

Buds of the grape vine primary shoot

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AXILLARY BUDS

A compound of buds is situated at each node of a primary shoot, at the axil of the leaf (Figures 1a, b & c). The portion of the stem which is situated between two nodes is called the internode.

The bud compound comprises:

1. A bud called **prompt**, or **anticipated** or **sylleptical bud**. This is not a true bud but a vegetative axil which is not protected by scales. Its initiation is systematic, but usually its development is limited to a few millimetres only. In the year of its formation it may, however, develop into a lateral shoot, called secondary shoot or laterals. Its fertility is usually very weak to zero, depending on the growth conditions and the cultivar. Its phyllotaxic plane is perpendicular to that of the principal shoot. The first axillary meristem produced by the prompt bud which appears at the axil of the leaf precursor evolves into a latent bud. The laterals could be used to form a cordon. The length of the lateral's internodes is more regular, which contributes to a more regular distance between two spurs when laterals are used to form a cordon.
2. The **latent bud** is a compound of vegetative miniaturised axils protected by scales. The principal axil of this compound is called the latent primary axil. The development of these structures is inhibited by the growth of the shoot on which it is differentiated (year n) and by the prompt bud. This nascent structure differentiates itself for 2 to 4 months during the growth of the bearer shoot before becoming dormant again. Its phyllotaxic plane is perpendicular to that of the prompt bud and consequently becomes parallel again to that of the bearer shoot. It is the bearer of the primary shoot's primor-

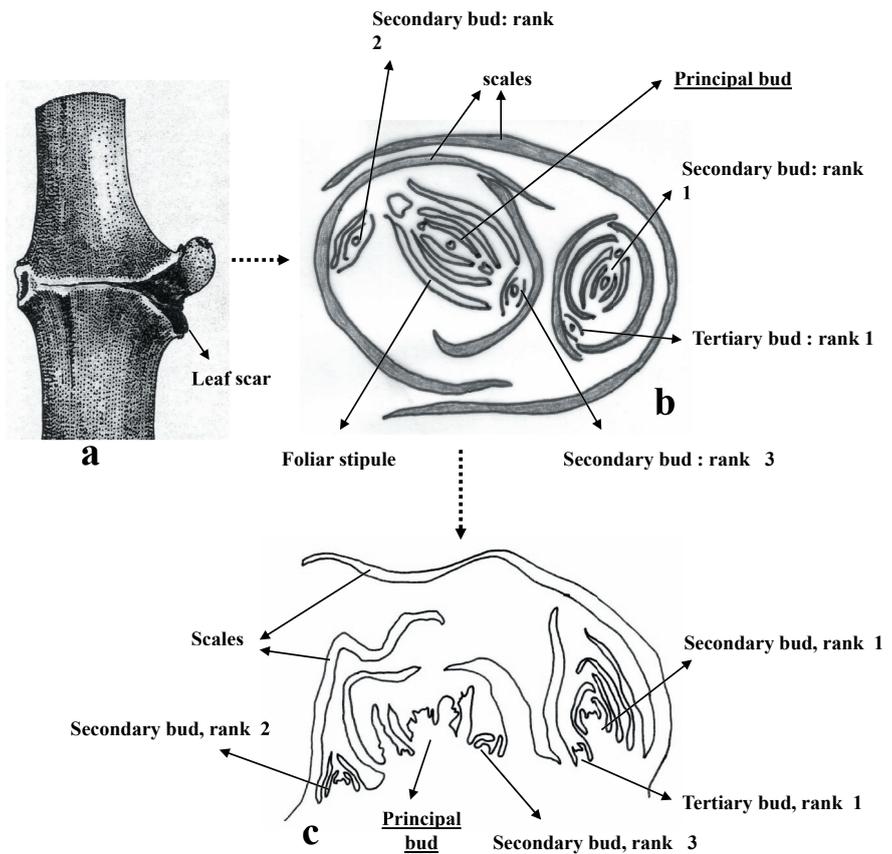


FIGURE 1A, B & C:

- a) Morphology of the latent bud at the completion of its differentiation.
- b) Transverse section of the latent vine bud.
- c) Longitudinal section of the latent bud.

At the end of its vegetative cycle, in the northern hemisphere in August and in the southern hemisphere in February, the differentiation of the primordia from the leaves and inflorescences is complete. At this stage the future flowers are not yet differentiated. Their differentiation starts at the beginning of the following spring through the formation of floral meristems (sources A. Deloire, 1982; Carolus, 1970). Fertility is generally considered to be the average number of inflorescences per bud. NB: Latent secondary and tertiary axils are represented on the same longitudinal plane, to facilitate understanding of the architecture of the latent bud; this is not actually the case.

dium of the following year (year $n+1$), qualified by the proleptic axil. The primary shoot's primordium bears the incipient inflorescences (Figure 2a, b & c) to the origin of the future grapes. Depending on the level of differentiation reached by the compound, the principal axil may comprise 4 to 12

preformed metameres (Huglin, 1986). The average number of incipient inflorescences that are present at the time when the differentiation ceases is called potential fertility* (on average 1 to 3 per latent bud). This fertility depends on the cultivar, and on the climatic and trophic conditions of the

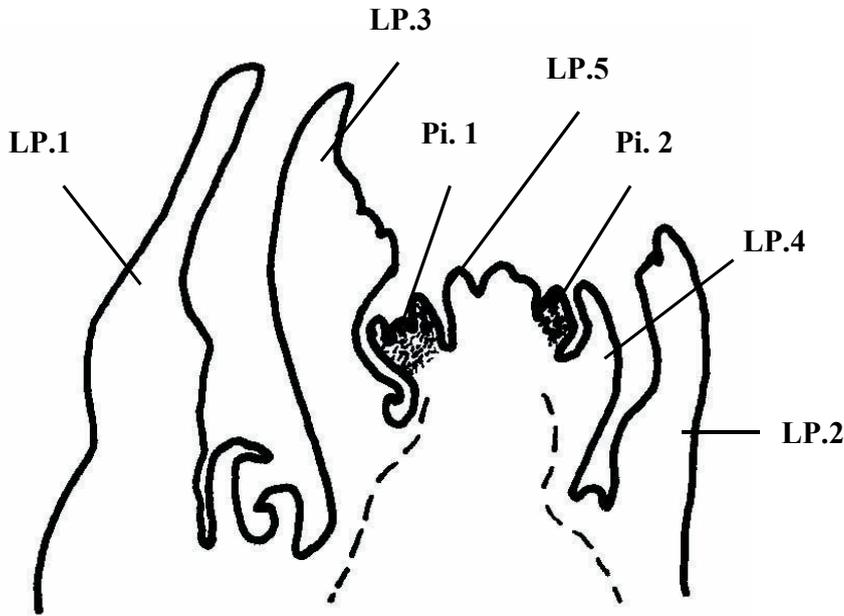


FIGURE 2: Longitudinal section of a latent bud showing the nascent of the future primary shoot (from Carolus, 1970).

Growth and differentiation of the latent bud are arrested in February (southern hemisphere) and in August (northern hemisphere). In this example, the primordium of inflorescence 1 is placed opposite the leaf primordium 4; the primordium of inflorescence 2 is placed opposite the leaf primordium 5. The future primary shoot will bear 2 bunches in position 4 and 5 from the bottom. LP: leaf primordium; Pi: primordium of inflorescence.

year in which the bud is formed. During the subsequent vegetative cycle, the newly formed organs and tissues (incipient inflorescences, primordium of leaves and tendrils, preformed internodes) will develop into the precursor of the shoot, which will be lengthened by the meristem if conditions (climate and cultural practices) favour growth. So the grapevine yield depends on climate and on cultural practices for two years (versus two growth cycles).

Inside the latent compound are the secondary buds (or counter buds or replacement buds) situated at the axil

of the primary bud, which behave in similar vein as the primary bud, but do not grow unless conditions are exceptional (climatic accidents such as frost or hail, which could destroy the principal shoot undergoing development) or in instances of vegetative disequilibrium (excess vigour). The fertility of latent secondary axils is usually weak. The phyllotaxic planes cross one another: That of the principal shoot is perpendicular to that of the prompt bud, which in itself is perpendicular to that of the latent bud, which in turn is perpendicular to that of the secondary

bud. The planes of the latent buds are therefore parallel to those of the principal shoot and the planes of the secondary buds are perpendicular to those of the principal shoot.

* Some authors use the term fertility for the number of inflorescences per shoot. The number of flowers depends on the size and the number of the inflorescences, as well as the parameters of the particular cultivar. Fertility expressed as the number of flowers per principal shoot (instead of the number of inflorescences) may be called "floribundity".

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The primary shoot of the vine (called cane in winter)

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The primary shoot (called cane in winter) is described in Figures 3 and 4. The young green growth from the latent bud is called a primary shoot. The shoot consists of an apex (shoot tip), nodes, internodes, buds, tendrils, leaves, inflorescences or/and bunches, and secondary shoots (laterals).

The rhythm of the primary shoot growth occurs according to the sympodial theory (Figure 5). The growth of the primary shoot takes place in accordance with a precise rhythm: two consecutive nodes, which bear one leaf and one tendril each, are followed by a node which has one leaf but no tendril. Two bunches are situated at the bottom section of a primary shoot, instead of tendrils. The bunch is opposite the leaf.

This sympodial rhythm has an effect on the internode length (N1-N2 > N2-N0) (Louarn, 2005). The lateral developed from the prompt bud in position N2 (Figure 5) is generally longer than those situated in position N1 and N0. The surface of the leaf in position N2 is more important than those in position N1 and N0 (Carbonneau, 1976).

In practice the apical dominance principle impacts on the growth of laterals (Figure 6). The growth of the laterals depends mainly on the vigour of the vine, the choice of training system and canopy management. At the beginning of their development, laterals compete with the rest of the vine (for sucrose, minerals, etc.), and when they reach a certain length ($\geq 30\text{cm}$), they may be a source of carbohydrates and provide sucrose, and some other compounds, to the bunches. Laterals could be useful in the completion of the ripening process and could also protect the bunches from excessive exposure to the sun (Hunter, 2000; Hunter & Archer, 2001; Hunter *et al.*, 2004).

Acrotonie is different from apical dominance in the sense that it concerns the winter cane. On a long winter cane, the top buds will develop first and their growth will inhibit the development of the buds situated underneath (Figure 7). This principle should be borne in mind when pruning canes and selecting a pruning system that will influence the shape of the canopy.

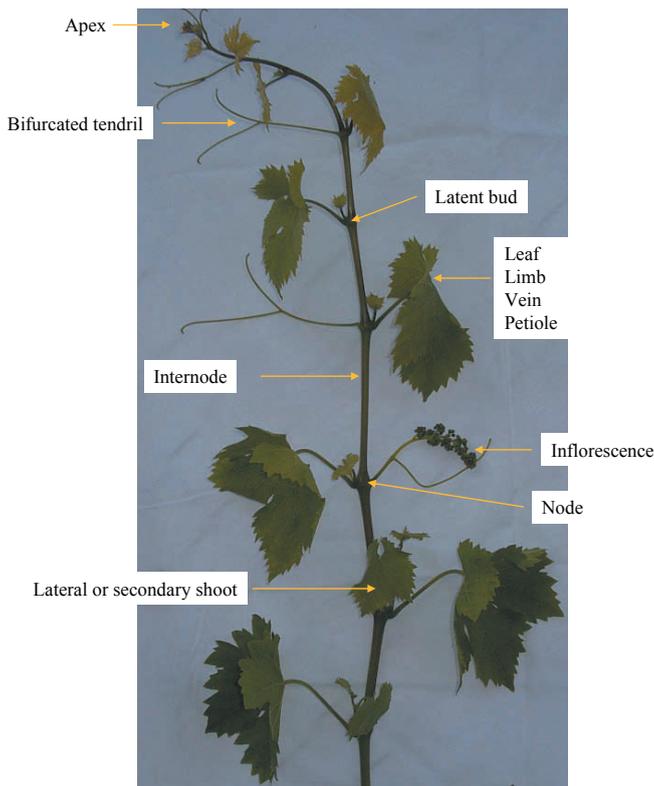


FIGURE 3. Description of a grapevine growing primary shoot.

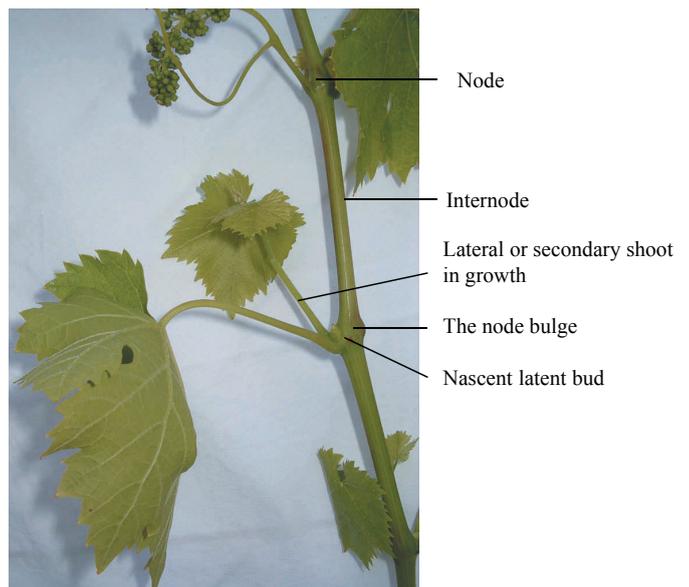


FIGURE 4. Organisation of a node of the primary shoot. The phyllotaxic plane of the lateral (secondary shoot) is perpendicular to that of the primary shoot and to that of the latent bud. The phyllotaxic plane of the latent bud is parallel to that of the primary shoot.

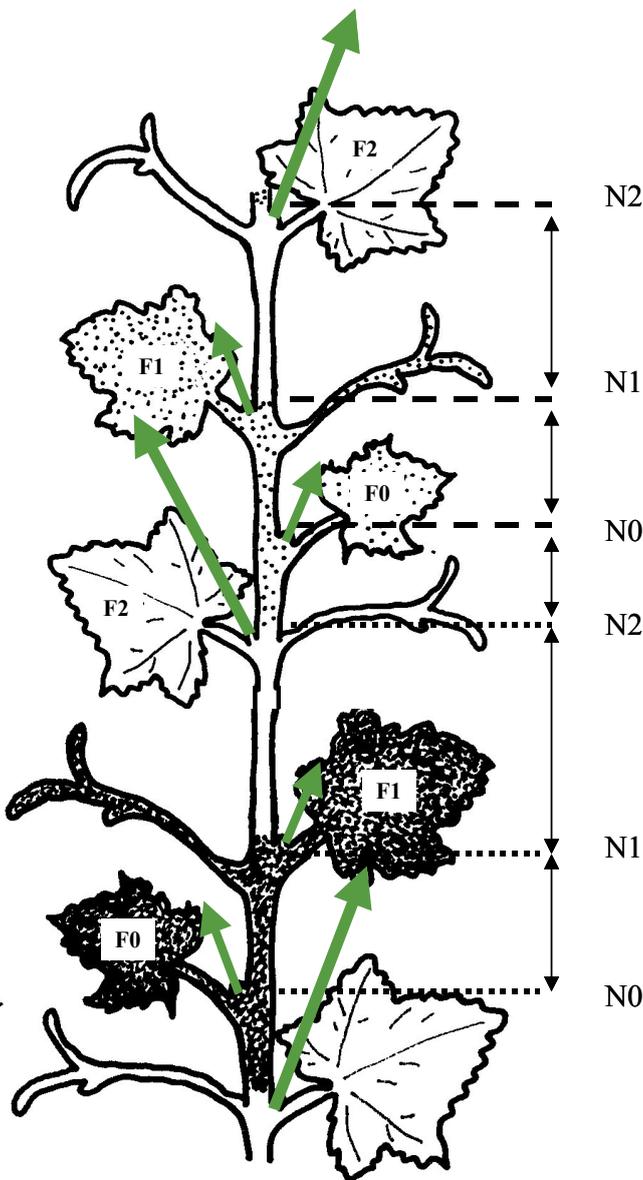


FIGURE 5. Sympodial theory (from Zimmermann, 1954 & Bouard, 1966). The growth of the primary shoot occurs according to a precise rhythm: two consecutive nodes which bear one leaf and one tendril each (see N1-N2) are followed by a node which bears one leaf but no tendril (see N0). This sympodial rhythm has an effect on the internode length ($N1-N2 > N2-N0$) (Louarn, 2005). The lateral developed from the prompt bud in position N2 is generally longer than those situated in position N1 and N0. The surface of the leaf in position N2 is more important than in position N1 and N0 (Carbonneau, 1976).



FIGURE 6. Example of apical dominance of a grapevine primary shoot.
 1) When the apex is present, the laterals from the bottom of the shoot grow first.
 2) When the apex is removed (cutting of the shoot tip), laterals which are directly under the apex begin to grow; the laterals situated at the bottom of the shoot continue their growth.
 3) A severe shoot cutting at the flowering period will involve the development of the laterals situated at the bottom of the shoot according to the vine's vigour.

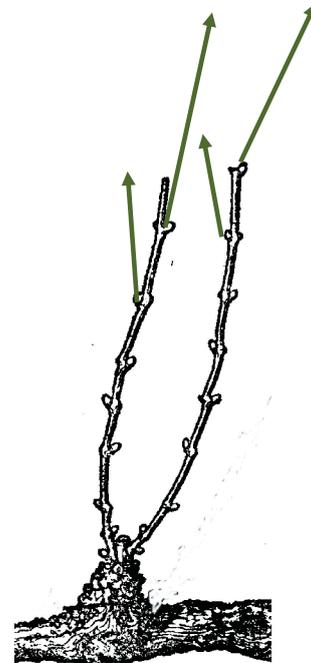


FIGURE 7. On a winter cane, growth is acrotone. In general, the top latent buds will grow first. This is why, for some pruning system, it is necessary to bend, or to position horizontally, the cane to prevent the acrotonie.

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Grapevine inflorescence and tendrils

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THE INFLORESCENCE AND THE FLOWERS

The development and the morphology of the inflorescence and its flowers are described in Figures 8, 9, 10 (a & b) and 11 (c & d) respectively.

The primordial inflorescences are formed in the latent bud of year « n » of the vegetative cycle. In the following spring they become differentiated during the growth of the primary branch on which they are borne (Figures 8 & 9).

At the time of bud break, when stage 5 leaves are displayed, the inflorescences are visible at the far end of the primary shoot (Figure 8) and carry the first outlines of a flower. The formation of floral meristems, having started at bud break, continues and the flowers are differentiated and completely formed when the primary shoot has developed 16 to 20 leaves (Figure 10a & b).

This differentiation is temperature dependent ($T^{\circ} \geq 12^{\circ}\text{C}$) (Pouget, 1963). If high temperatures are experienced during bud break and at the beginning of the growth of the primary shoot, the differentiation of the inflorescence may be disturbed and the latter may be transformed into a tendril. Morphologically, the inflorescence is a small modified shoot. In certain situations one of the axes of the inflorescence may differentiate itself into a shoot with a normal growth pattern bearing vegetative organs.

One inflorescence may carry 200 to 1 000 flowers depending on the cultivar and the climatic and trophic conditions during the differentiation of the flowers. The gender of the vine flowers depends on the genotype.

Flowering takes place, in other words the dehiscence of the floral caps (Figure 11c & d) fertilisation may take place.

PRUNING ON VINEYARD PERFORMANCE

The formation of the inflorescences and the vine flowers depends on the climatic conditions of two consecutive years (two consecutive vegetative cycles), which in turn impacts on winter and spring pruning.

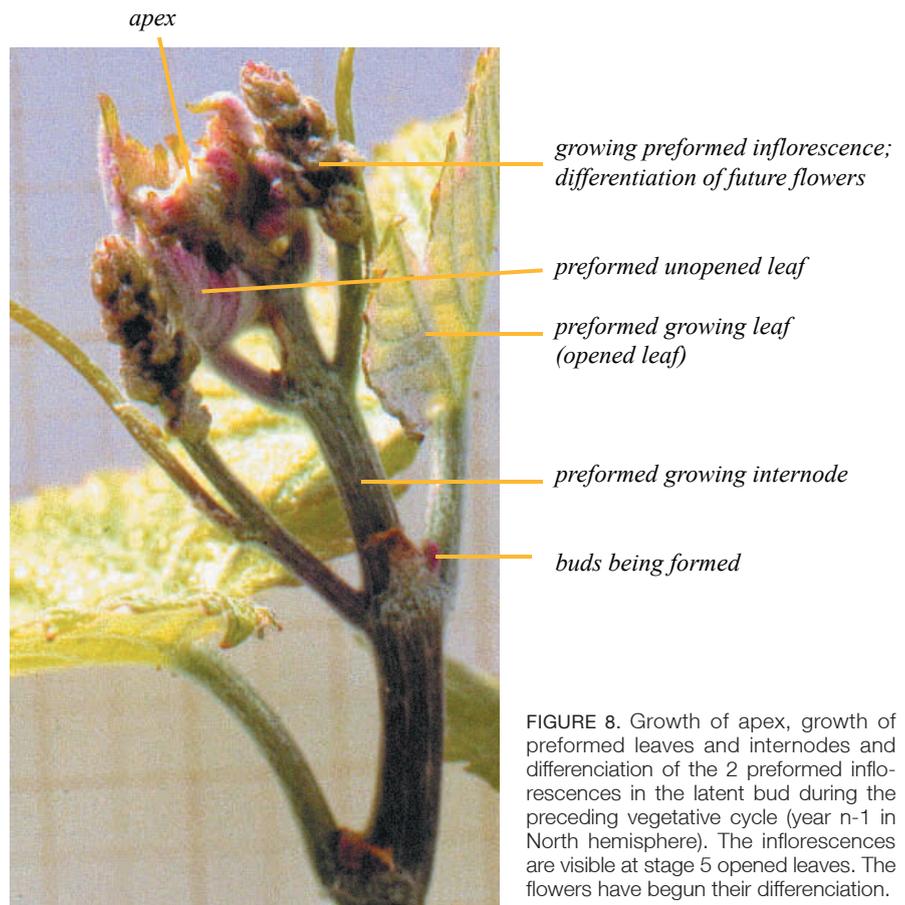


FIGURE 8. Growth of apex, growth of preformed leaves and internodes and differentiation of the 2 preformed inflorescences in the latent bud during the preceding vegetative cycle (year n-1 in North hemisphere). The inflorescences are visible at stage 5 opened leaves. The flowers have begun their differentiation.

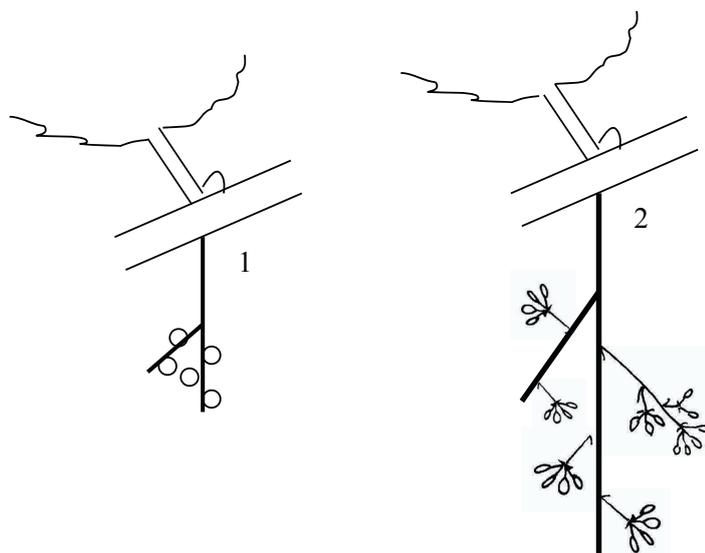


FIGURE 9. Schematic representation of the development of the inflorescence. The inflorescence (1) develops by lengthening its principal axis. The flower primordia are differentiated on the two axes of the inflorescence in a grape-like structure (1), and develop into flower cymes, a supplementary level of ramification on the inflorescence (2).



FIGURE 10a & b. Examples of vine inflorescences at full flowering stage (Syrah cultivar).

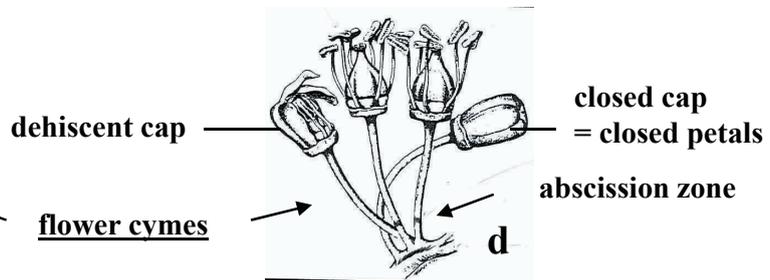


FIGURE 11c & d. c) Vine flowers arranged in a cyme. d) The dehiscence of the cap always takes place from the base (corolla = closed petals). The abscission zone of the flower is formed at the base of the pedicel.

As soon as the soil temperature is > 12°C, the roots develop (mainly the fine roots) and start functioning again, thereby allowing the absorption of water and mineral elements. The flux of xylem sap can be seen as tears (bleeding or exudation sap) which emanate from the pruning scars on the vine shoots. The growth of the future shoot is reactivated in the latent bud, before the onset of budding.

As a rule the vine should be pruned as soon as xylem activity recommences, which is beneficial to the fertility of the latent buds. If pruning occurs too early (for example directly after leaf drop) it may cause decreased fertility in the latent buds, when they become active again in spring. In actual fact, early pruning will lead to early bud burst, which may result in a disturbance of the differentiation of the inflorescences and the floral meristems caused by climatic conditions that are not optimal (Huglin, 1986; Archer & Champagnol,

1979; Champagnol, 1984). This principle is nevertheless often contradictory to economic constraints and manual labour related to the planning of pruning.

THE TENDRIL

Tendrils and inflorescence are similar organisms, in principle they are “oppositifoliées” throughout the entire *Vitis* genus. Both tendril and inflorescence have the same morphogenetic origin, they derive from the same meristem as the stem. The hormonal balance determines the vegetative or fructiferous evolution of the meristem of the latent bud. In the vine the gibberellines are inhibitors of floral differentiation. In the event of climatic or trophic problems at the time of bud break, the differentiation of the flowers on the inflorescence can be aborted or very incomplete, and where the future inflorescence was meant to be, a tendril may be formed (Bugnon, 1949). The tendrils of the *vinifera* vine are bifur-

cated. Their size is dependent on cultivar (for example Chasselas which has very large tendrils). The tendril helps the vine, which is a creeper, attach itself to any kind of support. It becomes lignified just like the vine shoot. It is worth noting that in *Vitis labrusca* the succession of tendrils is continuous, whereas in the majority of cultivars it is regularly discontinuous (Huglin & Schneider, 1998). “Filage” is a French term to describe the transformation of an inflorescence into a tendril proper (drying or non-differentiation of flower buds) (Rives & Hevin, 1966).

The transition from vegetative development to fructiferous development in a plant is a major, indispensable event in its survival through the production of seeds. Reproduction of plants depends on a compound of genes, notably homeotic genes. Some of these genes were recently identified in the vine (Sreekantan *et al.*, 2006).

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Grapevine flowers

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The flower of the vine, in which the differentiation of the floral parts is centripetal, is a pentameris (Figure 12a). It consists of 5 aborted sepals (calyx), 5 joined petals (corolla or cap), 5 stamens and an ovary comprising 2 carpels each enclosing 2 ovules. The opening of a vine flower corresponds to the detachment of the petals. This phenomenon may last from a few hours to several days. Flowering is usually spread out over 2 to 10 days. This depends mainly on the cultivar and the climatic conditions. At

the base of the pedicel of the flower is an abscission zone which is activated and which enables the flower to fall should it be dysfunctional. The question remains: does this abscission zone pre-exist or is it formed when a problem occurs? Current bibliography is still not conclusive (Bessis & Fournioux, 1992).

Vine flowers are male or hermaphrodite, the flowers having intermediary morphologies (Figure 12b).

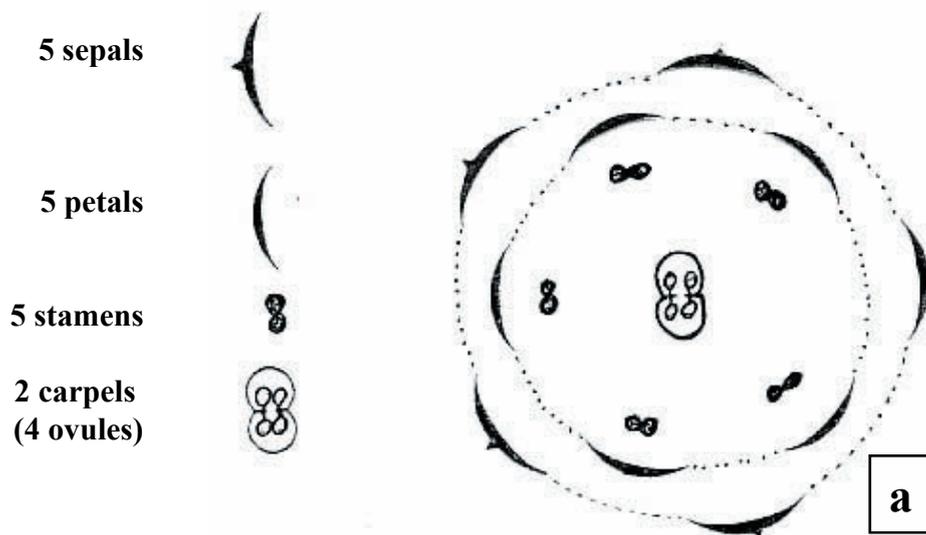


FIGURE 12A. The vine flower is a pentameris. The floral parts are formed in a centripetal manner. The flower consists of: 5 sepals (aborted) which form the calyx; 5 joined petals which form the corolla or cap; 5 stamens and an ovary comprising 2 carpels each with 2 ovules.

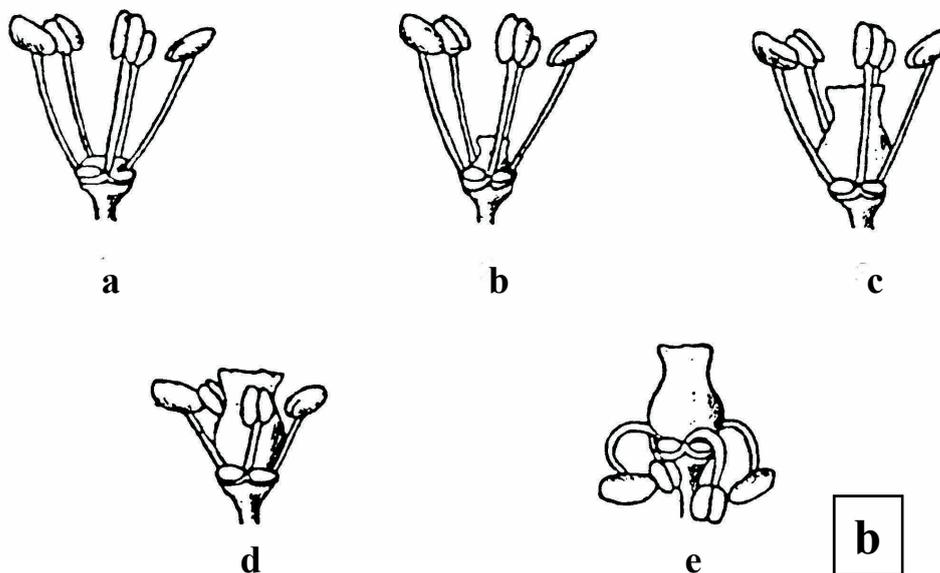


FIGURE 12B. Gender of vine flowers: a) male; b) hermaphrodite male; c) hermaphrodite; d) female with erect stamens; e) female with reflex stamens.

Grapevine flower fertilisation

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Flowering in the grapevine is the period during which fertilisation takes place.

THE MANNER OF FERTILISATION

The manner in which fertilisation in cultivated grapevines takes place is autogamous and/or heterogamous. When the flower cap drops, the stamens are separated from the gynaecium and rotate 180° (Figure 13a). Pollen is set free by the opening of the slit of the dehiscence (Figure 13b).

Figure 14 shows a longitudinal section of an ovule. There are 4 ovules in an ovary, each of which, after fertilisation, is able to differentiate one seed. In some grapevine varieties, there may be as many as 7 seeds.

The pollen grains which are deposited on the stigma germinate and the pollen tube has to reach the ovule through the style of the ovary. The two male gametes, transported to the furthest end of the pollen tube, will fertilise the 2 ancillary nuclei and the oosphere (female gamete), both of which are contained in the embryonic sac, to result in the albumen (3 n) and the embryo respectively (2 n).

The climatic and trophic conditions may impact on the formation of male and female gametes. This in turn could interfere with the positive outcome of fertilisation. The conditions at the time of fertilisation are important. The germination of pollen is mainly dependent on temperature and vine nutrition. Atmospheric temperatures below +15°C (Staudt, 1981) do not favour the growth of the pollen tube, thereby reducing the percentage of fertilisation. Mineral elements such as boron or zinc may encourage germination of the pollen tube. The formation of the ovule and particularly the embryonic sac may be disturbed by unfavourable climatic and trophic conditions. These organs are especially sensitive to temperatures below +15°C (Carbonneau & Ollat, 1993).

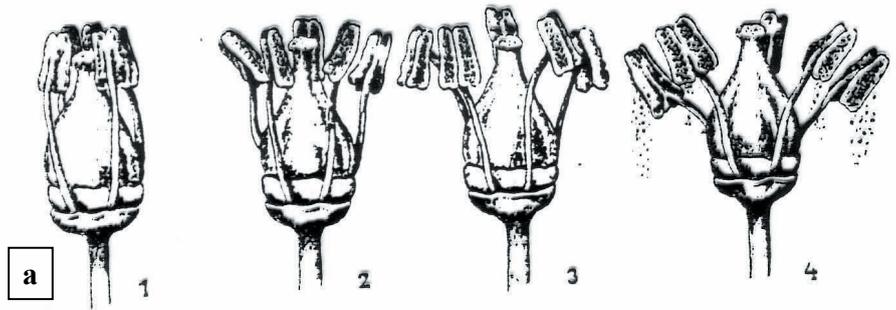


FIGURE 13 (a): Grapevine fecondation is autogamous (self pollinating plant: a1; a2) and/or heterogamous (mainly between flowers from the same inflorescence or between nearby inflorescences). When the cap falls, stamens move apart from the gynoecium and do a 180° rotation: a3; a4).

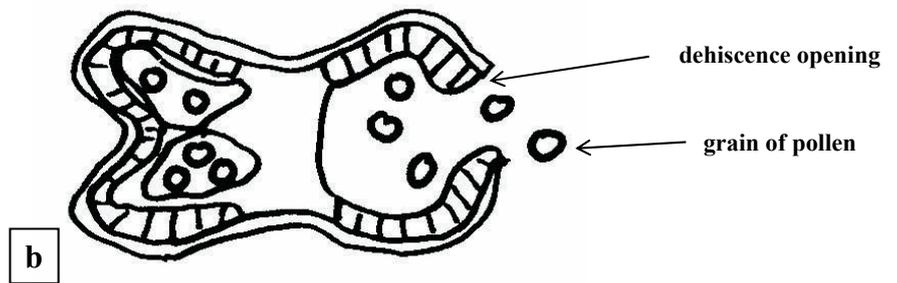


FIGURE 13 (b): Transverse section of an anther. Freeing of the pollen occurs when the dehiscence opening opens up. The pollen is mainly deposited on the stigmata of the parent flower. When climatic conditions are not favourable (high relative humidity of the air or low temperature) fertilisation may nevertheless take place under the cap that did not open at the required time.

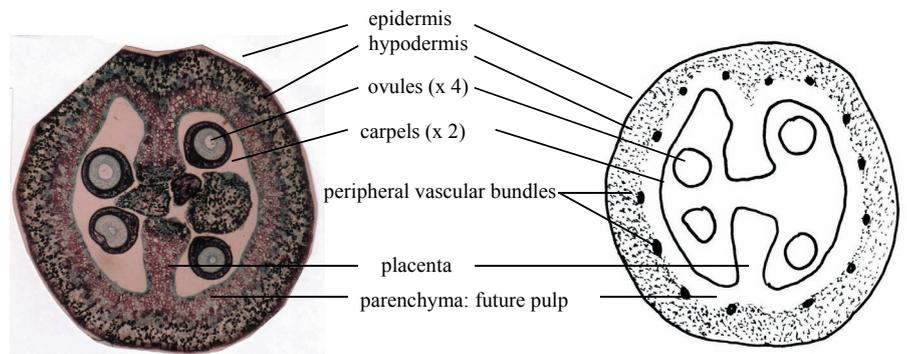


FIGURE 14. Transverse section of an ovary, setting stage (x 50; from A.C. Bernard, Agro Montpellier; Harris et al., 1968).

Disturbances in fertilisation cause problems with coulure (flower drop) and millerandage (inhibition of berry growth).

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Abnormalities of flower fertilisation and consequences on berry development

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Coulure or flower drop is determined by an abnormally high number of dropped flowers (Figure 15) compared to the “normal” rate of flower drop, taking into account that the inflorescence cannot possibly ripen all the flowers that developed (Carbonneau & Ollat, 1993). The drop of ovaries which started their growth to form a berry – in other words very young fruit with a diameter of less than 2 mm – is possible right at the start of fruit set, afterwards the berry will no longer fall. The loss of flowers occurs as a result of the functioning of an induced or pre-existing abscission zone, situated at the base of the pedicel of the flower. Bessis and Fournioux (1992) have demonstrated the role played by ethylene in the functioning of the abscission zone. Its functioning is restricted to the flowering period and at the very start of setting. To this end, the application period of ethephon, which sets the ethylene free and provokes an “artificial coulure”, with a view to a chemical thinning in order to reduce the yield, is delicate because the window of application is narrow and flowering throughout the vineyard, and at the level of the plant itself, is not homogeneous.

The causes of coulure are:

- Climatic: Especially temperatures below +15°C at the time of flowering; rains particularly which wash out the pollen (possible if the cap is open, thus exposing the pollen). Luminosity has little influence on coulure as far as vineyard conditions are concerned (Deloire *et al.*, 1995).
- Physiological: Complex disequilibrium between photosynthesis (vigour) reserves; deficiency of mineral elements such as nitrogen, boron, zinc (Carbonneau & Ollat, 1993).
- Defects of organogenesis: Malformation of pollen spores (microsporogenesis), and/or macrosporogenesis; malformation of the embryonic sac (the latter has a reduced receptivity of 48 hours only, which necessitates rapid fertilisation once flowering starts and in particular once pollen is set free). The formation of gametes starts 3 weeks

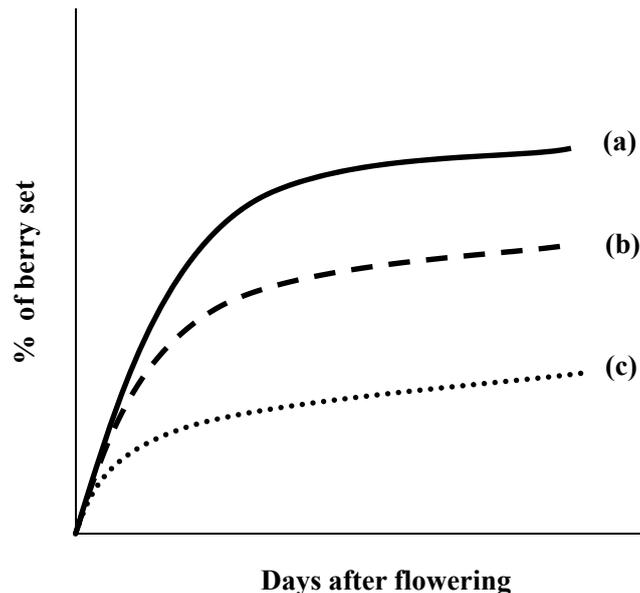


FIGURE 15. In the vine, dropping of flowers or imperfect young fruits is called «coulure». This may occur naturally or accidentally.

(a) Absence of coulure: Setting rate of about 70%. Natural dropping of flowers 30%, the plant knowing instinctively that the inflorescence is often unable to transform all the flowers that had formed into fruit.

(b) Moderate coulure: Setting rate of 20 to 50%. This setting rate impacts largely on the potential yield. It may be due to adverse climatic conditions or to a trophic problem (nitrogen deficiency), but remains acceptable.

(c) Significant coulure: Setting rate below 30%. There would have been a serious climatic cause, which impacts negatively on yield. This setting rate often occurs when vines have a disease (virus, wood diseases, etc).

before flowering, which lengthens the period during which the inflorescence is sensitive to climatic conditions.

- Pathological: Viruses; wood diseases; Shiraz decline, etc.

Millerandage is characterised by the abnormal development of berries. The cellular growth of the pericarpal cells is inhibited. The question of the effect that “millerandage” has on the number of cells, therefore on the cellular multiplication of the setting, has not yet been studied. “Millerandées” berries may either mature normally or remain green because of inhibition of cellular growth as well as their biochemistry. It has been shown on Merlot that “millerandées” berries which mature “normally” have a certain amount of tan-

nins and sugar compared to berries that are systematically inferior. Their secondary metabolism is therefore disturbed and parallels a disturbance of cellular growth (Cholet, 2001; Fougère-Rifot *et al.*, 1996). Millerandage is linked to problems with fertilisation. Berries contain aborted seeds (transparent and soft), thus signalling that fertilisation was incomplete or that premature abortion of the embryonic sac occurred. Sufficient pollinisation has nevertheless taken place to initiate the process of setting (the signal has not been identified: hormones perhaps? secondary messengers?) and in conjunction with it the partial development of the fruit, with different degrees of malfunctioning.

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