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

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Abstract

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

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

1. Introduction

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

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

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

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

The understanding of regulatory mechanisms of the shoot organization is essential either to optimize the use of energy resources and nutrients or to ensure some stability and sustainability 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 sheating 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

propagation (cutting or grafting) will have the same biological properties (Torregrosa et al., 2011); theoretically the lifespan of a genotype is underterminate;

ii) Due to the structure of their caulinar meristem (Doerner, 1999; Nougarède, 2001; Torregrosa et al., 2011), higher plants vegetatively-propagated as grapevine, can accumulate different non-lethal somatic mutations in the different bud meristematic layers (L1/L2/L3 territories). If located in the initial cells of a bud meristems, this allows to establish somaclonal variants by vegetative propagation (cutting or grafting);

iii) To challenge environmental fluctuations, an adult plant needs to develop a range of axillary meristems with different structures and functions.

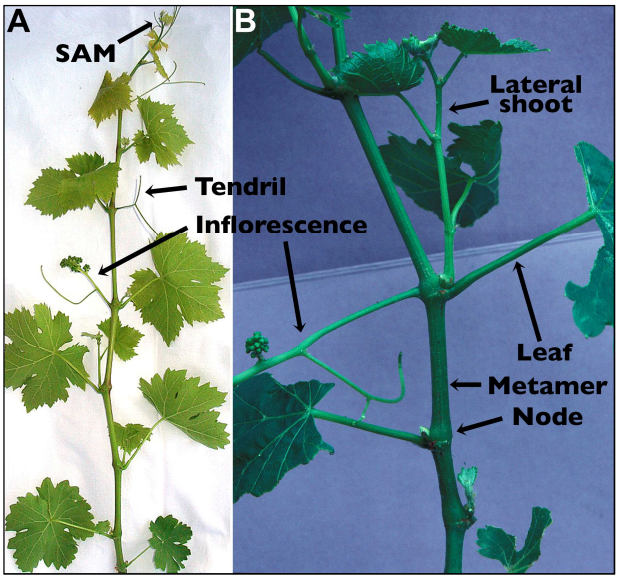


Figure 1 - Structure of the *Vitis vinifera* grapevine shoot. A) General view of a growing shoot. B) Details of the phytomer organisation.

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

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

Meristem				**Resulting**
Order	**Position**	**Function**	**Common name**	**stem name**
R_0	End of the growing axe	Growth, Organogenesis, Primary anatomy	Apex, SAM (Shoot Apical Meristem)	Main shoot or cane
R_1	Axillary to R_0 leaf	Immediate ramification	Lateral meristem	Lateral shoot
R_2	Axillary to R_1 pre-leaf	Delayed ramification	Winter or latent bud	Main shoot (at the next crop cycle)
R_3	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
N/A	*Intercotyledonary tissues*	*Growth, Organogenesis, Primary anatomy*	*Caulinary meristem*	*Epicotyl*
N/A	*Epidermis*	*Bud neoformation*	*Adventitious bud*	*Neoformed shoot*

R_0 corresponds to the primary meristem, R_1 axillary meristems initiated by R_0, R_2 axillary meristems initiated by R_1 and R_3 axillary meristems initiated by R_2.

Table 1 - **The different types of meristems or buds of the *Vitis vinifera* grapevine**. At each crop cycle, the ranks of the shoot apical meristem are reset to R_0. In italic, caulinar meristems that are not present on an adult plant grown in field conditions.

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

The shoot apical meristem (R_0) - This is the tip of the main growing stem. It develops all the organs of the stem including axillary meristems, and the tissues of the primary anatomy (Fournioux, 1995).

The lateral shoots (R_1) - There are the first lateral meristems formed by R_0, axillary to each leaf and of each node (Bugnon, 1953; Bugnon and Bessis, 1968; Deloire et al., 2020). Except in the case of excessive vigor or early shoot tipping (trimming), this axis develops only a few centimeters without lignification. At the end of the ongoing vegetative cycle, it undergoes an abscission that leaves a scar on the R_0 main stem (**Fig. 2A**). The phyllotaxis of R_1 is orthogonal to R_0. In general, no attempt is made to encourage the development of lateral shoots because they degrade plant microclimate by increasing leaf density while they produce little bunches late to ripe.

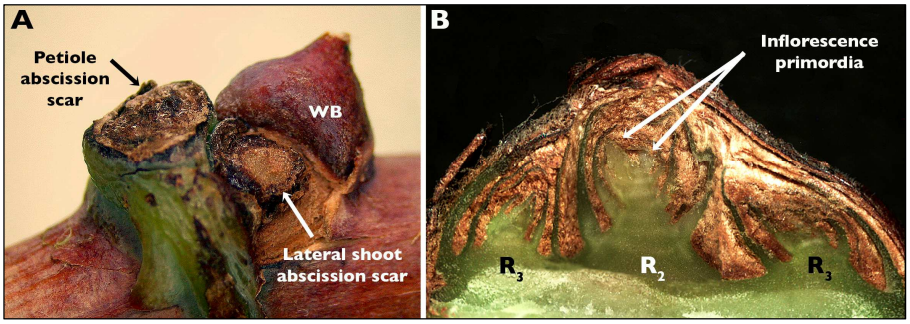


Figure 2 - External (A) an internal (B) views of the *Vitis vinifera* winter bud (WB). A) Presence of the scars of the leaf petiole and of the lateral shoot at the base of the WB. B) Longitudinal section of a WB in the R_2 plan of phyllotaxis. At the end of the R_2 axis, in positions 4 and 5, two primordia of inflorescences are visible; at the base of the R_2, two secondary WB axes (R_3) are present.

The winter buds (R_2+R_3) - R_2 are the first axillary meristems formed by the lateral shoots. This meristem is initiated axillary to the first R_1 pre-leaf (Carolus, 1970) which form the first scale of the R_2 winter bud (**Fig. 2B**). This structure evolves into a complex of buds (the gemmary

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

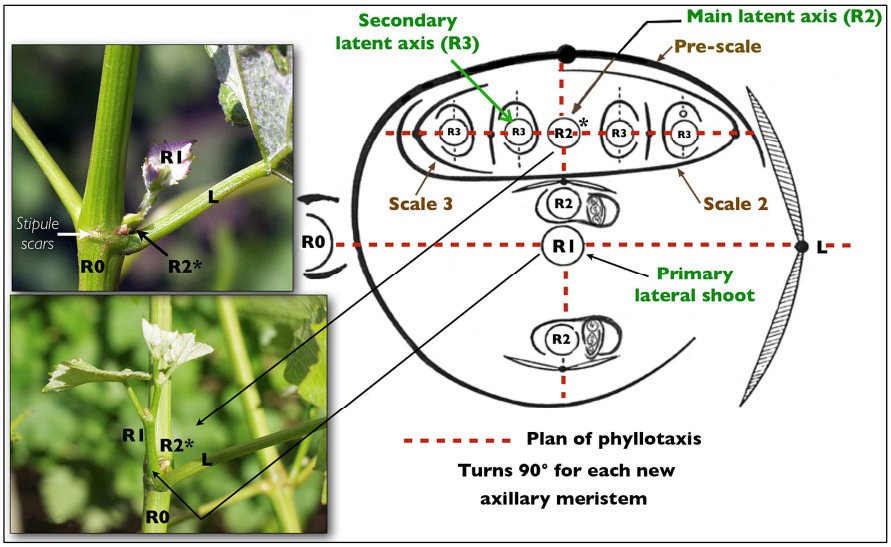
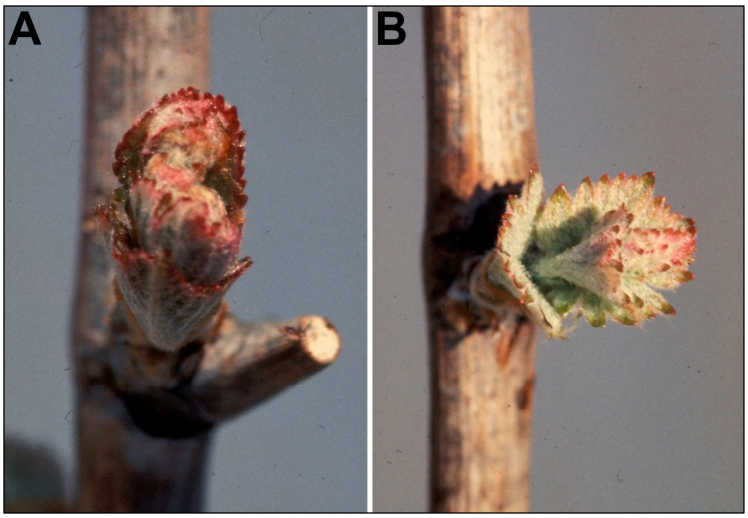


Figure 3 - Organization of the axillary meristem complex of the *Vitis vinifera* grapevine (adapted from Bugnon, 1953). Main shoot (R_0), lateral shoot (R_1), main winter bud meristem (R_2), secundary winter bud meristems (R_3), leaf (L).

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



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

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

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

2.2. Shoot system architecture: sympod vs. monopod

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

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

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

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

The monopodial model: Here, the terminal meristem does not stop organogenesis until a terminal bud is formed at the end of a growth cycle. This terminal bud will resume the growth of the bearing axis by setting up one or more new growth units (indeterminate primary growth). According to this classification, the domesticated *V. vinifera* follows the sympodial model in temperate climate. Non-hardened tips do support the maintenance of apical buds to ensure the continuity of growth from a cycle-to-cycle (**Fig. 4**). During the latent period, all buds enter in dormancy (see section 5) and the structure will remain frozen until the next growing cycle. Further development of the previous main stem R_0, will only be possible from axillary meristems. As mentioned before, as lateral branches R_1 do not generally lignify, R_2 winter buds of the bearing axis normally resume the growth. If R_2 is damaged, R_3 (and in some cases R_4) meristems can take over to establish a new R_0 and continue branch development.

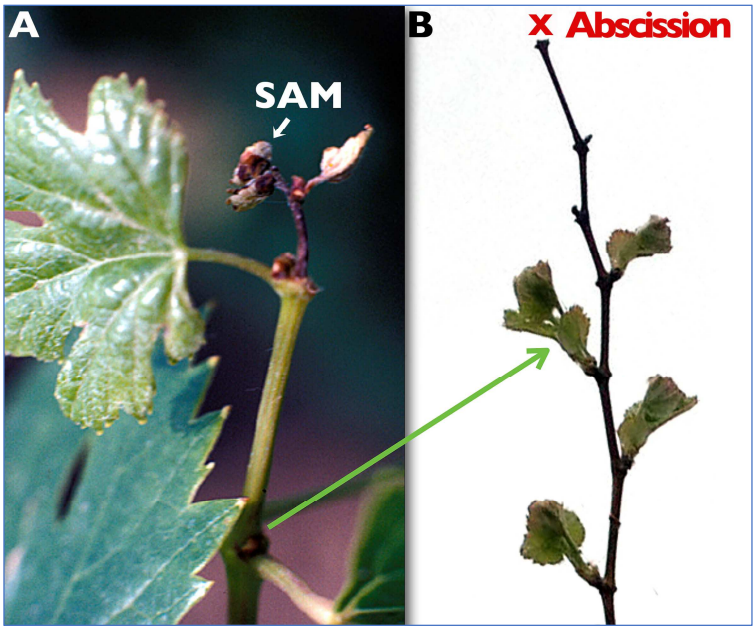


Figure 4 - **The sympodial *Vitis vinifera* grapevine model**. A) At the end of a growth cycle, phyllochron first slows down, then apex becomes necrotic and drop down. B) At the next cycle winter buds will resume the growth of the nearing axe by lateral development. SAM (Shoot Apical Meristem). X indicates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

2.3. Ternary rhythm organization of the adult grapevine stem

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

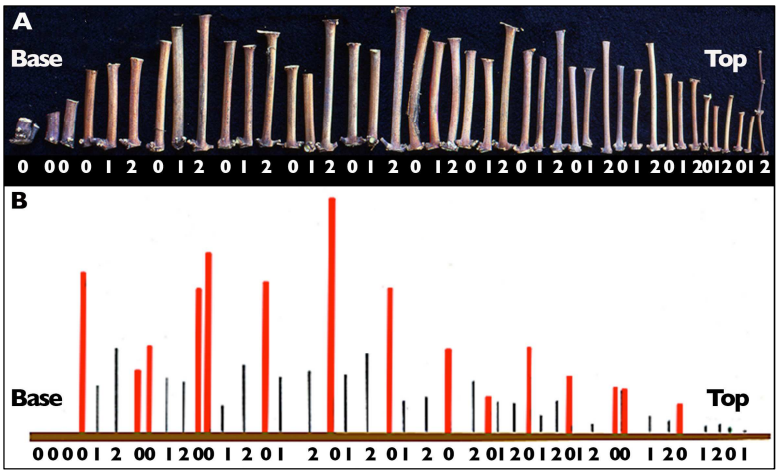


Figure 5 - **Ternary rhythmic organization of the phytomers (P_0-P_1-P_2) of the *Vitis vinifera* grapevine**. A) The distribution of the phytomer length from the base to the top of a stem of the variety Carignan after growth arrest, showing a maximum metamer length in medial sector of the vegetative axis, with locally, P_2 phytometer to be the longest. B) The distribution of the lateral shoot length on a vigorous main stem of the variety Ugni Blanc, showing that branches from P_0 phytomers are regularly the longest (adapted from Bouard, 1966).

2.4. Origin of the ternary rhythm and the three leaf helices

At juvenile stage (seedling), the stem meristem, which does not form oppositifoliated organs and has only one territory of vegetative organ differentiation, displays leaves following a single helix according to an alternate spiral model of phyllotaxis (foliar angle of 2/5). In adult vines, the apical meristem, which can develop oppositifoliated organs (tendrils or inflorescences), has three distinct territories of vegetative organ differentiation, display leaves arranged according to an alternate distichous model of phyllotaxis (foliar angle of 1/2). Oppositifoliated organs are distributed along three leaf helices resulting in the previously described ternary rhythm of organogenesis. However, under extreme growth intensity, in tropical climates for instance, this structure is disturbed due to a position shift of the leaf and the tendril or bunch (Supplementary material n°2 - **Fig. S2**), revealing the reality of the construction of the shoot architecture in 3

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

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

2.5. Nature of vegetative axes: Syllepsis vs. Prolepsis

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

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

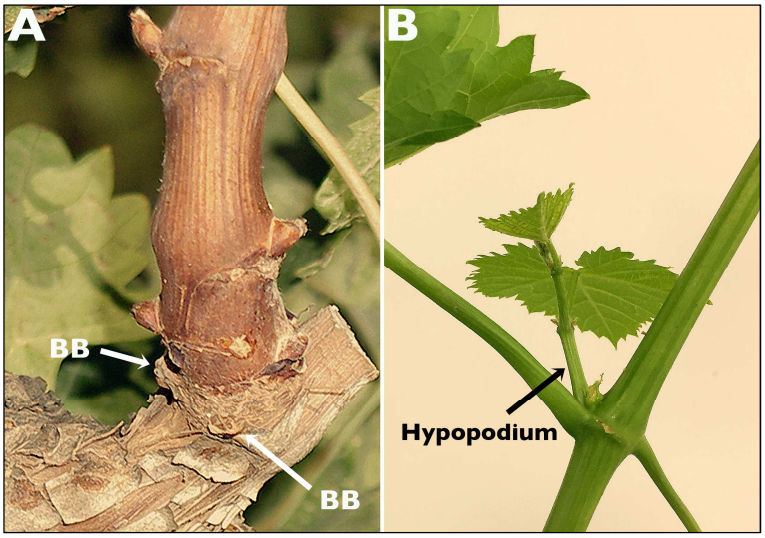


Figure 6 - External view of proleptic and sylleptic axes' base of the *Vitis vinifera* grapevine. A) A proleptic axis displaying phyllotaxis parallel to the bearing spur with the first phytomers been very short. The base present scales scars and several rudimentary basal buds (BB). B) A sylleptic shoot displaying phyllotaxis orthogonal to the bearing stem and a long hypopodium.

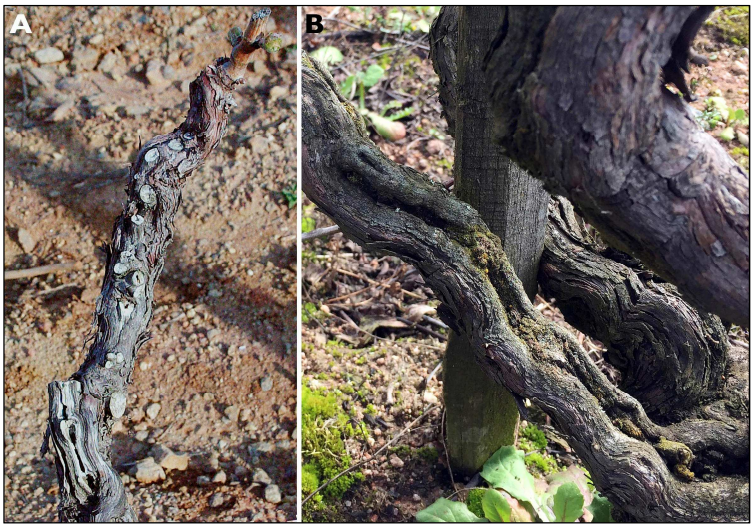
A number of morphological features differentiate sylleptic from proleptic shoots (**Table 2**). The most obvious appear at the base of the axes. In proleptic shoots, first phytomers emerging at budburst and located in the proximal section are very short (**Fig. 5a**) with rudimentary caulinary organs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

	Type of shoot	
Characteristics	**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

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

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

The second consequence concerns the management of the vascular tissue architecture. As mentioned above, internal anatomy of the grapevine stem follow a dorsiventral symmetry (Fournioux and Bessis, 1979). Winter buds of the main axes are systematically preferred to those of sylleptic axes, as the lineage of successive R_2 meristems follows the same plan of phyllotaxis. This has two interests: i) to maintain optimized vascular continuity between stems of different ages limiting the complexity of the sap pathways and ii) to localize pruning wounds and resulting wood necrosis in same phyllotaxis plan (Supplementary material n°3 - **Fig. S3**). But the non-respect of this rule is not fatal as grapevine has a good capacity to bypass the sap circuits damaged by pruning wounds (Zhang and Carbonneau, 1987).



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

2.6. Priority of shoot development: Apical dominance vs. acrotony

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

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

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

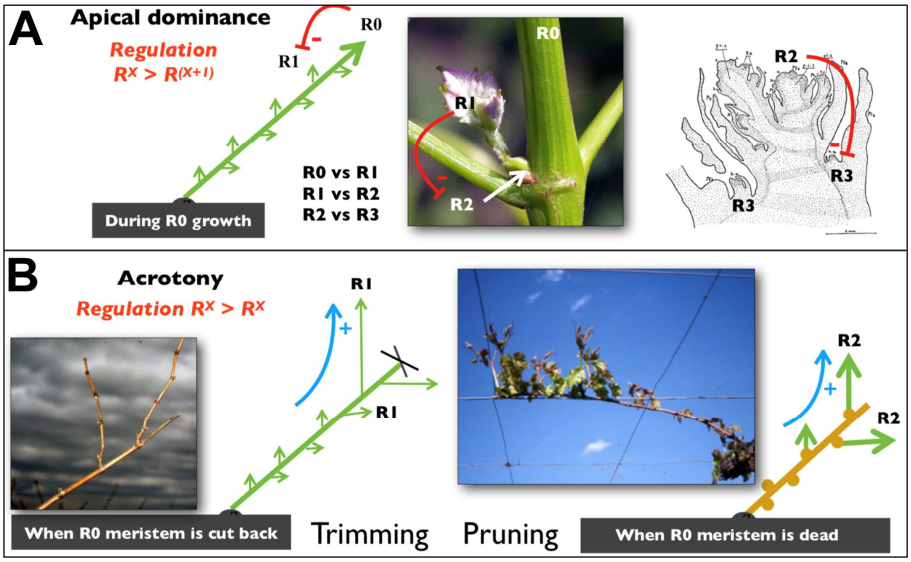


Figure 7 - Diagram of the combined effects of apical dominance, acrotony and vigor on vegetative development of the *Vitis vinifera* grapevine. A) During the season, the apical dominance prioritizes the growth according to the rank of the meristems with the gradient R0>R1>R2. B) The acrotony and the bearing shoot vigor favour the distal meristems when growth resumes: on the left, during the vegetation cycle for the sylleptic shoots (R_1) after apex (R_0) removal; on the right, at the next vegetative cycle, after winter buds (R_2) budburst establishing new proleptic axes.

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

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

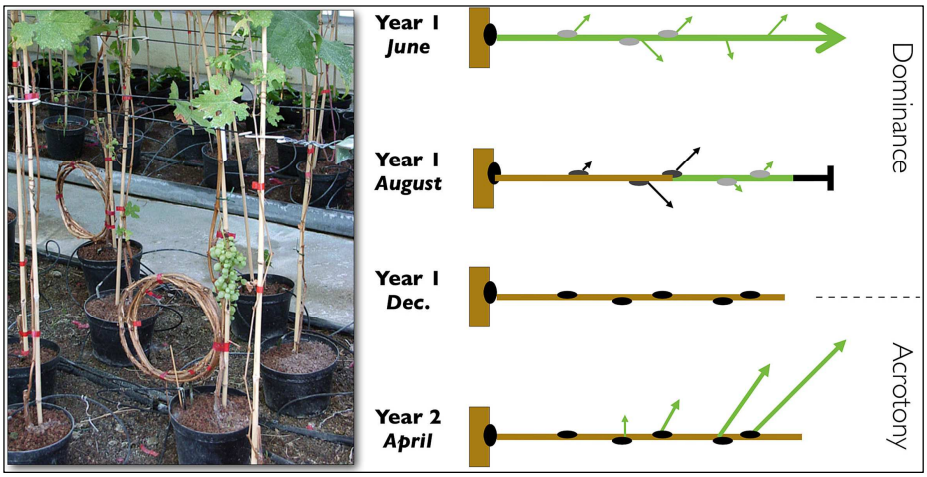


Figure 8 - Combination over 2 growth cycles of apical dominance, acrotony and correlative inhibitions, that condition the primary growth and branching of the *Vitis vinifera* grapevine stem.

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

Supplementary material n°4 - Figure S4 - Trunk extension of a very old *Vitis vinifera* grapevine plant managed through spur pruning in the South of France. Despite a constant control of the acrotony by spur pruning the perennial structures elongate.

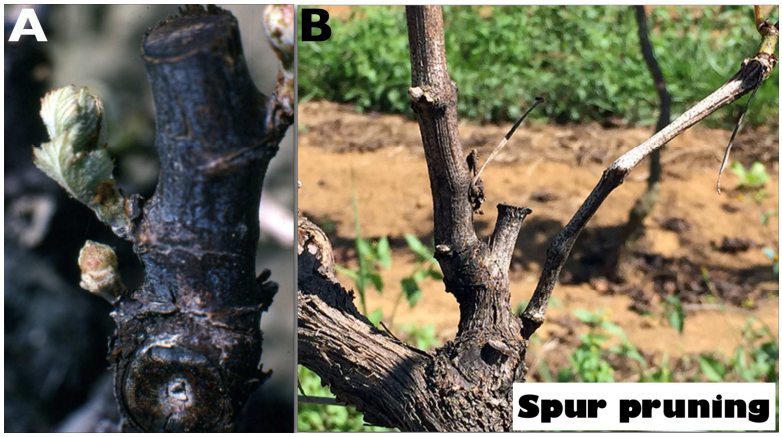


Figure 9 - Effect of acrotony on axes spur-pruned of the *Vitis vinifera* grapevine. A) In a temperate climate (Montpellier, France), shoots from winter buds ranked 2 and 3 are more early in bursting than the winter bud from the base. B) In a sub-tropical altitude climate (Pocos de Caldas, Minas Gerais, Brazil), at the end of the vegetative cycle, the proleptic axis from winter bud ranked 2 is more developed than the one developed from rank 1.

2.7. Other parameters impacting the vegetative structure

2.7.1. Morphological factors

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

As other perennial plants, the grapevine develops secondary tissues by successively differentiating vascular (VC) and subero-pellodermic (SPC) cambiums, the last been also called phellogen or cork cambium (Bernard, 1980). Located in the deepest layers of the cortex and developing poorly lignified cells (Pratt, 1974), the grapevine SPC plays a modest role in shoot architecture. On the other hand, VC, totally reconfigures the internal anatomy of the grapevine. VC produce several kinds of secondary tissues, in particular secondary xylem which will progressively become the main tissue of the stem (Fournioux, 1995). While the stem primary anatomy is rich in water and has little mechanical resistance to lateral deformations, secondary tissues gradually becomes rigid due to lignification (Bouard, 1966). In grapevine, there is some diversity in the length of the phytomers (Huglin, 1958) and in diameter of the metamers (Galet, 1990). Variability has also been mentioned for the ratio between supporting tissues and vascular and filling parenchyma, especially the balance between the pith and secondary xylem, which 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_2 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_1). 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 prolopetic axes, including reproductive structures (see section 4),
447 and finally lignify becoming perennial (**Fig. 10**).

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

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

2.7.3. Cultivation practices: plant biomass strength vs. shoot vigor

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

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

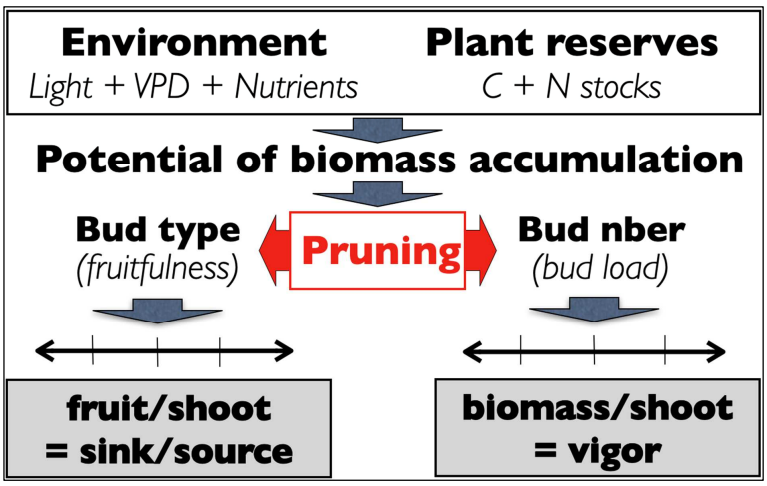


Figure 11 - Main factors to regulate plant biomass strength and shoot vigor of the *Vitis vinifera* grapevine.

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

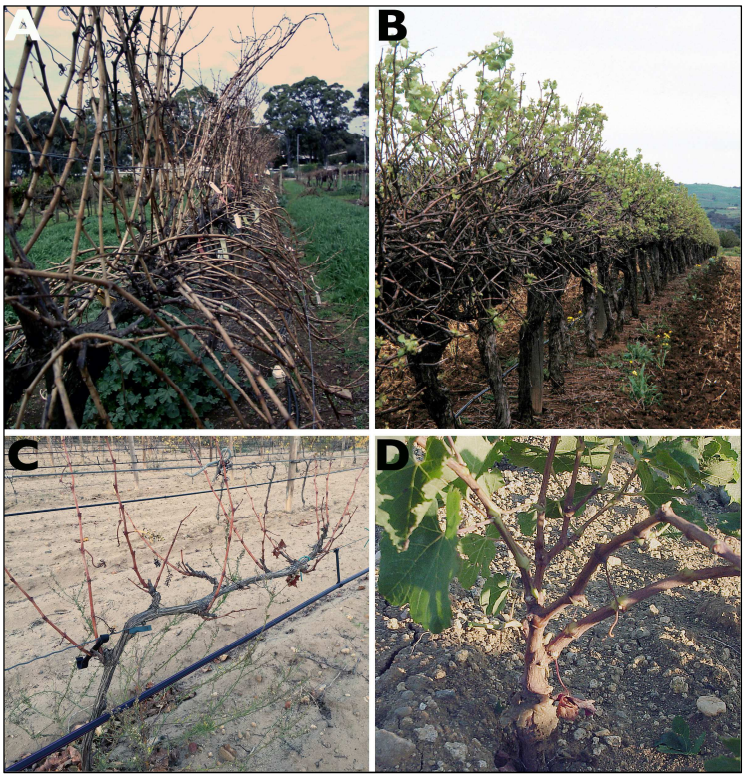


Figure 12 - The 4 extreme cases of the ratio plant biomass strength/shoot vigor of the *Vitis vinifera* grapevine: A) A powerful vine managed by hand pruning, displaying vigorous shoots. B) A powerful vine managed through minimal pruning with little vigorous shoots. C) A weak hand pruned vine with weak shoots. D) A young vine, with a low total biomass strength displaying very vigorous shoots.

2.7.4. Biotic factors

In a vineyard, various types of organisms can modulate the plant biomass strength and/or shoot vigor through direct or indirect effects. For example, the presence of weeds or cover grass impact on nutrient and water supply (Celette and Gary, 2013) with significant effects on development of the vines (Carbonneau et al., 2020; Morlat et al., 1993). The same with a range of pests and diseases that influence the assimilation of carbon or mineral resources. For example, leaf fungal diseases (e.g. downy or powdery mildew) reduce the quantity of the 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 (GFlV) 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

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

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

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 *Vvgai*1 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

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

4.1. Fructification of proleptic axes

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

During the primary growth of the main shoot, once a tendril has been formed, no more reproductive organs can be differentiated by higher ranked phytomers. This is true for the wild and domesticated genotypes, except for *Vvgai1* mutants (microvines and derivatives) which display a continuous flowering behavior regardless of the position and type of axes (Pellegrino et al., 2019).

In the non-dwarf genotypes, the potential of fruitfulness, i.e. the number and size of inflorescences primordia, of proleptic axes vary according to their position along bearing axes. In the *V. vinifera* grapevine, under temperate climate, the number of bunches per R_2 proleptic varies from 1 to 3, exceptionally 4. The maximum fruitfulness is observed for the proleptic axes

developed in the medial zone of the bearing stem, i.e. for 5-15th phytomers from the stem base (Huglin and Schneider, 1998). The fruitfulness of R_3 proleptic axes is 5-10 times lower than that R_2 stems but the distribution of clusters is not modified. Proleptic shoots developed from old wood buds are infertile the first year, but they develop a new generation of winter buds which display the same fruitfulness as the shoot arising from regular winter buds (Huglin and Schneider, 1998).

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

4.2. Fructification of sylleptic axes

As proleptic axes, the reproductive organs of sylleptic are the first oppositifoliated organs. Fruiting intensity of the lateral shoots is dependent on both, the resources available at axis level and the correlative inhibitions undergone by R_1 meristem at local level (Olivain and Bessis, 1987). In low or moderate conditions of vigor, in the absence of early SAM trimming, lateral shoots remain weak (<20cm) and exhibit a low fruitfulness (Olivain and Bessis, 1987). Olivain and Bessis (1988a, b) showed that the suppression of apical dominance can modify both the distribution and intensity of lateral shoot fruiting. Indeed, the potential of fruitfulness is decreasing with the insertion rank, which corresponds to a distribution of the potential fertility very different from that observed in non-trimmed vegetative axes. These observations firstly reported with the variety Pinot Noir in Burgundy by Olivain and Bessis (**Fig. 14A)**, were

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

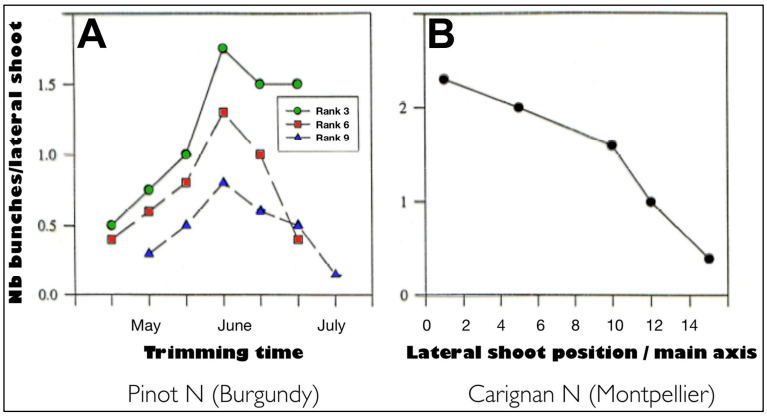


Figure 14 - Effect of the date and level (first proximal position=0) of apex trimming on sylleptic shoots' fruitfulness in the *Vitis vinifera* grapevine (redraw from Olivain and Bessis, 1988a,b and Boubals D., personal communication).

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

5. Seasonal effects: dormancy

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

successive stages (Fadon et al., 2020): i) **The pre-dormancy (para-dormancy)**, during which the development of the winter buds is prevented by correlative inhibitions (apical dominance of R_0 and R_1) and external physiological factors (limitation of the resources to growth at plant level, competition with reproductive organs during fruit maturation). During this period, an anticipated R_2 winter bud development can only be obtained after R_0 SAM trimming and all lateral shoot (R_1) removing (Gu et al., 2012; Pou et al. 2019); ii) **Dormancy or endo-dormancy**, which is mainly regulated by bud internal physiological factors (plant growth regulator balance). The release of endo-dormancy progresses gradually under the influence of cold temperatures (Nigond, 1966) or other abiotic stresses; iii) **Eco-dormancy**, which is only dependent of environmental factors, particularly to temperature regime (Camargo et al., 2017). After budburst, proleptic axis growth rate is determined by temperature and nutrient resources (plant biomass strength and vigor).

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

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

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

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

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

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

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

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

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

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

With *V. vinifera* varieties, the main problem is the absence of dormancy breaking due to insufficient low temperatures (Sudawan et al., 2016). The regulation of the vegetative architecture and the fruiting cannot be naturally established. A range of practices can be implemented to reduce bud endo-dormancy: severe water stress, defoliation with contact 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 ant 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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