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► **To cite this version:**

Max Rives. Vigour, pruning, cropping in the grapevine (*Vitis vinifera* L.). I. A literature review. *Agronomie*, 2000, 20 (1), pp.79-91. 10.1051/agro:2000109 . hal-00885987

**HAL Id: hal-00885987**

**<https://hal.science/hal-00885987>**

Submitted on 11 May 2020

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## Vigour, pruning, cropping in the grapevine (*Vitis vinifera* L.). I. A literature review

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(Received 20 November 1998; revised 15 May 1999; accepted 5 September 1999)

**Abstract** – We present a series of three papers that aim at providing a synthesis of the information collected or obtained from 1956 to 1974 at the Station de Recherche de Viticulture INRA in Bordeaux. This work was continued and expanded along new avenues mainly by Carbonneau [23, 25]. As it is, it endeavoured to study the relationships that prevail between traits which are easily assessed on the vine and are important in determining the production of a crop. It showed that to be meaningful, experimenting with factors that are expected to influence yield must last at least three years; it provided a simple and practical means to eliminate subjective influences from the experimenter on the trial by the use of pruning scales defining the load as a function of the weight of prunings; it showed for the first time how to study in isolation a single three-year cycle leading to the production of a crop.

**Grapevine / vigour / pruning / photosynthetate / inflorescence initiation**

**Résumé – Vigueur, taille et production chez la vigne (*Vitis vinifera* L.). I. Synthèse bibliographique.** Nous présentons une série de trois articles qui ont l'ambition de fournir une synthèse d'informations collectées ou obtenues de 1956 à 1974 à la Station de recherche de Viticulture INRA de Bordeaux. Ces travaux ont été continués et amplifiés depuis dans des voies nouvelles par Carbonneau [23,25]. Ils tendaient à étudier les relations entre les divers caractères qui sont facilement déterminés sur une plante de vigne et qui sont importants pour le déterminisme de la production d'une récolte. Ils ont montré que, pour avoir un sens, l'expérimentation sur des facteurs susceptibles d'avoir un effet sur le rendement doit durer au moins trois ans. Ils ont fourni des moyens simples et pratiques pour éliminer les influences subjectives de la part de l'expérimentateur en utilisant des échelles de taille définissant la charge en fonction du poids des bois enlevés à la taille. Ils ont montré pour la première fois comment étudier en isolement un seul cycle de production de trois ans.

**Vigne / vigueur / taille / photosynthétat / initiation florale**

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Communicated by Silviero Sansavini (Bologna, Italy) and Hervé Thiellement (Geneva, Switzerland)

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## 1. Introduction

Experimenting on woody perennials is made difficult by the fact that 1) the individual plant is most of the time a big unit; 2) there are obviously follow-up effects through the years that have to be understood to make experiments meaningful; 3) human intervention especially with pruning may have a strong effect on the results of experiments. The understanding of the interrelations within the plant is thus of great importance for the planning and performing of such experiments. Knowledge acquired in studies aiming at this understanding will also have its importance for commercial production.

I have gathered in the following most of the knowledge that was available at the time of the experiments described in the second and third part.

## 2. The cropping cycle

The model is as follows:

- in the first year, carbohydrates are photosynthesised that will contribute to producing a crop and other products, as well as maintaining vigour<sup>1</sup> in the vine<sup>2</sup>;

- in the second year of the cycle, this vigour is expressed by the rapidity of growth of the shoots<sup>3</sup>. This in turn is positively correlated to the diameter of the resulting cane<sup>4</sup>. Consequently, vigour can be measured as the weight of the prunings<sup>5</sup> from the vine. The degree to which inflorescence initiation<sup>6</sup>

<sup>1</sup> Vigour: this intuitive notion can be variously made objective by measuring it through the speed of growth of the shoots, the diameter of the canes or the weight of these.

<sup>2</sup> Vine: in English a vine is a liana. From the French, a vine is a plant (shrub) of e.g. *Vitis vinifera* used for producing grapes. The vine is the natural unit of physiological functioning. It is normally the experimental unit in experimenting on grapes.

<sup>3</sup> Shoot is used to designate the growing organ from a bud, in the first part of the growing season, say while it is not "aoûté" i.e. ripened.

<sup>4</sup> Cane is the ripened shoot (sarment).

<sup>5</sup> Prunings are the canes taken away by pruning the vine.

(i.e. the development of a number of initials<sup>7</sup> of inflorescences in the buds borne by these shoots that develop during the second year in the cycle) takes place is strongly correlated with the vigour of the cane that bears the bud;

- in the third year this results in regulating the number of clusters<sup>8</sup> or bunches<sup>9</sup> produced by the vine, and hence in determining its yield.

Obviously, the whole process is subject to all external factors of variation.

As a consequence, on an adult vine, at any time, 3 cycles are simultaneously in operation, and they are in competition for the sole available source of energy: carbohydrates synthesised by photosynthesis. This is shown in the diagram of Figure 1 from Rives and Lafon [51].

## 3. Reserves of energy in the cultivated vine

For these reserves in the form of stored photosynthetates, one can identify two different kinds of sinks:

- Some of the energy is definitively lost. Immobilised for good in the build up of the permanent structure of the vine, "old wood"<sup>10</sup> of the trunk<sup>11</sup> and arms<sup>12</sup> and root system. Or lost as

<sup>6</sup> Inflorescence initiation: on the primordium of a new shoot that develops within the bud, primordia of basal tendrils are transformed into cluster initials. Contrary to what the term seems to imply, flower initials do develop only just before and after bud burst.

<sup>7</sup> Initials: within the bud, small islets of tissue are formed that will evolve later into the organs of the shoot, especially clusters.

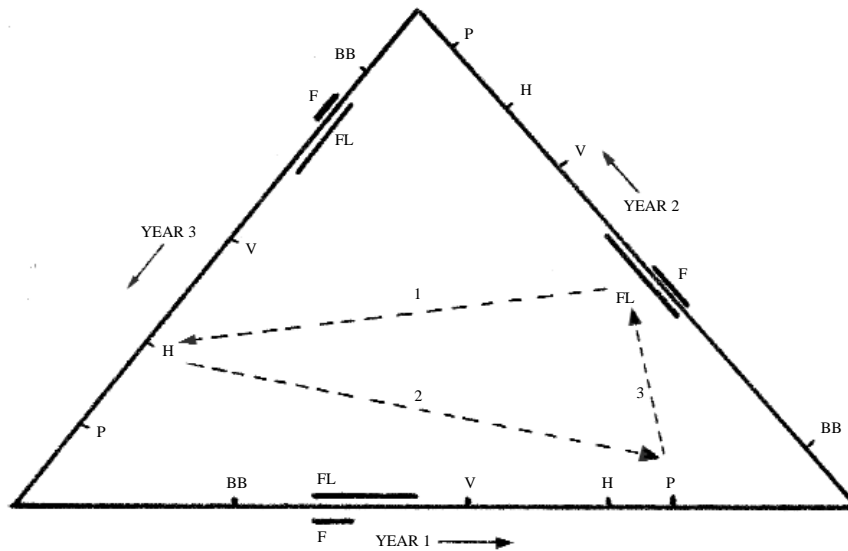
<sup>8</sup> Clusters: usually used to designate the inflorescence of the grapevine, until berry set.

<sup>9</sup> Bunches: this is the fruit of the grapevine, following flowering and fruit set in the clusters.

<sup>10</sup> Old wood: any part of the vine that is more than one year old.

<sup>11</sup> Trunk: the basal part of the vine, stemming from the ground and supporting the arms.

<sup>12</sup> Arm: vines are usually branched into one or more branches of old wood, called arms.



**Figure 1.** The 3-year cycle, anticlockwise from the bottom. P = pruning, BB = bud burst, F = flowering, FI = floral initiation, V = véraison, H =harvest.

Arrows inside the triangle represent the main interactions: 1: inflouescence initiation for production; 2: production vs. vigour through reserves; 3: reserves for inflouescence initiation through vigour.

The whole cycle is subject to the influence, positive or negative, of the environment.

exports in crop, leaves that go with the wind, and prunings, and not forgetting respiration.

– The other part of the energy is stored in a recoverable manner in the old parts of the vine; that part that is stored in pieces of canes left at pruning does not count for much, as these represent only a small part of the canes lost at pruning.

As already said, the operation of this system is obviously under the influence of external factors, and this can be put to use to investigate the internal relations between the parts of the cycles through manipulating the external factors.

#### 4. The make up of the vine

It is interesting at this point to consider the relative importance of the different parts of the vine.

In nature, the grapevine plant is a vine (or a liana). Most of the species of grapevine, live in forests and climb trees; only a few of them, such as *Vitis rupestris*, do grow without support and set fruit in the open. There is a clear dimorphism on a wild vine: shade shoots are straight, vertical, with elongated internodes and large lobed leaves; as soon as the vine has reached the top of the canopy of the forest, sunlight shoots have short internodes, more complete smaller leaves, and bear flowers, and on female plants fruit. The wild vine builds up a long trunk that may become rather thick and weigh several tens of kilos.

In vineyards, in contrast, and to use May's [36] terms, one can say that "cultivation has reduced the vine to a shrub, comprising a trunk with arms of old wood, including only a few hundred grammes of functional ligneous tissue, on which pruning

leaves only a small portion of the canes of the preceding year”.

The shoots or canes of the grapevine have a very peculiar architecture. Summing up the classical data, as it has been very well expressed and investigated further by May [36], one can say that these canes are made up of articles stacked on top of each other, end to end. Schematically, each article is comprised of a length of cane, the internode, ending up in a node<sup>13</sup>. The node bears a leaf, and at the axil of the petiole, an “eye”<sup>14</sup> or compound bud. Opposite to the leaf and eye, there is a tendril<sup>15</sup> except on every third node in *Vitis vinifera*. This tendril may be differentiated into a cluster initial during the formation of the shoot initial in the bud on the lower internodes (normally up to fourth). The eye is made up of a primary bud, the prompt-bud, or “prompt-bourgeon”, that can grow during the season of its development, into a summer lateral or “entre-cœur”. Then there is at least one secondary and often a tertiary, bud that remains latent until the next season unless forced into growth. For an excellent full description of the morphology and anatomy of the vine see Bouard [13]. The shoot has a bilateral symmetry so that each bud in the sequence has its plane of symmetry at a right angle with the preceding or following one.

The shoot so described is itself originated from a bud borne on a morpho-anatomically identical shoot from the preceding season. The buds of

shoots that originate from buds forced from old wood, that are called “suckers”<sup>16</sup>, or “gourmands”, usually do not contain flower initials and these suckers are barren. Contrary to a belief common among vignerons<sup>17</sup>, the buds borne by the suckers will contain initials in the next season, provided they have started growing sufficiently early. Thus they can therefore be used at pruning. Huglin [29, 30], Balthazard [9], Buric [16].

Each bud borne on a one year cane is thus able to produce a shoot in the next season, that is in turn made up of the same elements. Such a shoot bears a number of bunches that can vary but in only small proportions (rarely more than 3 or 4 clusters per cane). Pruning, in leaving a given number of buds on the vine, amounts to a prediction of the load<sup>18</sup>, in the number of bunches, that the shoot will bear, and as a consequence to a prediction of the yield of the vine in the following season. This prediction is accurate, at least in a relative measure.

This architecture results in a rather schematised organism, that is easy to grasp and analyse.

## 5. Cane architecture and bud formation

In this scheme, vigour and inflorescence initiation are central to the process leading to a crop in the cultivated grapevine.

<sup>13</sup> Node: on a shoot or cane, the swelling site at which a leaf, an eye, and eventually a tendril, are located.

<sup>14</sup> Eye: a complex structure comprised of several buds, at a node, at the axil of the leaf.

<sup>15</sup> Tendril: an organ specific to the genus *Vitis* and some other liana, located at two of every three successive nodes in *V. Vinifera*, opposite to the eye and leaf, that has a special sensitivity to touch. Whereby it will coil itself around any support that it meets, thus providing an anchorage to the growing shoot. Basal tendrils initials, up to 3 or 4 become differentiated into inflorescence initials in the forming bud.

<sup>16</sup> Suckers: shoot evolving from latent buds of the old wood. They are most of the time barren. When they start growing early enough, however, their buds will contain normal inflorescence initials.

<sup>17</sup> Vigneron: French for a man working at viticulture, extended to all those who are engaged in viticulture and its study.

<sup>18</sup> Load: taking out canes and the buds they carry at pruning leaves some parts of canes and the buds they carry on the vine; these buds will eventually burst and grow into shoots and canes and bear grapes, i.e. a crop in the following growing season. As every bud contains a number of cluster initials that is roughly predictable, the number of buds left, or load is a rough prediction of the relative crop one can expect the vine to carry.

The strong dimorphism between shade and sunlight shoots for grapevines in main natural habitat hints toward the importance of light as a factor in flowering and fruiting.

While the morpho-anatomical structure of the shoot is sympodial, the ontogenic structure, however is monopodial, the apical meristem being permanent for the season, unless damaged or cut out. This is demonstrated by observing sectorial chimeras, the mutant sector of which runs all along the shoot. There may be some controversy on these points, see Mullins, Bouquet and Williams [44]. Thus the genetic origin of the tissues in all internodes is the same. Breider [15], Thomson and Olmo [53] have shown that the shoot originates from only 2 initial cells in the apical meristem, at variance with the usual situation of 3 or 4 layers in woody perennials such as apple or pear (Dermen [26, 27], Rives [48]).

The apex remains active throughout the growing season, until the “end of growth”<sup>19</sup> when it necroses and falls. This is true in temperate climates. Under the tropics, or in the greenhouse, growth may continue indefinitely. This means that in cultivation, under temperate climates or with pruning, the shoots of a year will be produced from the lateral buds borne on the pieces of cane left from the preceding year at pruning.

At the axil of the leaf, the growth of the primary bud (prompt-bud) is inhibited only by the apex. The other buds in the eye are also inhibited by the leaves at the axil of which they are located, and normally do not grow in the same season, before they enter dormancy<sup>20</sup>.

## 6. Inflorescence initiation

During the differentiation of the buds, a new lateral apex evolves within the bud, producing an axis

<sup>19</sup> End of growth: French “arrêt de croissance”. In temperate climates, typically in October in the Northern hemisphere, while leaves begin to become yellow and fall, the apices stop functioning and die.

or shoot initial, made up of some ten internodes, each bearing a leaf initial and at every third node a tendril initial. Tendril initials are transformed into inflorescence initials in the main (secondary or latent) bud, i.e. the bud that will enter dormancy and grow in the following year to give a shoot that will evolve into a cane.

The timing of inflorescence initiation has been amply investigated since the first study by Barnard and Thomas [10], especially by Huglin [30], May [36], and Lavee et al. [32].

Barnard and Thomas [10] used direct observation of bud sections under the binocular. Carolus [24] using the same technique, stated that: “In Merlot, in the Bordeaux region, inflorescence initiation begins approximately 6 weeks after bud burst”.

For the first 5 to 15 buds of a cane, that are the only ones of interest for the grower, because these are those that will be left at pruning, inflorescence initiation ends at the end of July or beginning of August, in Bordeaux, as “each bud stops evolving approximately 2 and a half months after the beginning of its differentiation” (cf. [24], Fig. 21). Thus differentiation progresses up to a time that corresponds with “shoot ripening”<sup>21</sup> (“aouïtement”) and the entry of the buds into dormancy. At this time, mitotic activity entirely stops and remains nil in the bud until a little before bud burst in the following year.

Buttrose [17–22] counted clusters on shoots originated from latent buds of the same season after forcing these through cutting the tips and defoliating the shoots. Using this technique, Huglin

<sup>20</sup> Dormancy: a state in which the bud will not start growing, even though the external conditions are optimal. Pouget (1963) has made a thorough and remarkable analysis of this phenomenon, showing that in nature, dormancy is broken by the action of a series of cold days in winter. Various chemical or physical treatments can lift dormancy artificially, notably hydrogen cyanamid applied to the buds can do this in the vineyard.

<sup>21</sup> Shoot ripening: (French aouïtement) in August, (Northern hemisphere), the shoot becomes brown, as, starting from the base up, the epidermis becomes suberised and transformed into a periderm. As this process passes each node, the bud in this node becomes dormant and the shoot becomes a cane.

[30] could observe the effect of a hail storm that inhibited inflorescence initiation starting from a certain level in the shoots. Lavee et al. [32] showed that defoliation led to the same effect and the same result. Alleweldt and Ilter [4] did the same through the use of gibberellin sprays, the inhibitory effect of which on inflorescence initiation we had found earlier (Rives and Pouget [52]). It is worth noting at this point that two of these treatments (hail and defoliation) suppress or at least decrease photosynthesis, and that they were applied during the period of initiation.

Alleweldt and Ilter [4] could add that there was a time lapse between the moment when the stimulus reducing initiation is applied and the moment when its effect becomes actually visible under the microscope. They found that the lag could be 10 to 20 days.

## 7. The physical impact of pruning on the cultivated grape

In the grapevine, pruning is the most important operation that the grower performs on the plants. It results in removing from each vine almost all the canes and the buds they carry, leaving only a small number of eyes, that will be at the origin of the shoots that will bear fruit in the following season. This number is called the load<sup>22</sup>. For instance, every year pruning removes 90% or more of the buds borne on a vine in Bordeaux. Load should theoretically be determined in proportion to the “vigour” of the vine. We will discuss this point at length later.

To emphasise the potential effect of pruning on the dry matter balance of the vine plant, we may quote figures from Mullins et al. [44] apparently quoting Williams and Biscay [55]: on excavated vines of Chenin trained as bilateral cordons at a density of 1737 vines/ha ( $2.40 \times 2.40$  m) in the San Joaquin Valley in California, i.e. in a very

<sup>22</sup> Load: at pruning, the number of buds left on a vine; later, may also mean the amount of bunches borne by the plant.

favourable environment for the grapevine, in September, the following *dry* (including for the clusters) weights were found for:

|                                 |          |
|---------------------------------|----------|
| the old parts, (trunk, cordons) | # 6500 g |
| the (recovered) roots           | # 3000 g |
| the canes                       | # 2500 g |
| the leaves                      | # 1700 g |
| the crop                        | #5200 g. |

Thus, the exports or that part of the dry matter accumulated in the non-permanent parts (canes, leaves, clusters) amounted to 9500 g, i.e. almost exactly the same weight of dry matter as that of the permanent parts. It is to be noted that [44] from budburst to harvest, the increase in dry weight of the permanent parts (roots, trunk, cordons) was approximately 1500 g, i.e. almost 16%. This poses the problem of understanding how such a large accumulation in one year can account for the moderate weight in the 10th year. A possible explanation is that a good part of this are reserves that are used during the heterotrophic phase of growth at the beginning of the growing season. This explains how, in adult vines, the influence of the variation in the balance of reserves at the end of one year can be damped by the reserves accumulated in the previous history of the vine, thus obliterating part of the variation imparted by treatments in a single year of experimental trial.

## 8. Fertility and the impact of pruning on production

The peculiar importance of pruning in the grapevine is due to the fact that the content in potential clusters of fruit in each bud left on the vine by pruning is rather constant. As a consequence, the decision on the load to be left on a vine amounts to a prediction of the number of bunches that will be produced and harvested on this vine. The number of fruit units (initials, inflorescences, clusters, bunches) is called “fertility”<sup>23</sup>.

<sup>23</sup> Fertility: depending on the date when assessed, the number of inflorescence initials, then of inflorescences, that of clusters or bunches per bud, either considering one bud in particular or several ones on an average.

Huglin [29, 30] has shown that fertility is characteristic of a variety, that it varies according to a number of factors, e.g. rootstock, that it is more or less constant along the cane in some varieties, and increases up to say node 10 or even 15 on others (see [33]). He has also made a thorough investigation of the factors that increase or decrease fertility.

The number of initials in the buds sets an upper limit to the number of bunches at harvest. This can only decrease later. Here again various factors have been found to cause different types of losses, that result in different kinds of fertility, as defined by Bessis [11].

The decrease in fertility is referred to “losses before flowering” (with regard to the potential fertility in the buds) and to “losses following flowering”, the causes of which are not the same. In addition, some buds may not effectively grow, and this in part depends on the quantitative relation between load and vigour, as we will see.

## 9. Factors of inflorescence initiation in natural conditions

### 9.1. Light

The Australians have been first and foremost in investigating the factors that regulate inflorescence initiation, that determines fertility in the buds. Their main variety at the time was the Sultana, grown for raisins. This has a very low (less than 1) fertility which, in addition, only peaks around node 14 or even farther. This is an extreme example of why certain varieties require a pruning system with long canes, while others (those with an even distribution of fertility along the cane including the very basal buds) can be trained to short spurs<sup>24</sup>. Moreover the fertility of the Sultana is highly variable from year to year (0.30 to 0.75 initials per bud). In the Australian climate, where post-flowering losses are minimal, fertility is the main factor of productivity. Antcliff and Webster [6] have

obtained correlation coefficients between average fertility and yield of grapes in the order of 0.7 to 0.8 over 13 years.

In Alsace, an environment that is in marked contrast to the Murray Valley of Australia, Huglin [30] investigated fertility on Alsacian varieties that are very different from the Sultana. He found a positive correlation between fertility and the mean temperature prevailing during the period of initiation. In the very dry conditions of Colmar, he could also show a positive correlation of fertility with precipitation. [I suggest that this correlation results from a positive effect of water supply on the rapidity of growth of the shoots.] These results are based on only 5 years of observation and could be deemed insufficient if they did not agree with those of Alleweldt and Balkema [3] in the Rhine valley in supporting those of the Australians as these were reported in the synthesis by Baldwin [8].

From these last observations that extend over 18 years, the evidence is strong that sunlight is the main factor acting upon floral initiation. This is measured in the number of hours of sunshine per day with the solarimetre. Baldwin calculated regressions of fertility vs. hours of sunshine for periods varying both in their beginning (taking into account the average precocity in each year) and in their length,. He showed that maximum correlation was found with total sunshine duration in a period of 20 days beginning from the 14th to the 20th November depending on the year. The dependent variable in the regression was the proportion of fertile eyes at positions 4, 9 and 14. Adding the variable temperature after sunshine duration during the same period increased the correlation from 0.786 to 0.866 (i.e. in terms of variance, from 0.618 to 0.785 of the total variance was “explained” by the variables). The share of the effect of temperature that is independent of sunshine is small. It is obvious, however, that there is a strong correlation between sunshine and temperature, everywhere.

The influence of light has been investigated further. May and Antcliff [39] showed that shading whole vines with fabric would lower inflorescence initiation. We (unpublished results) did confirm this effect in the very different environment of

<sup>24</sup> Spurs: cane segments left on the vine at pruning are usually short (2 eye spurs or French coursons) or long (typically more than 4 eyes, long bois in French, aste in Bordelese).



Bordeaux, on Sauvignon, in which fertility is much higher than in the Sultana.

May [37] found that, at least for a good part, it is light that reaches directly the buds that is acting on initiation within the bud. Covering the developing eye with aluminium foil caps he observed a consequent decrease in fertility. The spurious effect of a possible elevation of temperature under the aluminium caplet was discarded through the use of transparent caps, assuming they had the same effect on temperature, and that had no adverse effect on fertility. Indeed, according to Huglin [30], as I have mentioned, an elevation of temperature ought to increase inflorescence initiation. Wave length was also eliminated as a factor, as differently coloured transparent caps had no differential effect.

## 9.2. Photoperiod

Alleweldt [2] observed that photoperiod had only a very small influence if any. This is well corroborated by the observation of fertility in intertropical vineyards (e.g. in Peru in the 13th degree South) in which it is quite comparable with that observed in higher latitudes for both local<sup>25</sup> and imported varieties.

Wagner [54] observed the favourable influence of supplementary lighting on hastening inflorescence initiation on seedlings in the greenhouse. This has become part of the technology used to force seedlings into early flowering in the breeding of new varieties from seed.

## 9.3. Vigour

May [34, 38] showed that vertically training one shoot from a Sultana vine while the other canes were maintained prostrate as is usual for that vari-

ety, would increase floral initiation in the buds of that shoot. This effect decreased when more than one cane was vertically trained on one vine. May concluded that this was due to the greater vigour imparted to that shoot by vertical training, at the expense of the other shoots. One may also observe that a vertical shoot extends from inside the mass of the canopy and thus receives more direct light on its buds.

These results introduce the effect of vigour on inflorescence initiation. Huglin [30], in particular, studied the correlation between the fertility of the buds of a cane and its diameter at the base, or between the fertility of the buds on one vine and the weight of its prunings. He found positive correlations throughout.

Lavee et al. [32], Alleweldt and Ilter [4] and especially Carolus [24] have shown that the speed of elongation of the cane during the period of initiation is positively correlated with inflorescence initiation. This is not surprising as we have seen that inflorescence initiation is correlated mainly with vigour, measured either by cane diameter or by the weight of prunings, and one may expect that both of these are strongly correlated with the speed of growth of the canes.

Baldwin [8] made the interesting observation that the average fertility in the first 9 years of his 18-year series was definitely lower than that of the last 9 years. The difference was associated with the switching from Bordeaux mixture to synthetic fungicides. It is a common observation, indeed, that Bordeaux mixture, in the absence of mildew, has a detrimental effect on vigour.

This refers equally to the influence of a hail event or to shading, insofar as this last did reduce photosynthesis. No data on this point, however, was presented by May and Antcliff [39].

The influence of the speed of growth is taken advantage of in the forcing of the seedlings in the greenhouse. While the seedlings begin to bear tendrils say somewhere from the 8th to the 20th node, it looks as if inflorescence initiation did not take place on the following nodes before the whole plant had reached a certain weight. In this case, the favourable effect of optimal mineral nutrition

<sup>25</sup> Local: in Peru all varieties of *V. vinifera* have been imported; some were imported early by the Spaniards, among these obvious populations originated locally from seeds. These may be assumed to have been submitted to a selection for adaptation to the local climate, including day length.

through hydroponics, warm temperature and, as we have seen, additional lighting (in addition to its direct effect), all contribute to a very rapid growth that succeeds in inducing inflorescence initiation in the buds developing within the first year.

#### 9.4. Competition with the developing crop

In such a context, one would expect that it ought to be possible to show a competition on inflorescence initiation from the developing crop. Antcliff [5] found a significant effect of removing all inflorescences. Antcliff et al. [7], however, were unable to repeat the observation when removing part of the inflorescences. The difference in intensity of the treatment may account for the discrepancy. It may also be assumed that the timing of the intervention is important, and that unsuccessful debunching came too late in the course of the development of the cane and of that of inflorescence initiation in its buds to affect fertility; the more so as we have seen that Alleweldt and Ilter [4] showed that there was a time lag between the cause and the effect. Huglin [29] also failed in observing such an association.

It is not surprising that the competition from the developing crop does not affect the same year's inflorescence initiation, as the 2 phenomena do not occur in the same period (autumn vs. spring).

#### 9.5. Water supply

Vigour, especially the speed of elongation of the shoots, can be influenced also by water availability as Huglin has observed.

In an experiment on soil management in a Grave soil containing a proportion of clay, we [49] compared the usual soil management through repeated plowing (down to 15 cm) to no plowing at all with either the whole surface kept clean through the use of herbicides, or herbicide cleaning of a 50 cm wide strip only on the row, and grass on the rest i.e. 1.00 m. Measurement of the water content of the soil showed that these treatments induced sharp differences in water content that were very quickly, already in the first year, reflected in differences in the weight of prunings (Tab. I).

#### 9.6. Growth substances

Growth substances have not been studied to a great extent.

Following an experiment in using gibberellin to loosen the bunches of Chasselas, we [49] have found (to our surprise and dismay) that high concentrations applied in May-June, i.e. at the very period for inflorescence initiation, would decrease inflorescence initiation and delay bud burst (or even suppress it altogether) in the following year. This has been observed several times since, e.g. by Julliard and Balthazard [31], and we have seen that Alleweldt and Ilter [4] used the effect to determine the time of initiation.

Cholinechlorochloride (CCC) used by Pouget and Castéran [46] to reduce the speed of growth of the canes, induced the differentiation of flowers on the tendrils developing later in the same season on the treated shoot itself when sprays were frequently repeated.

### 10. Studies in artificial conditions

Buttrose [17–22] was the only one to study inflorescence initiation in artificial conditions on established varieties (as opposed to seedlings). He worked on young plants in climate controlled chambers. He varied temperature and light intensity and duration. He assessed the effects through the number of initials per dissected bud. He was able to confirm the influence of light intensity. Fertility increased when light intensity increased from 900 to 3600 ft cd, with a 16-hour day. Fragmentation of

**Table I.**

|                                       | Grass | Plow | Clean |
|---------------------------------------|-------|------|-------|
| Pruning weight                        | 228 g | 331  | 393 g |
| Water content in soil<br>(% dry soil) | 4.70  | 5.10 | 6.10  |

the day (e.g. 12 + 4 hours) did not change the effect in Muscat or Alexandria, but was slightly less efficient in Riesling or Syrah.

## 11. Making initials into a crop

All initials present in the buds do not reach the stage of inflorescences and bunches of fruit. This has been interpreted in particular by Branas [15] as the back-transformation of inflorescence initials into tendrils at bud burst. Hence the French name “filage”<sup>26</sup> after “fil”: a thread, to evoke the thread-like shape of the tendril. Bessis [12] noted the absence of experimental evidence on the phenomenon and questioned its importance. An observation that everyone is able to make is that while initials are indeed present in the buds of the cuttings and graftwood used in propagating the grapevine, seldom does one see inflorescences developing on the rooted cuttings or grafted rooted plants in the nursery. Careful examination of cuttings grown in the greenhouse for example reveals that in the majority of the cases the initials shrivel, dry up and fall at a very early stage, which can easily pass unnoticed.

### 11.1. The origin of the losses at bud burst

Mullins [40-43] has shown that on cuttings grown on water or nutrient solution, or on specially designed hot-cold beds, initials can be induced to develop into inflorescences by one of the following three techniques:

- Removing the leaves before they have expanded, when they are still wrapped around the bud in a spoon-like shape, as soon as one can distinguish the petiole sufficiently to slip the tip of the tweezers

behind it to sever it and remove the leaf. This apparently removes competition from the developing leaves, for something that is necessary for the initial to grow into an inflorescence, as this treatment succeeds in obtaining the development of the inflorescence.

- The second technique consists of inducing the growth of roots on the base of the cuttings by growing these (this can not be done with one-bud cuttings that are too short) on a bottom-heated bed while keeping the top with the bud in a cool environment. This way the growth of roots is obtained while the buds are refrained from bursting. When a warm environment is re-established at the tops, the buds that burst on these now rooted cuttings will retain their inflorescences. This is evidence that the roots contribute a factor to the growing bud that may be the same as that for which there is a competition between leaves and initials.

- The third technique involves repeatedly applying a solution of cytokinin directly to the bud: this replaces the removal of the leaves and the presence of the roots. It is thus highly likely that the factor in question for which there is a competition between the developing leaves and the flower initials, and that produced by the roots, is a cytokinin. It is established that cytokinins are produced by the roots and transferred to the tops (Nitsch and Nitsch [45], cf. Mullins et al. [44], p. 144).

### 11.2. The timing of flower initiation

These techniques, by making it possible to observe the development of the initials that become clearly visible once the leaves have expanded or have been removed, provide the means of confirming the observations of Winkler [56] that the differentiation of the flowers themselves takes place in a very short period, from just before visible bud burst to shortly afterwards. While it has been suspected that there could be a correlation between the size of the initials and that of the inflorescences or of the bunches and though the Australians have attached importance to this (they used special microscales to weigh these initials!) they have never been able to demonstrate it

<sup>26</sup> Filage: originally, the theory that flowers were pre-initiated in the bud and that the forms of imperfect inflorescences that may be observed were due to the failure of the flower initial to develop, led to use of this word to mean that inflorescence initials had reverted to tendril-like organs, looking like a “fil” (thread). This theory has been shown to be wrong, by Bessis, and by Carolus, in particular, but the name has stuck.

(May [35]). May [36] and Carolus [24] have definitely shown that flower differentiation on the initials does not start before bud burst has begun, contrary to what Alleweldt and Balkema [3] have claimed. This has recently been confirmed on Syrah using scanning electron microscopy [25].

### 11.3. Late pruning

It is commonly assumed that late pruning favours yield. I have reported [50] on a trial of pruning date on Merlot in Bordeaux. There was an ill-ascertained trend in that direction, while Ravaz [47] in a very well conducted trial on Aramon, and Bouard [13] on Ugni blanc, both had observed clear-cut results in favour of a favourable effect of late pruning. From a trial using Mullins' [40] technique of defoliation on one-bud cuttings, I could demonstrate the existence of a variation in sensitivity to endogenous cytokinins among various varieties, that may explain the discrepancies among these three trials. An explanation might be that delaying pruning keeps the buds that will eventually be retained at pruning from bursting before the full flux of cytokinins has come from the roots. A side effect is that it also keeps these buds from being damaged by late frosts.

## 12. Conclusion

From the information gathered in the literature, one can conclude that the intensity of pruning, the load, is foremost in directly determining the crop of the following year, and is likely to have indirect effects as well. Hence the importance of finding a way to adjust the load according to some purely objective method, so as to eliminate bias in experimentation, as well as to reach the optimal balance in the vine for the type of production desired. The experiments to be described thereafter in Section 2 [12] are designed to answer some of the questions thus raised.

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