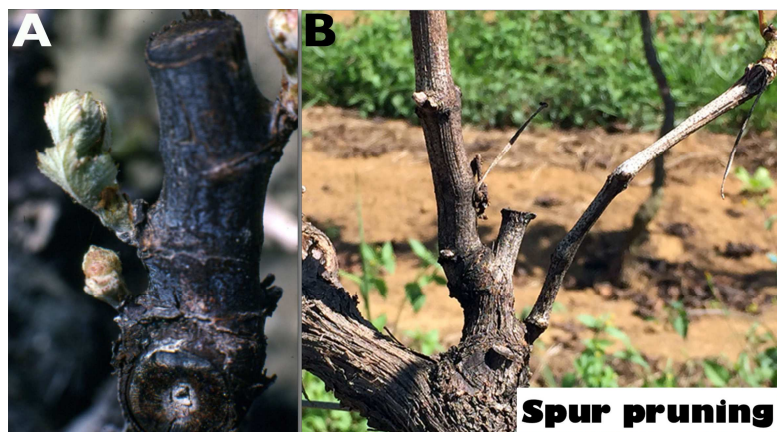
387

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

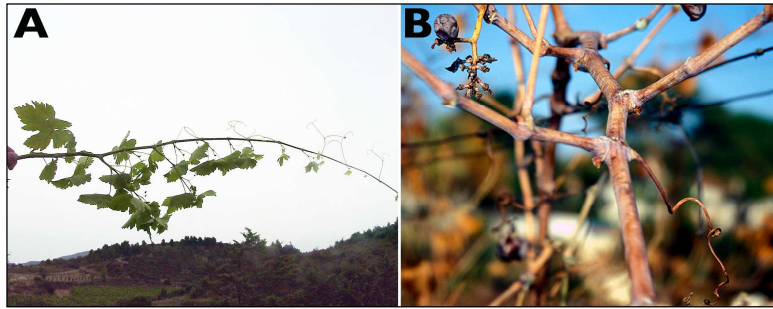
423 the shape of the shoots of scion and rootstock varieties, which varies from erect to curved forms
424 (Galet, 1990).

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 R₂ 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 (R₁). 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.

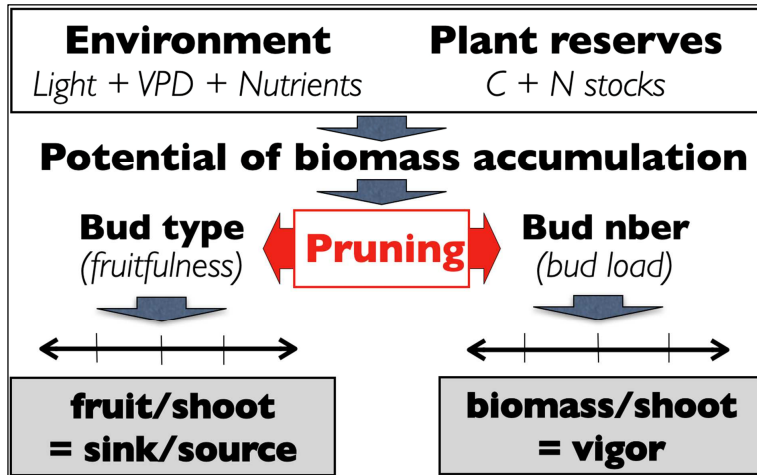
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454 Moreover, intra-shoot trophic competition can modify lateral shoot development (Pallas et al.
 455 2008). While, phytomer production on the primary axis and the probability and timing of
 456 proleptic axes is not affected by trophic competition, 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**

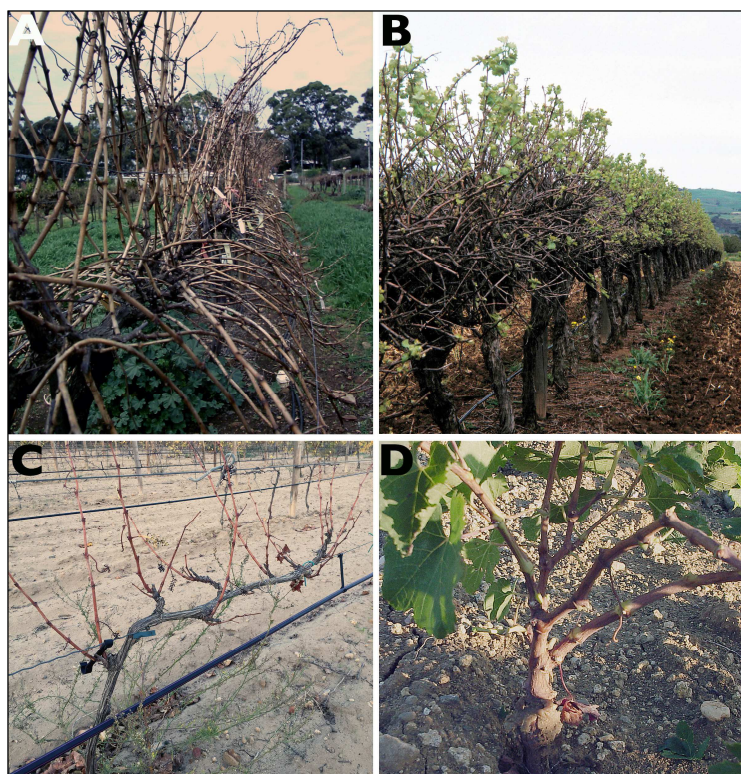
463 All practices influencing the potential of biomass accumulation can modify the vegetative
 464 architecture of the *V. vinifera* grapevine (Branas, 1975; Champagnol, 1984; Keller M, 2020;
 465 Carbonneau et al., 2020). Nevertheless, winter pruning is probably the most powerful tool to
 466 modify 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

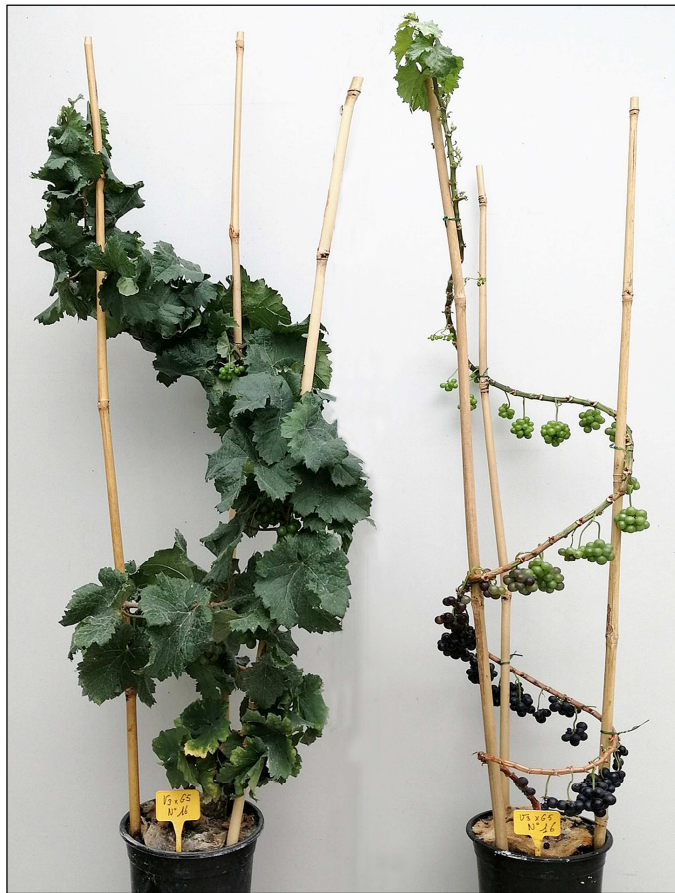
537 **Supplementary material n°5 - Figure S5 - Monumental wild *Vitis vinifera* ssp. *sylvestris***
538 **grapevine plant near the ancient Lycian site of Kaunos** (near Antalya on the south coast of
539 Turkey). In the creek, the vegetation covers various shrubs and multiple trunks climb to a pine
540 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 4-6th 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 R₂ proleptic
606 varies from 1 to 3, exceptionally 4. The maximum fruitfulness is observed for the proleptic axes

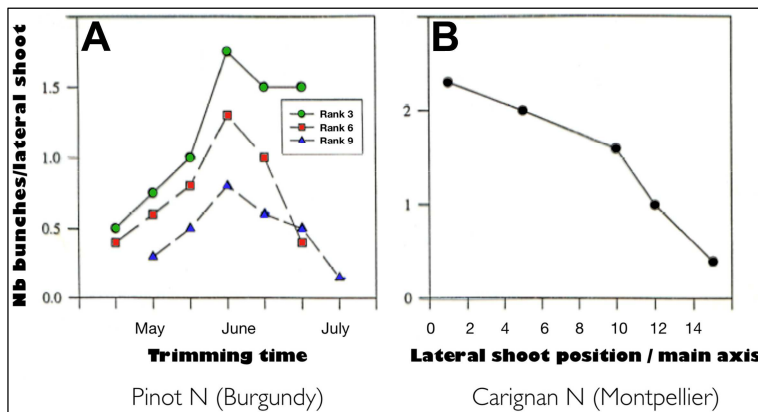
607 developed in the medial zone of the bearing stem, i.e. for 5-15th phytomers from the stem base
608 (Huglin and Schneider, 1998). The fruitfulness of R₃ proleptic axes is 5-10 times lower than
609 that R₂ stems but the distribution of clusters is not modified. Proleptic shoots developed from
610 old 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 R₁ 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 **syллеptic 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 syллеptic 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 R₀ and R₁) 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 R₂ winter bud development can only be obtained after R₀ SAM trimming and all
656 lateral shoot (R₁) 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 (CH_2Ca) or hydrogen (CH_2N_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

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