# From bud to berry, with special reference to inflorescence and bunch morphology in *Vitis vinifera* L.

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**Abstract**

A brief review of the reproductive system of the grapevine is presented. Phases discussed include floral induction and initiation during early spring, inflorescence primordium growth during summer to dormancy, flower formation at budburst in the subsequent growing season, and finally flowering and berry development. Difficulties in clearly defining and describing some of these developmental stages will be outlined, especially the complex bud system, the morphology of buds at budburst, and the course of flowering. The course of floral development during dormancy and at the time of budburst requires further attention, especially the reported effect that low temperature at budburst leads to increased numbers of flowers. Also, the recent finding that 'intercarpellar' floral organs can be induced by applying auxin is of particular interest and will be described. Case studies from Burgundy vineyards with Chardonnay, Pinot Noir and Gamay ovaries and berries will be included.

A detailed analysis of what constitutes a grape bunch will be presented from observations of Chardonnay inflorescences and bunches collected at random after set and at harvest in two seasons from spur-pruned, cane-pruned and hedged vines growing on two sites varying in climate and productivity (Adelaide Hills and Southern Vales of South Australia). This analysis covered variability in numbers of branches and flowers and in per cent berry set, as well as relationships between branch numbers and flower numbers. Relationships between flower numbers and per cent set, per cent set and berry size along the inflorescence, and berry size and seed complement are outlined. Likely implications of inter-bunch and intra-bunch variability for bunch compactness, berry composition and yield components are discussed.

***Keywords***: *grapevine, reproductive structures, developmental morphology, berry size variation*

## Introduction

Developmental morphology of grape shoots and the reproductive organs attached to them has been researched and described in many articles, beginning in the 19th century and continuing in the ground-breaking work of Snyder (1933a, b), Barnard and Thomas (1933), and Winkler and Shemsettin (1937). Reproductive biology of grapevines was further extended by May (1964), Alleweldt and Balkema (1965), Carolus (1970), Pratt (1971), Scholefield and Ward (1975), Srinivasan and Mullins (1981), Staudt (1982), Staudt and Kassemeyer (1984), Morrison (1991) and Ebadi (1996), to name some, and reviewed by Bugnon and Bessis (1968), Pratt (1971), Buttrose (1974), Coombe (1976) and Srinivasan and Mullins (1981).

The present paper comments on some of the events which form the developmental cycle from inflorescence induction within a bud to berry maturity. A description then follows of the distribution of flowers on inflorescences and berries on bunches, using data from the cultivar Chardonnay as a case study. Surprisingly little attention has been paid to this aspect of the reproductive system of grapevines, despite the likelihood that variation in berry size and composition is in part related to berry position within a bunch. Crop uniformity is influenced by many factors, and variation in berry position may be one of them. Due to changes in the relationship between rachis branching and berry numbers, bunch structure may also influence bunch compactness, with consequences for grape quality and soundness.

## Bud system

The bud system of a grapevine conforms to the general morphological characteristic of angiosperms where a bud (i.e. a primordial shoot), and one bud only, develops in the axil of every leaf. What makes grapevine buds more complicated is the loss of true leaves and extreme shortening of internodes in the most basal portion of shoots. This leads to the formation of so-called 'compound buds', with a whole array of names being used for their component parts (Table 1). This assembly of different names for given organs was compiled from literature sources listed in the Introduction. Identifying an organ by different names is confusing, and hinders communication.

**Table 1**. Names to be found in the literature for the several buds present in the leaf axils of the grapevine. For explanation of N+1 etc see text. The names are taken from references listed throughout the paper.

| N+1 | N+2 | $N+3_1$ | $N+3_2$ |
|---|---|---|---|
| Summer lateral | Latent bud | | |
| Lateral shoot | Dormant bud | | |
| Prompt | Primary bud | Secondary bud | Tertiary bud |
| First order bud | Second order bud | Third order bud | Third order bud |
| Shoot in leaf axil | Bud in prophyll axil | | |
| Axillary shoot | | | |
| (Prompt-bourgeon) | Fruit bud—Flower bud | | |
| (Anticipé) | *versus* | | |
| (Entre-coeur) | Leaf bud | | |
| | ← Winter bud → | | |
| | ← Dormant bud → | | |
| | ← Compound bud → | | |
| | ← Eye → | | |

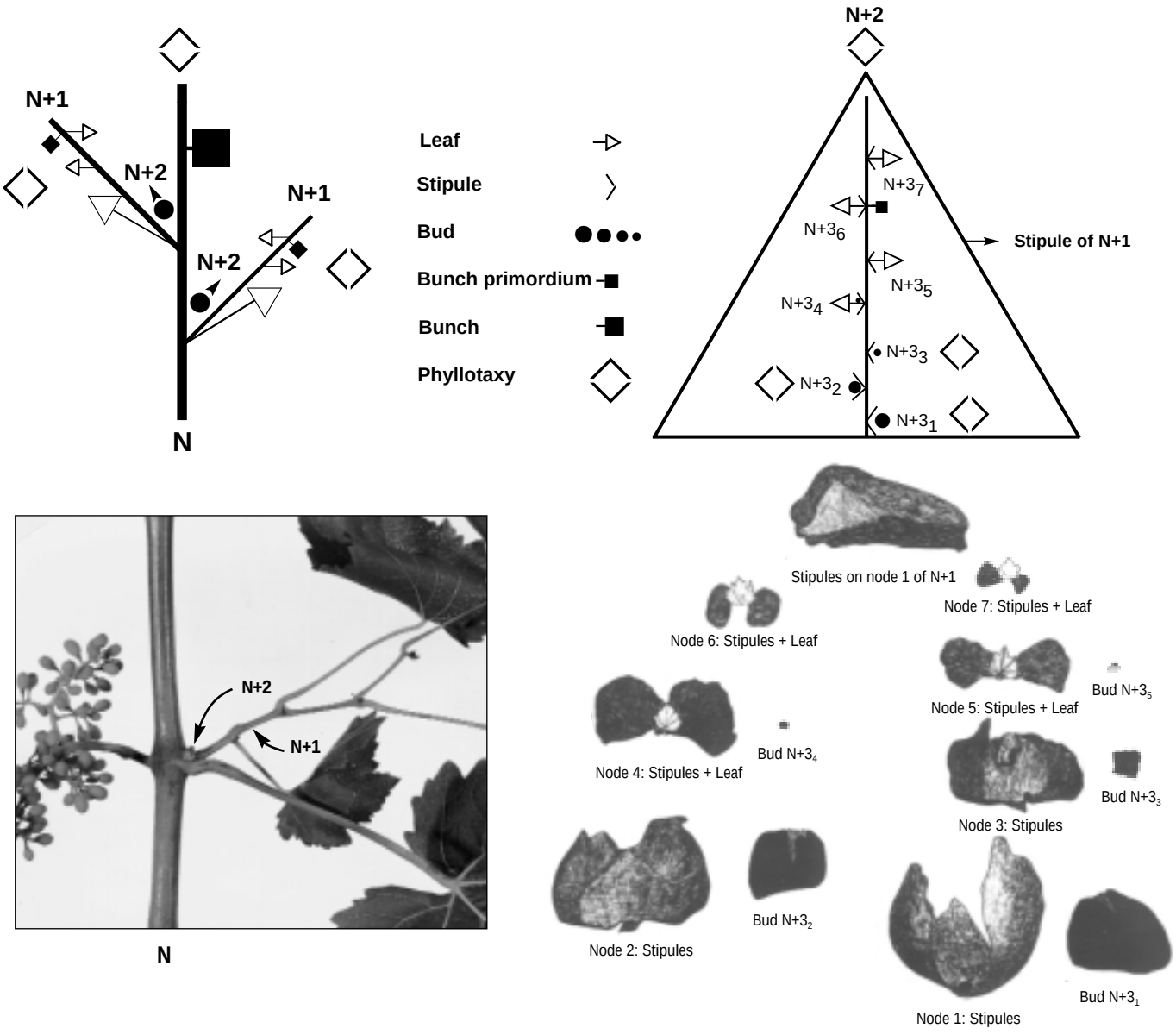


**Figure 1**. *Top:* Schematic representation of a section of a grapevine shoot (*top left*) and of a 'compound' N+2 bud (*top right*). *Bottom left:* Photograph of one node of a shoot N of cv. Sultana with leaves, axillary 'lateral shoot' N+1 and 'compound bud' N+2. *Bottom right:* Shadowgrams of the various parts of a 'compound bud' (cv. Freisamer, modified from May (1964)). Note that the stipule on node 1 of N+1 encloses the 'compound bud' N+2 on the first node of the lateral shoot N+1. The axillary bud primordia of $N+3_6$ and $N+3_7$ are too small to show at the scale used.

To clarify this issue, Bugnon and Bessis introduced naming codes based on the generation sequence of the buds. This nomenclature was recommended by Lavee and May (1997), and is adopted here. Relationships between components of a 'compound bud' are illustrated in Figure 1. According to this system, the shoot itself is called N. Shoot initials are formed on every node in the axil of each leaf. They are colloquially called laterals and coded N+1. On proximal nodes they arise as buds in the preceding season in the axils of primordial leaves, as is shown below in Figure 2. Only some of these buds, and some of the buds formed after budburst on more distal nodes, develop into shoots.

The most proximal node of N+1, situated close to its base because of failure of the subtending shoot portion to elongate, carries a bud, to be called N+2. Its primordial shoot is the main part of the 'compound bud'. This primordial shoot is enclosed by a prophyll, to be interpreted as the stipules of a non-developed leaf (Figure 1). Before entering dormancy, this same primordial shoot forms up to 10 nodes, all with leaf primordia and some with leaf-opposed inflorescence and tendril primordia. As is the case with the basal node of N+1, the two or sometimes three basal nodes of N+2 carry only stipules without lamina primordia, the stipules enclosing the buds coded N+3 (Figure 1). Depending on cultivar and perhaps seasonal conditions, N+3 buds may or may not form inflorescence primordia.

It is interesting to note that lamina and petiole initials are not present on nodes where buds are well-developed, i.e. where the N+2 bud is situated on N+1 or where $N+3_1$, $N+3_2$ and, sometimes, $N+3_3$ buds are situated on N+2 (Figure 1). In contrast, more distal nodes on N+2 carry well-formed lamina primordia apart from large stipules (Figure 1, $N+3_{4-7}$) but have much smaller bud primordia in their axils. I speculate that the presence or absence of a lamina at that stage has a determining effect on the development of their axillary bud.

Bugnon and Bessis (1968, p. 13) drew attention to the generation sequence of grapevine shoots, describing the N+2 as the child of N+1 and thus the grandchild of N. This is recognisable by changes in phyllotaxy as indicated in Figure 1. Phyllotaxy is alternate-opposite on each shoot generation but changes by about 90° from one generation to the next. Thus, the plane of the phyllotaxy is the same on N and N+2, as well as on N+1 and N+3.

During bud dormancy (most recently reviewed by Lavee and May (1997)) morphological development is arrested. In temperate climates, it recommences when exogenous conditions, namely temperature, permit growth, leading to budburst. In tropical climates, budburst occurs when endogenous growth inhibition is removed by the treatments of defoliation and pruning. The timing of budburst has a major influence on the subsequent course of seasonal growth and reproductive development. For example, when I encased buds of Pinot Noir vines in plaster casts in a Burgundy vineyard budburst was delayed for about three weeks. This delay in commencement of growth persisted throughout the season, and led to delayed flowering and berry maturation.

Date of budburst is an important determinant of subsequent seasonal development and is a pivotal component of any system designed to document phenological stages in both experiments and in practical viticulture. The numerical E–L system (Lorenz et al. 1975) distinguishes between beginning of bud swelling ('buds begin to expand inside the bud scales'– stage 01), end of bud swell ('buds swollen but not green'– stage 03), 'wool stage' ('brown wool clearly visible'– stage 05) and beginning of budburst ('green tips clearly visible'– stage 07). In the modified E–L system of grapevine growth stages (Coombe 1995), budburst is noted as stage 4, 'green tip – first leaf tissue visible'. Pouget (1963), in his detailed study on grapevine dormancy, defined budburst for the cultivar Merlot as a state when a globular, fawn-coloured, hairy body appears between the opening scales, arguing that this is the most accurately determinable state. That state corresponds presumably to a (non-included) stage 04 of the E–L system or to stage 3 of the modified E–L system. In Sultana however, green leaf tips appear as soon as the bud scales open because of reduced bud villosity. Accordingly, Antcliff and Webster (1955) defined budburst as the stage when 'the edge of a leaf could be seen between the covering bracts'. Buds then resemble the state illustrated as stage 2 or at most stage 3 of the modified E–L system. As several days may elapse between stages, depending on ambient temperature, varietal differences in interpretation may cause appreciable differences in determining a precise date for budburst. A survey of the variation among cultivars in the morphology of developing buds may therefore be useful. Moreover, determination of an average date of budburst for a given vineyard situation is further complicated by a need to visually integrate within-vine and between-vine variations. Taken overall, recorded dates for budburst of a given cultivar in a given vineyard must be viewed circumspectly.

Contrary to occasional claims (summarised below) grapevines form adventitious buds only in tissue culture (Favre 1977, Vilaplana and Mullins 1989, Tang and Mullins 1990) and never *in vivo*. When axillary buds remain dormant for long periods and become embedded in old wood, they appear to have arisen in extra-axillary positions and have been incorrectly called adventitious buds (e.g. Weaver 1976, p. 16). Such buds, among them the so-called 'base buds' of Pool et al. (1978), may burst in later seasons, producing 'water shoots'. Indeed, embedded buds may remain viable for many years. Such longevity was demonstrated by May (1987): trunk portions were obtained from old Pinot Noir vines uprooted in a Burgundy vineyard and were propagated in a growth room. Most trunk sections developed both shoots and roots even though they carried no recently formed buds.

## Inflorescence initiation and development

As shown long ago, tendrils on grapevines are structurally homologous to inflorescences and the structure of a grapevine shoot with its extra-axillary appendages, inflorescence(s) and tendrils, has been variously described as either monopodial or sympodial (reviewed by May

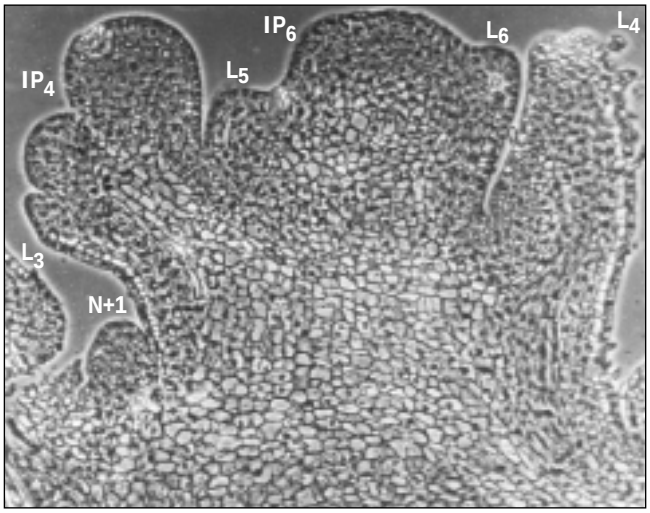


**Figure 2**. Apical portion of a Grenache N+2 bud in early November (spring, southern hemisphere). It shows leaf primordia (L) labelled by subscripts corresponding to the acropetal sequence of their subtending nodes, N+1 bud in the axil of $L_3$, a differentiated inflorescence anlage ($IP_4$) on node 4, and a second, so far undetermined, anlage ($IP_6$) on node 6.

(1964) and Pratt (1971)). This old controversy is theoretically important but appears to be without practical significance. This issue has until recently remained unresolved, and most authors favoured a monopodial structure. However, Fournioux and Bessis (1990) have now shown from *in vitro* observations that shoots often undergo sympodisation on nodes with tendrils in which the meristematic residue of the apical dome is small. By contrast, sympodisation does not occur when this meristematic residue regenerates rapidly, as is mostly the case *in vivo*.

As mentioned earlier, there are many descriptions of the origin and further development of the grape inflorescence from its initiation within developing N+2 buds at about flowering time in season 1 until maturation of the berry in season 2. Underlying processes are outlined below, and call for a clear distinction to be made between floral induction (the physiological stimulus that leads ultimately to flowering) and floral initiation (the morphological consequence of that stimulus). Floral induction has been extensively studied in those annual plants where flowering is induced by strictly defined, leaf-sensed photoperiodic effects. In grapevines such studies are difficult and no such definitive response to external or internal factors is known. Nevertheless, induction has been examined by Lavee et al. (1966) by sequentially defoliating Sultana shoots in the field, and by Buttrose (1969, 1974) by periodically changing the temperature regime in growth cabinets housing plants of cv. Muscat of Alexandria. Both determined that induction occurs well before initiation. The time interval between induction and initiation was 18 d for Sultana and 20 d for Muscat of Alexandria.

Following 'floral' induction, the as yet undifferentiated anlage, initiated at the apex of the shoot primordium (Figure 2), first forms a bract primordium (Mullins et al. 1992), then divides into an 'inner' and 'outer' arm (see below). The inner arm (and often also the outer arm) subsequently form branch initials. Further morphological development ceases when dormancy commences.

When buds start to swell before budburst, marked by an increase in moisture content, inflorescence growth recommences (May 1964). At the cellular level, cells divide in large numbers and their nucleoli enlarge. Morphologically, further branching, branch elongation and flower formation can be observed. The organs of individual flowers are then formed in the sequence sepals – petals (calyptra) – stamens – carpel – ovules.

Microsporogenesis and macrosporogenesis occur just before anthesis, followed by pollination, fertilisation and berry set. A three-stage development of berries from set to maturity ensues (Coombe 1976) and is commonly portrayed in curves of berry volume as two growth phases separated by a lag phase. This whole developmental scenario (from bud to berry) was described as an 11-stage sequence by Mullins et al. (1992) while Fougère-Rifot et al. (1995) divided flower development into 20 stages.

Returning to developmental morphology of grapevine shoots, inflorescences and subsequently bunches are also formed on N+1 shoots during their early growth. Their occurrence in the vineyard is well known and mostly undesirable because this 'second crop' is still immature when the main crop is harvested. Their occurrence varies with cultivar but they appear in many cases after the removal of some apical portion of the N shoot. For Pinot Noir in Burgundy, Olivain and Bessis (1987) found that about 90% of all N+1 buds on node 6 of the N shoot formed inflorescence initials. They persisted but remained hidden within the non-expanded apex on N+1 shoots that elongated less than 5 cm, but abscinded on shoots that grew longer. Tipping the main shoot (N) led to retention and further development of the N+1 inflorescence(s). This effect is variable and depends on the length of the removed apical shoot portion. The effect becomes maximal when shoot removal includes the apex plus nine leaves (Olivain and Bessis 1988). A similar shoot-tipping experiment with Sultana was done at Merbein (Victorian Murray Valley) by P. May and I. Cameron (CSIRO; the latter now Agriculture Western Australia) in the 1960s. This experiment (unpublished) yielded qualitatively similar results (Figure 3) to those from Burgundy and similar relationships between the timing of shoot tipping and the formation of inflorescences. However, outcomes could not be evaluated numerically due to their infrequent occurrence.

### Inflorescence components

As mentioned above, an inflorescence primordium arises as a two-lobed apical dome. A bract is situated at the base of the abaxial lobe; the adaxial lobe is situated opposite to the bract (Figure 2, $IP_4$, and Figure 3 centre-right which shows the scar of the removed bract). The adaxial lobe develops more rapidly than the abaxial lobe. Field observations have led May (1964) to interpret the structure of the inflorescence as a transformed shoot, and this is in agreement with general theory on the phylogenetic origin of angiosperm inflorescences. In the grapevine inflorescence, the shoot axis is mostly reduced or totally

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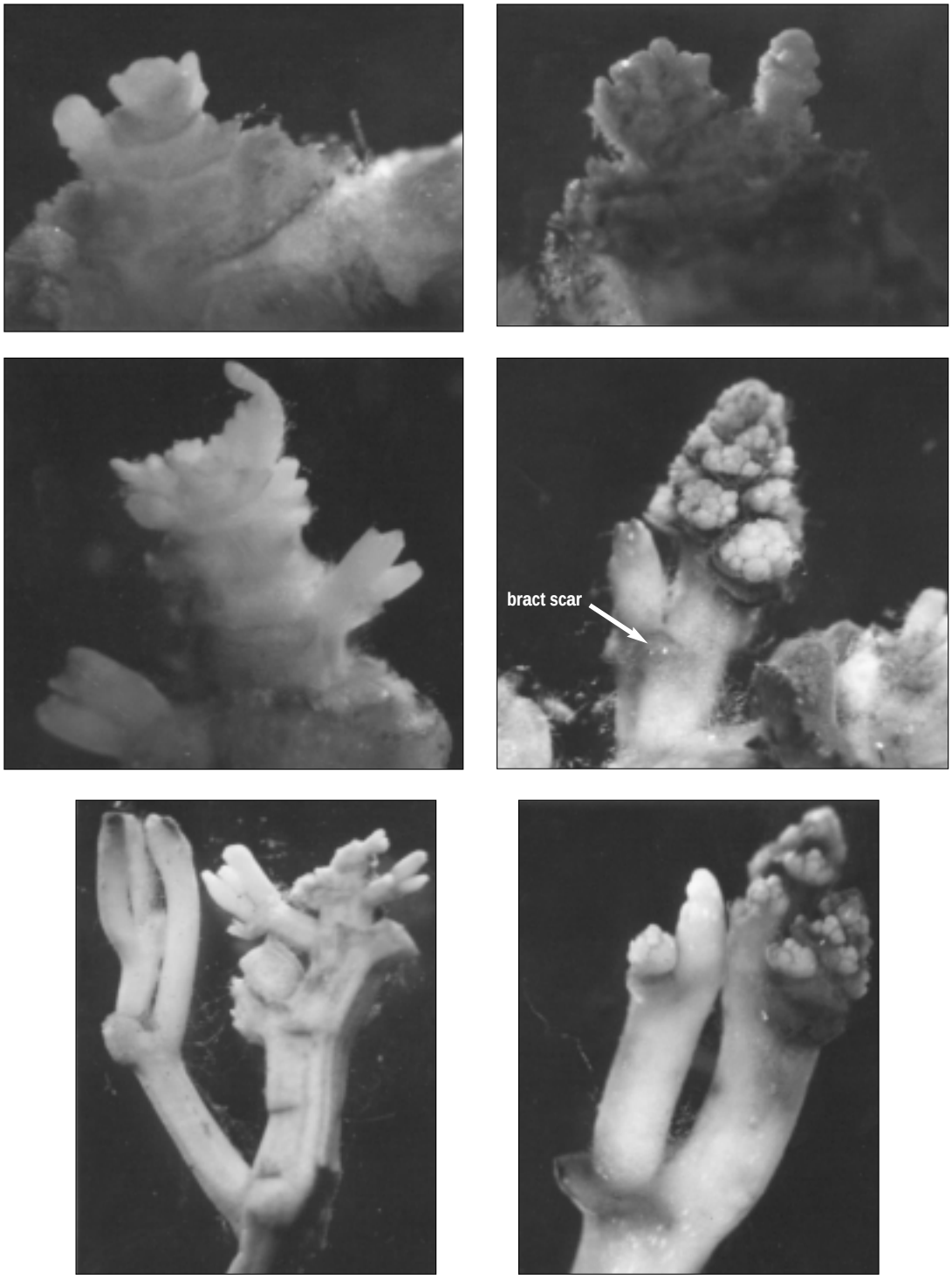



**Figure 3**. Formation of anlagen on N+1 shoots. The photographs on the left show examples of anlage development when the N shoot was not tipped, while those on the right developed when the N shoot was tipped.

absent, but may be present in various forms, as shown in Figure 4. When a shoot component is present, its first, bract-opposed appendage becomes the main portion of the inflorescence, called the 'inner arm' in literature on this subject because of its adaxial position to shoot N. The shoot component may produce at its second 'node' a leaf and a leaf-opposed inflorescence. This second appendage is colloquially named the 'wing' of an inflorescence complex without shoot component. It is called the 'outer' arm because it is abaxial to shoot N. The 'inner arm' develops more rapidly than the much smaller 'outer arm'. Hence the 'outer arm', although originating in a distal position, appears to be the most proximal part of the inflorescence prior to anthesis and has been named incorrectly 'the lowest branch of the inflorescence' (e.g. Pratt 1971, Srinivasan and Mullins 1981).

The following circumstantial evidence, based on inflorescence/tendril formation and on the time course of anthesis, supports this hypothesis of inflorescence genesis. Cultivars with a considerable proportion of

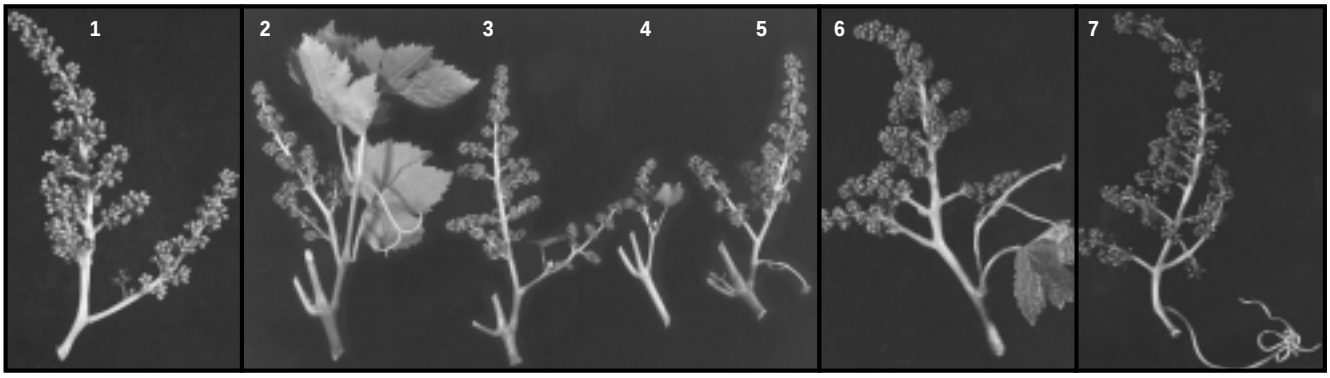



**Figure 4**. Variation in 'inflorescence' morphology with varying development of 'outer arm': (1), as 'inflorescence wing', cv. Riesling; (2–5) as shoot with varying amount of development, cv. Moscata Paradiso; (6) as rudimentary shoot plus tendril, cv. Doradillo; (7) as tendril without any shoot component, cv. Sultana. These inflorescences coincide with Modified E–L System stage 17 (Coombe 1995).

inflorescences with 'wings' also produce multiple inflorescences on the N-shoot. In contrast, cultivars with inflorescences where wings are infrequent (Sultana, Ohanez, Purple Cornichon) produce mostly N-shoots with only one inflorescence (May 1964). The formation of inflorescences with a tendril in place of a 'wing' thus parallels the formation of N-shoots with only one inflorescence and a tendril instead of a second inflorescence. Also, in relation to the time course of anthesis, the sequence of flower opening on the inner and outer arms of inflorescences and on the two inflorescences of two-inflorescence shoots is similar: flowers on the 'inner' inflorescence arm and on the proximal inflorescence of two-inflorescence shoots open earlier than flowers on the 'outer' inflorescence arm (wing) and on the distal inflorescence of such shoots.

The apparent morphogenetic variability of inflorescences may thus be interpreted as a consequence of a reductive process whereby the shoot portion of the apical meristem of the anlage is overwhelmed by the more rapid meristematic development of its lateral appendage(s). This process would be in parallel to that suggested for the shoot itself by Fournioux and Bessis (1990) who found sympodisation to occur only when the apical meristem remains small after anlage initiation (as described above). The sequence of the development of the leaf-opposed anlage could then be interpreted as: shoot initial (mostly lost) → first inflorescence → second inflorescence or tendril (may be lost) → shoot apex (mostly lost). This sequence is in contrast to the interpretation of Srinivasan and Mullins (1981) who suggested a pathway for anlagen development as: anlage → tendril primordium → shoot or inflorescence or tendril.

### Formation and distribution of flowers

While there is general agreement amongst authors that flower initials are not formed before the onset of dormancy, the question remains to be answered whether first-order branching continues after dormancy has ended. Neither the scanning pictures of Scholefield and Ward (1975) nor those of Srinivasan and Mullins (1981) allow such a determination. The section of a dormant Sultana bud shown by Barnard and Thomas (1933, their Figure 2, top right) shows eight branch initials. This number needs to be doubled because a median section fails to show one half of the branches, which are inserted on the rachis pair-wise, the pairs at about the same level, alternating cross-wise up to the inflorescence apex.

In an experiment where the buds of single-node Sultana cuttings were made to burst at 22/18°C day/night temperature (May 1964), the inflorescence primordia of dormant buds showed branches of the first order and occasionally some of the second order. On day 8 branches of the third order had been formed, while those of the fourth order had been formed on day 12, the mean day of budburst. This course of development agrees with the statement of Barnard and Thomas (1933) that 'most of the growth and branching of the inflorescence occurs during the period from mid-August to bud-burst'; they then added, however, 'that the extent of the growth of an inflorescence during this period is largely dependent upon the stage of development it had reached at the end of the previous season'. It also agrees with the finding of Carolus (1970) that the inflorescence primordium of the cultivar Merlot forms its main branches, but not its lower-order branches, before the onset of dormancy.

Except for statements by Alleweldt and Balkema (1965), Alleweldt (1966) and Alleweldt and Ilter (1969) that in Germany some flowers are formed before the onset of dormancy, there is general agreement that flower formation commences around the time of budburst. The fact that some branching occurs after the end of dormancy makes it appear likely that flower number is not yet fixed at the onset of dormancy, and this has now been confirmed experimentally. Both Pouget (1981), holding container-grown, two-year-old grapevines of cvs Merlot and Cabernet Sauvignon during budburst at 12°C and 25°C, and Ezzili (1993), working with cuttings of the cvs Alicante Grenache and Cardinal held at 12° and 28°C, obtained more flowers per inflorescence at the lower than at the higher temperature. However the fresh weight of inflorescences of Sultana made to burst on cuttings at 15°/10° or 22°/16°C day/night did not vary at the stage comparable to Pouget's definition of budburst, even though the lower temperature regime caused a delay of 12 d in reaching this stage. Thus, the propensity of flower formation is evidently affected when temperature is close to either the lower or upper limit likely to be

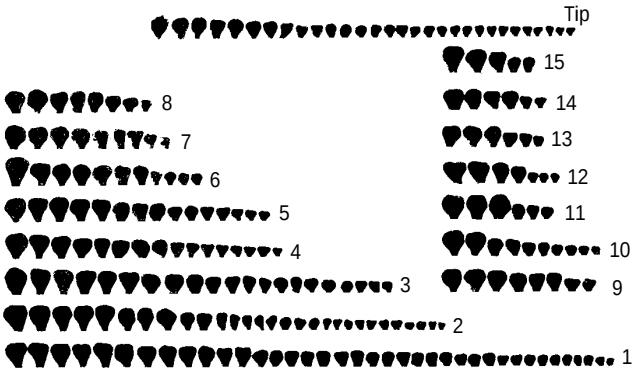



**Figure 5**. Shadowgrams of the flowers of a Pinot Noir inflorescence, sampled in a Burgundy vineyard on 15 May, about one month before flowering. They are arranged in ascending order of the branches (labelled 1 to tip) on which they originated, indicating the variability in flower size. (Reproduced from May 1987)

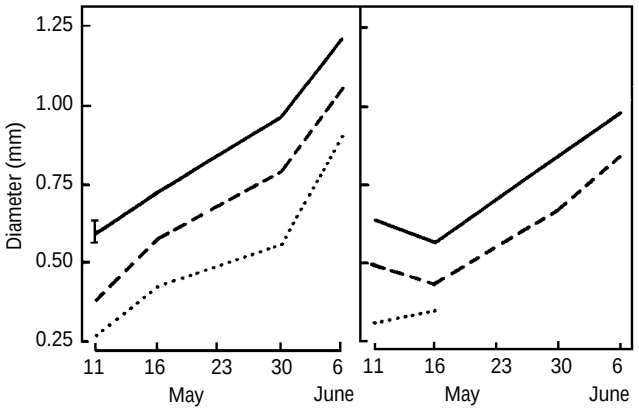



**Figure 6**. Diameter of flowers in the central, i.e. terminal, position or in lateral positions of branches of Pinot Noir inflorescences. The inflorescence was sampled in a Burgundy vineyard four weeks after budburst and six weeks before flowering.
—— Central on first- or second-order branch; – – – – Central on higher order branch; ••••• Lateral on branch of any order
(Reproduced from May 1987)

encountered in the field before and during the period of budburst. However, the importance of lesser temperature variations, which are more likely, remains to be established. A further question relates to the manner by which such differences in flower numbers eventuate. Is it the level of branching or the berry complement per branchlet?

Flowers of an inflorescence vary in both size and in their state of development according to their position on the inflorescence (May 1987). Variation in flower size is illustrated in Figure 5, while Figure 6 shows the relationship of that variation to the point of insertion within the branching system of the inflorescence. The illustration provided and discussed by Ezzili (1993) shows reduced variability in flower size at 12°C (on day 50 after budburst) compared with that at 28°C (on day 4 after budburst), but variability still existed at the lower temperature. This variability with respect to size and the stage of flower development, evident from the varying stages of closure of the calyptra, is shown on vineyard samples of Pinot Noir inflorescence branchlets in Figure 7.

Faulty development of flower parts has been implicated as one of the reasons why flowers fail to convert to berries (Kozma 1961). One such development is the formation of 'internal ovaries', perhaps better named intracarpellary pistils (May 1987). This abnormality (Figure 8) was discovered frequently during a study of flower and berry development with cvs Pinot Noir, Chardonnay and Gamay in Burgundy vineyards. Such abnormality had detrimental consequences on fruit set, which was only 17.5% for berries with this abnormality compared with almost 50% for all berries of 20 examined Pinot Noir bunches. A literature search established that this phenomenon was found by Kozma and Scheuring (1972) in the tablegrape cultivars Afuz Ali (syn. Dattier de Beyrouth, Regina, Waltham Cross) and Cardinal, and listed as one of several flower abnormalities interfering with berry set. Indeed, this teratological occurrence was frequently mentioned in the literature of the 19th and early 20th century for the grapevine as for many other plants (Penzig 1921). Several names were given to the phenomenon, viz. floripar diaphysis, endocarpic proliferation, ectoblastesis, encased supplementary carpel. More recently, Gil et al. (1992) were able to induce this condition in flowers of the tablegrape cultivar Flame Seedless by application of the auxin 2,4-dichlorophenoxyacetic acid at week 5 before bloom, i.e. when pistil enlargement had commenced. This was considered to be due to continuing meristematic activity. It was assumed to last until either auxin was no longer supplied or the meristem was inhibited by 'the complexity of the system, probably through ovule differentiation'. This finding is of interest in the context of floral differentiation, especially since Yahyaoui et al. (1998) found in experiments *in vitro* that auxin (applied as indolebutyric acid) was of lesser influence on floral differentiation than either gibberellin or cytokinin.

### Size distribution of flowers and berries

Little is known about how flowers and subsequently berries are affected by their position on individual inflorescences and bunches. Moreover, the sparse information found in the literature is difficult to access

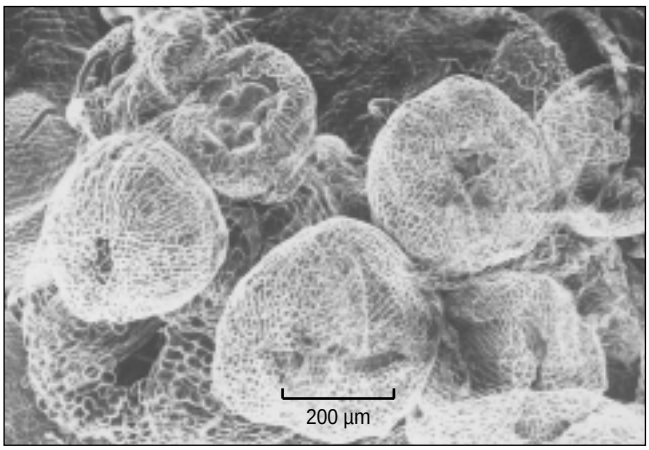



**Figure 7**. Scanning micrograph of a branchlet of a Pinot Noir inflorescence four weeks after budburst and six weeks before flowering. Note difference not only in size but also developmental stage of flowers.

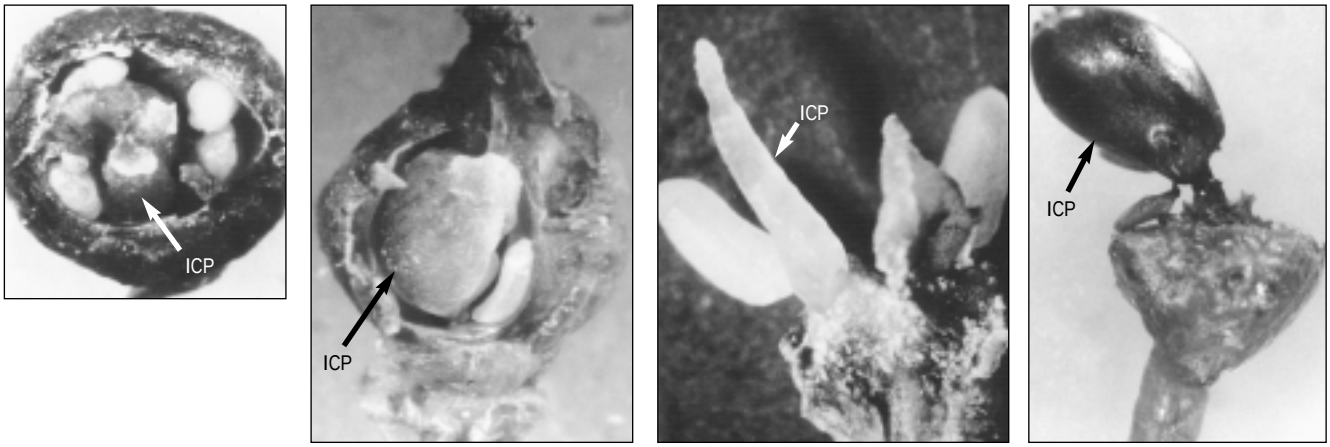



**Figure 8**. Intracarpellary pistils (ICP). From left to right: Pinot Noir pistil with four ovules and central ICP; Gamay pistil with large ICP and trace of stigma; Poulsard pistil with long, undifferentiated ICP; mature Gamay berry (removed) with coloured berry-like ICP on receptacle.

(Benabedrabou 1972, Tourmeau 1976). This lack of information is surprising as berries are, after all, the basic units of crop production and their position on the framework of the rachis may well have implications on metabolic activity and substrate accumulation.

Initial observations on the distribution of flowers on the inflorescence were made on samples of cv. Chardonnay collected in a vineyard near Waikerie, South Australian Murray Valley. This was followed by more detailed studies on inflorescence and bunch structure in two seasons, 1989/90 and 1990/91, in two Chardonnay vineyards that differed in climate and site management (for details see 'Materials and Methods') and referred to here as either 'Hills' or 'Plain'. On both sites, bunches were randomly selected and analysed, two from each of 12 vines pruned either to spurs, to canes, or to hedge. To illustrate the difference between the two sites, Table 2 contains data on yield and yield components. The vines at the Plain site, being wider spaced and bigger than those at the Hills site, had almost twice the number of bunches, which carried on average more berries, and yielded almost three times as much fruit.

*Distribution of flowers on branches*

The distribution of flowers on the sequence of branches that make up an inflorescence is shown in Figure 9, based on randomly collected Chardonnay inflorescences from Waikerie. The mean number of flowers per branch was

**Table 2**. Components of yield for Chardonnay vines, growing in two vineyards (Hills, Plain), pruned to spur, cane or hedge, and sampled during seasons 1989/90 and 1990/91. Least significant differences (LSD) are shown for yield and bunch number per vine, and standard errors ($P < 0.05$), indicated as subscripts, are shown for the other variables that were determined on 18–24 bunches per pruning treatment.

| Variable/ | Hills | | | | Plain | | | |
|---|---|---|---|---|---|---|---|---|
| Season | Spur | Cane | Hedge | LSD 1% | Spur | Cane | Hedge | LSD 1% |
| **Yield/vine (kg)** | | | | | | | | |
| 1989/90 | 4.23 | 5.13 | 6.71 | 1.26 | 13.10 | 14.85 | 15.71 | 3.10 |
| 1990/91 | 2.99 | 3.38 | 4.52 | 0.97 | 9.87 | 13.88 | 14.38 | 3.32 |
| **Bunches/vine** | | | | | | | | |
| 1989/90 | 49 | 58 | 88 | 13 | 92 | 106 | 164 | 13 |
| 1990/91 | 49 | 56 | 79 | 15 | 78 | 92 | 145 | 24 |
| **Branches/inflorescence** | | | | | | | | |
| 1989/90 | $14.0_{0.7}$ | $17.5_{0.5}$ | $15.9_{0.7}$ | | $18.4_{0.6}$ | $19.3_{0.7}$ | $15.7_{0.8}$ | |
| 1990/91 | $14.4_{0.8}$ | $17.1_{0.9}$ | $13.7_{0.9}$ | | $15.7_{1.1}$ | $22.6_{0.8}$ | $17.9_{0.9}$ | |
| **Flowers/inflorescence** | | | | | | | | |
| 1989/90 | $141_{9.7}$ | $204_{14.9}$ | $178_{13.2}$ | | $751_{9.8}$ | $369_{33.6}$ | $181_{19.4}$ | |
| 1990/91 | $168_{14.0}$ | $214_{13.7}$ | $131_{8.4}$ | | $183_{16.9}$ | $407_{44.7}$ | $239_{20.2}$ | |
| **Berries/bunch** | | | | | | | | |
| 1989/90 | $20_{2.0}$ | $26_{2.2}$ | $27_{2.9}$ | | $45_{3.3}$ | $48_{3.7}$ | $31_{2.6}$ | |
| 1990/91 | $20_{2.1}$ | $20_{1.9}$ | $17_{1.9}$ | | $27_{2.6}$ | $33_{3.2}$ | $35_{6.1}$ | |
| **Per cent set** | | | | | | | | |
| 1989/90 | $47_{2.4}$ | $45_{2.2}$ | $45_{2.6}$ | | $42_{3.0}$ | $37_{2.6}$ | $40_{2.6}$ | |
| 1990/91 | $40_{3.0}$ | $37_{2.6}$ | $48_{2.6}$ | | $48_{2.9}$ | $35_{3.2}$ | $45_{2.2}$ | |

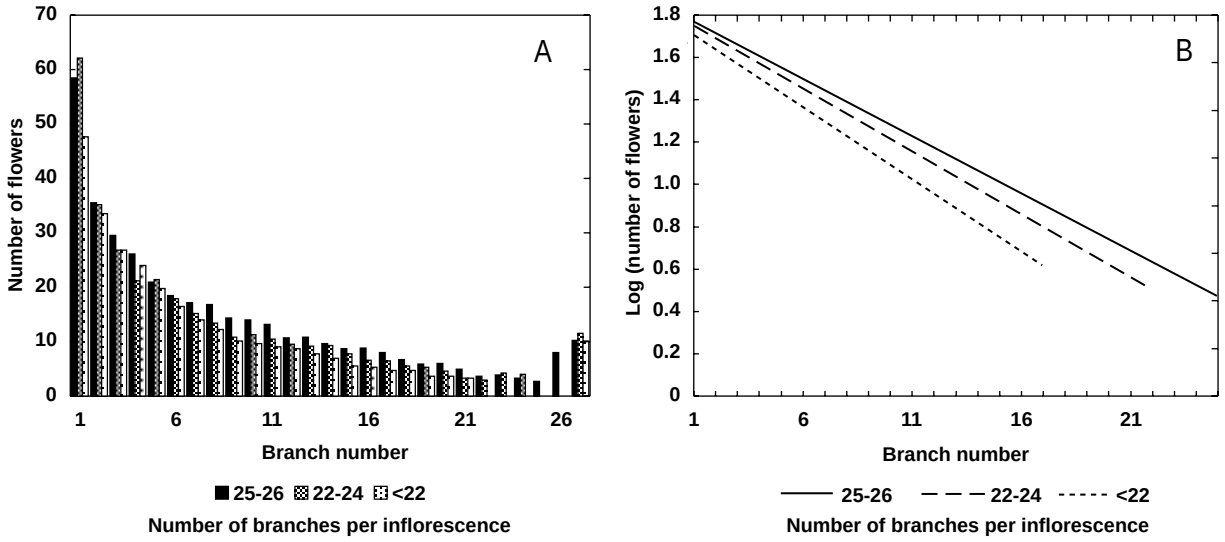



**Figure 9**. Means of number of flowers per branch (A), and linear regression of log(mean number of flowers per branch) on branch number (B), of randomly sampled Chardonnay inflorescences from a Waikerie (South Australia) vineyard. The inflorescences were divided into three groups according to their number of branches (25–26, 22–24 & <22). The last column of (A) gives the values for the most apical part of the inflorescence where branching is no longer discernible. The number of inflorescences in the three classes was as follows: $n_{25\text{-}26} = 6$, $n_{22\text{-}24} = 7$, $n_{<22} = 12$. For (B) coefficients of determination ($R^2$): $R^2_{25\text{-}26} = 97.0$, $R^2_{22\text{-}24} = 94.9$, $R^2_{<22} = 97.4$.

determined on 25 inflorescences, grouped according to their branch numbers. In each group, the mean number of flowers per branch decreased exponentially from the most proximal to the most distal branch, as shown by the highly significant linear regressions of log-transformed flower number on branch number. This is a reflection of the form of the grape inflorescence, described as a panicle (e.g. Pratt 1971).

*Branch number and flower number*

Despite yield differences between vines of Hills and Plain cited above, the mean number of primary branches per inflorescence differed little, and differences in berry number were obviously the result of differences in lower-order branching. The bunches of cane-pruned vines had more branches, presumably because some of the bunches came from more distal node positions of the canes; these contain larger inflorescence primordia than the basal two nodes present on spurs (May and Cellier 1973).

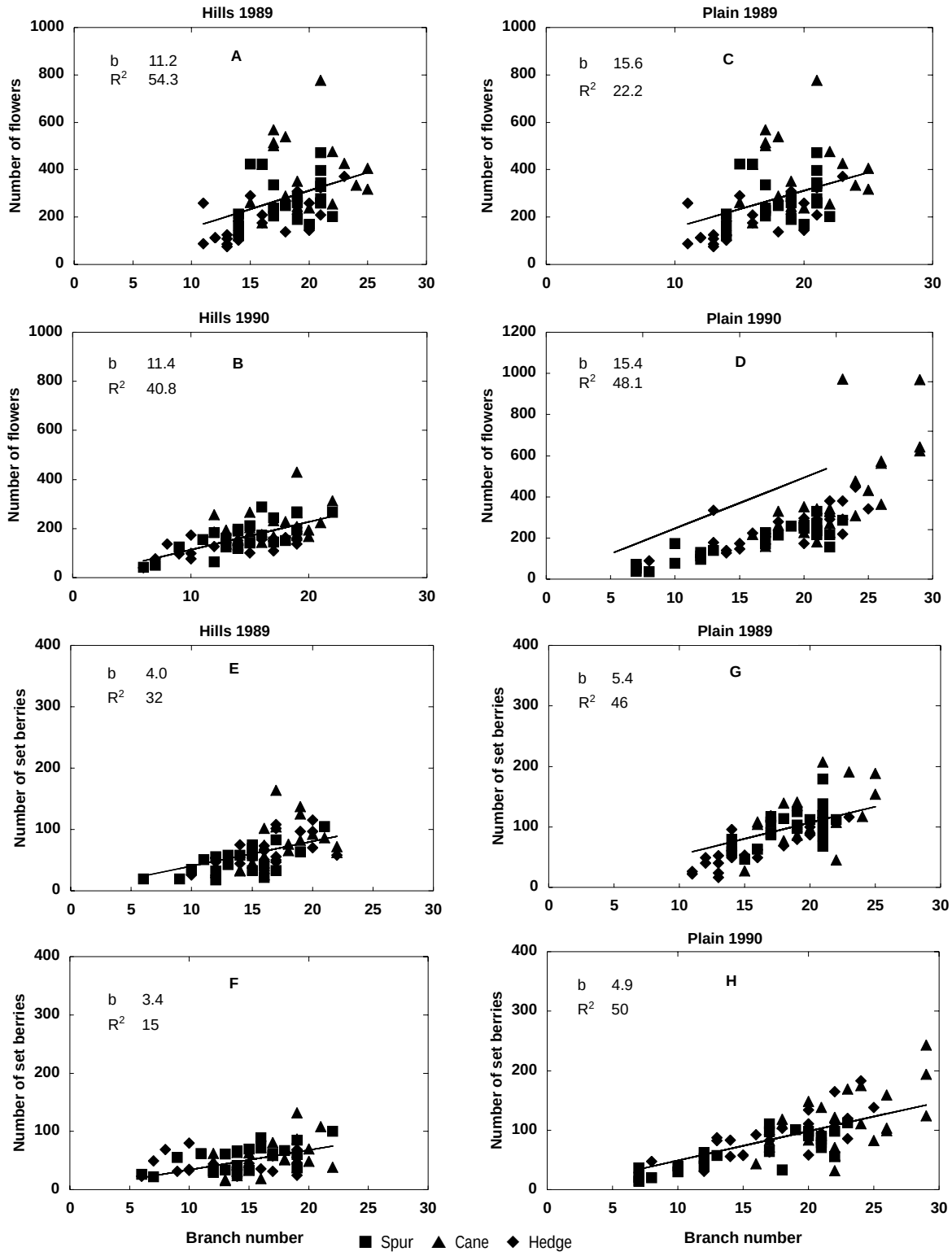
Regression lines, forced through the origin, for mean flower number on branch number of the three pruning treatments (combined) are shown in Figure 10 (A–D). According to the values for the regression coefficient b, the average number of flowers per inflorescence was about 11 for Hills and 15 for Plain, with little variation between years. Relevant values for the three pruning treatments are also tabulated. All combined regression coefficients were highly significant, even though the spread of values around the regression line was considerable, especially for cane-pruned, and this resulted in somewhat low values for the coefficients of determination $R^2$. Among the twelve regressions of the individual pruning treatments, only nine were significant. Thus branch number per inflorescence is not a good indicator for flower number, as had already been found for Pinot Noir in Burgundy (May 1987).

Also shown in Figure 10 (E–H) are regression lines for set berries (i.e. the berries of size classes 1-4, see below) as a function of branch number. Again, while all four regressions were highly significant, the variation around the regression line was considerable ($R^2$ of 50 or less). Values for the regression coefficient b indicate an average number per branch of set berries of 3–4 for Hills and about 5 for Plain. Two of the twelve regressions for the individual pruning treatments were not significant. Thus branch number per bunch also failed to be an accurate predictor of number of set berries per bunch despite the significant relationship between the two variables. This applied also for the counts done on bunches at harvest (Table 3).

*Variation in berry size*

Berries present on bunches either soon after set or at harvest were visually divided into seven size classes whose mean weight was then determined. Classes 1–4 were of sufficient size to contribute to the weight of the crop, class 5 were small berries assumed to have no viable seed, having arisen without successful pollination (Staudt and Kassemeyer 1984) and colloquially called 'chickens' (*millerandées* in French). Class 6 were live green ovaries that had failed to expand (colloquially called 'shot berries') and class 7 were blackened dead ovaries that had failed to drop. The respective numbers determined at the various times of sampling are shown in Figure 11.

Differences between the bunches from the three pruning treatments were mostly not significant except for size classes 6 and 7. Obviously the much greater average number of flowers on inflorescences from the cane-pruned and to a lesser extent the hedged vines did not translate into more berries. Compared with inflorescences from spur-pruned vines they had much larger numbers of ovaries (classes 6 and 7) that were loose. Their placement on the rachis could no longer be determined, but their numbers could be used to determine per cent set. It




| | | Regression flowers on branches | | | | | | Regression set flowers on branches | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Hills | | | Plain | | | Hills | | | Plain | | |
| | | Spur | Cane | Hedge | Spur | Cane | Hedge | Spur | Cane | Hedge | Spur | Cane | Hedge |
| b | 1989 | 10.1 | 11.8 | 11.4 | ns | ns | 11.4 | 3.6 | ns | 4.1 | 5.4 | 6.0 | 4.2 |
| | 1990 | 11.2 | ns | 9.3 | 11.5 | 18.6 | 13.5 | 3.7 | 3.4 | ns | 4.1 | 5.1 | 5.2 |
| $R^2$ | 1989 | 59 | 40 | 64 | 4 | 3 | 37 | 10 | 14 | 38 | 38 | 28 | 60 |
| | 1990 | 45 | 2 | 34 | 77 | 34 | 56 | 40 | 17 | 2 | 64 | 26 | 55 |

**Figure 10**. Linear regression lines and data points of flower number (A–D) and of set berries in size classes 1–4 (E–H) on number of branches for Chardonnay bunches sampled at random after set in two seasons from vines pruned to spurs, canes or hedge in two vineyards (Hills, Plain). The table contains the regression coefficients b and coefficients of determination $R^2$ for the separate analyses of the values of each pruning treatment. These were combined in the analyses of A–H.

**Table 3**. Regression coefficients b and coefficients of determination $R^2$ for the regressions of number of berries at harvest (y) on number of branches per bunch (x). Chardonnay bunches sampled in two seasons from vines pruned to spur (S), cane (C) and hedge (H) in two vineyards (Hills, Plain). The parameters are shown for the analysis of each pruning treatment and for their combined analysis.

| | | Hills | | | | Plain | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | S | C | H | All | S | C | H | All |
| **b** | 1989 | ns | $6.0^{*}$ | ns | $5.6^{***}$ | $6.7^{***}$ | $7.0^{***}$ | $5.5^{**}$ | $6.4^{**}$ |
| | 1990 | $4.2^{***}$ | $4.4^{***}$ | $4.5^{***}$ | $4.4^{***}$ | $6.1^{**}$ | $6.0^{***}$ | $4.3^{***}$ | $6.2^{***}$ |
| **$R^2$** | 1989 | 10 | 36 | 8 | 31 | 34 | 43 | 64 | 48 |
| | 1989 | 53 | 43 | 44 | 45 | 49 | 50 | 41 | 61 |

Significance levels of b:

ns= not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

was surprising that many of the unfertilised ovaries were retained in their original position within the bunch despite the general field observation that many drop after berry setting has ended. There was good agreement between the numbers of berries in classes 1–4 collected after set and at harvest at Hills, but not at Plain. In 1989/90, the harvest bunches had more berries than the after-set bunches due to sampling differences. However in season 1990/91, there was also a shift in the numbers of berries in the classes, with a considerable increase in the numbers of the largest berries (class 1).

Means of berry fresh weight, number of live seeds, numbers of hollow seeds ('floaters') and of berry weight per seed for the berries of size classes 1–4 are shown in Table 4. Reduction in mean weight per berry with decreasing size was consistent in all samples; on average, berry weight in size classes 2, 3 and 4 amounted to about 75%, 60% and 40% of that in class 1. Corresponding values for seed number per berry were somewhat similar —70%, 50% and 30%. The fact that increases in seed number lead to increased berry size is well established (Müller-Thurgau 1898, Schumann 1973 and references therein). The decrease in the values of berry weight per seed with increasing seed number agrees with the results of Schumann (1973) who found a quadratic relationship between berry volume and seed number. Hence the stimulation of pericarp development induced by a single seed becomes less as the seed complement per berry increases. The fact that berry weight per seed number varied between seasons on both sites indicates that differences in seed number between seasons or sites are not the sole, and perhaps not even a major, determinant of differences in berry weight, despite their close relationship within any one season and site. This is in agreement with results obtained earlier when unsuccessful attempts were made to use seed number, established early in the cycle of berry growth and development, to forecast final berry weight (May unpublished data).

Hollow seeds that float on water ('floaters', Ebadi et al. 1995, 1996) are seeds with a woody testa that are non-functional, but which cannot be distinguished visually from viable seeds. They were present in berries of all size classes, but in greater numbers, and often as sole seeds, in those of size class 4.

**Table 4**. Means of fresh weight, number of viable seeds and number of 'floater' (hollow) seeds per berry, and berry weight/seed. Chardonnay bunches were sampled at random after set and at harvest in two seasons from vines pruned to spurs, canes or hedge in two vineyards (Hills, Plain). Every berry was visually allotted to one of four size classes. The values are means calculated from all bunches of the three pruning treatment (n = 18 to 24) on each site/season as there were no significant differences between the pruning treatments. 'Floater' numbers were only determined at harvest.

| | Weight/berry (g) | | | | No. viable seeds/berry | | | | Berry weight/seed (g) | | | | No. floaters/berry | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Size class** | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| ***After set*** | | | | | | | | | | | | | | | | |
| **Hills** | | | | | | | | | | | | | | | | |
| 1989/90 | 0.67 | 0.49 | 0.37 | 0.27 | 2.00 | 1.13 | 0.90 | 0.33 | 0.33 | 0.45 | 0.41 | 0.89 | | | | |
| 1990/91 | 0.54 | 0.39 | 0.30 | 0.19 | 1.59 | 1.23 | 0.98 | 0.56 | 0.34 | 0.31 | 0.31 | 0.47 | | | | |
| **Plain** | | | | | | | | | | | | | | | | |
| 1989/90 | 0.72 | 0.56 | 0.43 | 0.31 | 2.34 | 1.87 | 1.22 | 0.81 | 0.30 | 0.30 | 0.39 | 0.32 | | | | |
| 1990/91 | 0.26 | 0.17 | 0.12 | 0.07 | 2.22 | 1.55 | 0.71 | 0.31 | 0.12 | 0.11 | 0.16 | 0.22 | | | | |
| ***Harvest*** | | | | | | | | | | | | | | | | |
| **Hills** | | | | | | | | | | | | | | | | |
| 1989/90 | 1.68 | 1.34 | 1.14 | 0.78 | 1.43 | 1.12 | 0.89 | 0.58 | 1.19 | 1.20 | 1.29 | 1.38 | 0.26 | 0.24 | 0.38 | n.d. |
| 1990/91 | 1.33 | 1.06 | 0.84 | 0.41 | 1.80 | 1.18 | 0.83 | 0.36 | 0.75 | 0.90 | 1.06 | 1.17 | 0.22 | 0.21 | 0.26 | 0.50 |
| **Plain** | | | | | | | | | | | | | | | | |
| 1989/90 | 1.55 | 1.23 | 1.00 | 0.63 | 2.33 | 1.56 | 1.06 | 0.75 | 0.66 | 0.79 | 0.94 | 1.08 | 0.09 | 0.05 | 0.04 | 0.07 |
| 1990/91 | 1.60 | 1.29 | 1.10 | 0.82 | 1.68 | 1.23 | 0.99 | 0.74 | 0.96 | 1.08 | 1.15 | 1.13 | 0.17 | 0.12 | 0.10 | 0.32 |

n.d.= not detemined due to insufficient number of berries.

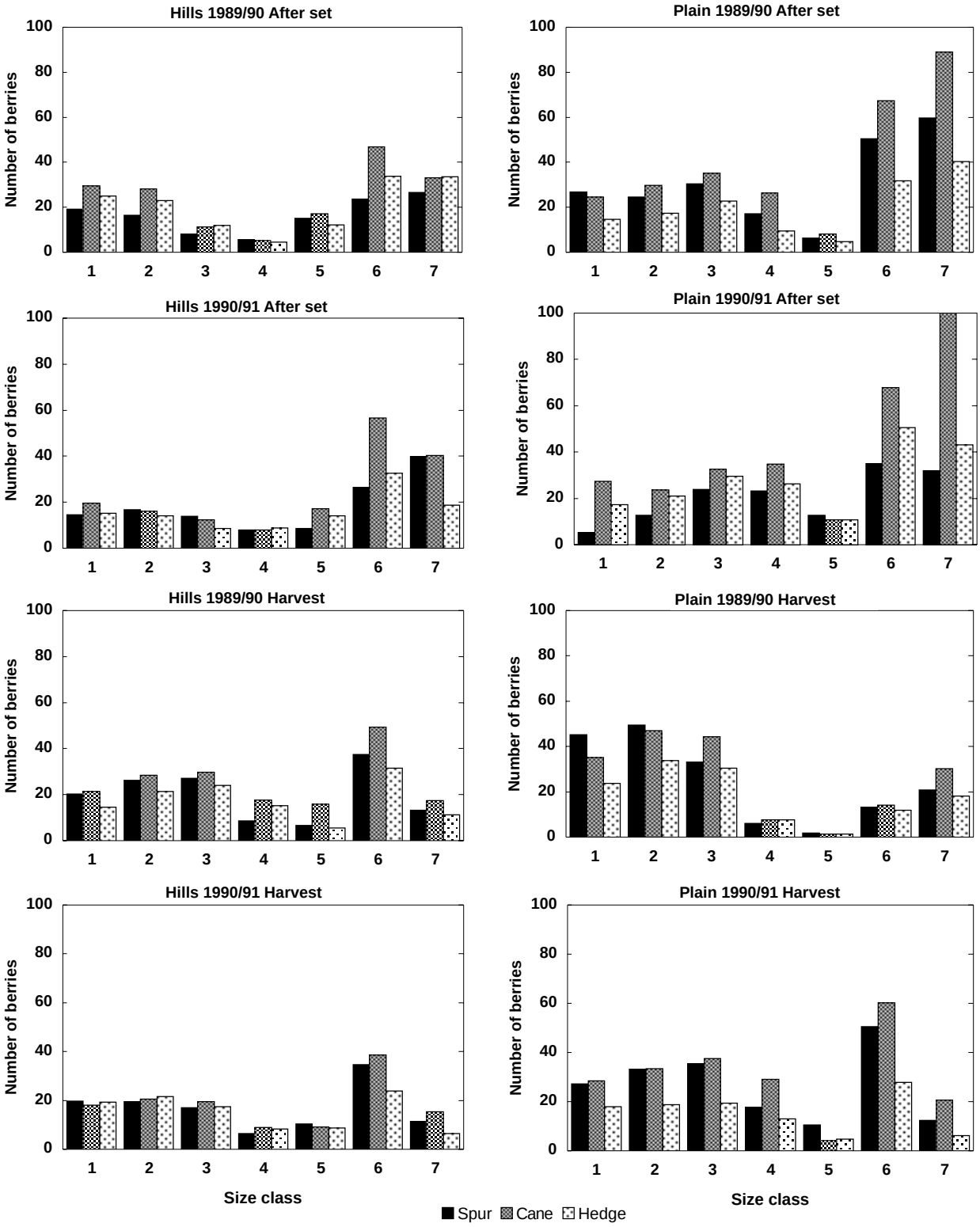



**Figure 11**. Number of berries (size classes 1–5, with class 1 being the biggest by visual assessment) and undeveloped ovaries (size classes 6, 7) for Chardonnay bunches sampled at random after set and at harvest in two seasons from vines pruned to spurs, canes or hedge in two vineyards (Hills, Plain). Note that the values for size class 7 are one half the real values.

*Berry numbers and berry weight*

The effect of variation in berry number and berry weight on total berry weight per branch is shown in Table 5. In the bunches collected at harvest, the proportion of bunch weight contributed by berries of size classes 1 and 2 was similar, due to the compensating effect of berry number and mean berry weight. On average, over all treatments in the four site × season lots, berries of classes 1–4 contributed 35%, 32%, 25% and 8% of total bunch weight. The variability among the lots was small, although the variation in vine yield (Table 2) was large, as was the difference in berry weight within each class. There was less consistency among the samples taken after set.

**Table 5**. Mean fresh weight of berries, absolute (A), and as percentage of the total berry weight per bunch (B), for each of four berry size classes to which they were allotted visually. Chardonnay bunches were sampled at random after set and at harvest in two seasons from vines pruned to spurs, canes or hedge in two vineyards (Hills, Plain). Every berry was visually allotted to one of four size classes. 18–24 bunches per pruning treatment. Standard errors as subscripts.

| | | A: Weight of berries/size class (g) | | | | B: Values of A as per cent of total bunch weight | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Size class | | | | Size class | | | |
| | | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| ***After set*** | | | | | | | | | |
| **Hills** | | | | | | | | | |
| 1989/90 | Spur | $13.6_{1.6}$ | $9.2_{1.4}$ | $3.3_{0.6}$ | $1.2_{0.2}$ | $51.0_{4.1}$ | $31.9_{3.3}$ | $11.0_{1.6}$ | $6.1_{1.3}$ |
| | Cane | $20.3_{2.5}$ | $14.4_{1.8}$ | $4.2_{0.7}$ | $1.5_{0.3}$ | $51.0_{3.4}$ | $34.8_{2.2}$ | $10.2_{1.7}$ | $4.1_{0.6}$ |
| | Hedge | $17.1_{1.9}$ | $12.0_{1.7}$ | $4.3_{0.9}$ | $1.2_{0.2}$ | $49.7_{4.6}$ | $33.2_{2.4}$ | $12.9_{2.4}$ | $4.2_{1.0}$ |
| 1990/91 | Spur | $9.0_{1.3}$ | $7.2_{0.8}$ | $4.3_{0.5}$ | $1.6_{0.3}$ | $39.3_{3.2}$ | $32.3_{1.6}$ | $20.7_{2.2}$ | $7.8_{1.1}$ |
| | Cane | $12.0_{1.6}$ | $7.3_{1.0}$ | $4.0_{0.8}$ | $2.2_{0.4}$ | $46.4_{4.4}$ | $28.3_{2.2}$ | $15.7_{2.4}$ | $9.7_{1.9}$ |
| | Hedge | $8.7_{1.1}$ | $5.5_{0.7}$ | $2.1_{0.5}$ | $1.3_{0.2}$ | $48.4_{3.5}$ | $32.3_{2.7}$ | $12.0_{2.3}$ | $7.3_{1.2}$ |
| **Plain** | | | | | | | | | |
| 1989/90 | Spur | $21.0_{2.1}$ | $14.8_{1.2}$ | $13.8_{1.1}$ | $9.3_{1.0}$ | $35.5_{3.1}$ | $25.0_{1.3}$ | $23.6_{1.4}$ | $15.9_{0.3}$ |
| | Cane | $17.3_{1.5}$ | $17.6_{1.7}$ | $16.0_{1.8}$ | $9.5_{1.9}$ | $32.1_{3.0}$ | $29.1_{1.5}$ | $24.8_{1.5}$ | $14.1_{2.2}$ |
| | Hedge | $11.1_{1.9}$ | $10.5_{1.6}$ | $15.4_{1.1}$ | $2.7_{0.5}$ | $23.9_{2.9}$ | $24.4_{2.0}$ | $44.8_{4.0}$ | $6.9_{1.1}$ |
| 1990/91 | Spur | $1.6_{0.4}$ | $2.3_{0.3}$ | $2.3_{0.3}$ | $1.6_{0.2}$ | $16.3_{3.0}$ | $28.4_{1.9}$ | $32.6_{2.7}$ | $22.7_{2.7}$ |
| | Cane | $8.8_{1.7}$ | $5.2_{0.7}$ | $4.2_{0.6}$ | $2.2_{0.4}$ | $39.4_{2.8}$ | $27.8_{2.1}$ | $21.3_{2.4}$ | $11.5_{3.0}$ |
| | Hedge | $5.7_{1.0}$ | $4.2_{0.5}$ | $3.9_{0.4}$ | $2.0_{0.3}$ | $32.0_{3.5}$ | $27.1_{1.9}$ | $26.7_{2.0}$ | $14.2_{2.2}$ |
| ***Harvest*** | | | | | | | | | |
| **Hills** | | | | | | | | | |
| 1989/90 | Spur | $35.3_{3.7}$ | $35.8_{4.4}$ | $29.4_{5.2}$ | $6.8_{2.4}$ | $32.7_{2.9}$ | $32.6_{1.5}$ | $28.5_{2.9}$ | $6.2_{1.4}$ |
| | Cane | $37.4_{2.9}$ | $38.4_{2.8}$ | $32.2_{2.8}$ | $13.2_{2.0}$ | $34.4_{3.7}$ | $30.9_{4.4}$ | $23.9_{5.2}$ | $10.8_{2.4}$ |
| | Hedge | $25.6_{3.4}$ | $29.3_{2.1}$ | $25.3_{2.7}$ | $8.7_{1.9}$ | $28.3_{3.4}$ | $33.1_{1.9}$ | $28.7_{2.7}$ | $10.0_{2.2}$ |
| 1990/91 | Spur | $28.2_{3.4}$ | $21.3_{2.3}$ | $14.0_{1.6}$ | $3.6_{0.5}$ | $41.4_{3.9}$ | $31.6_{1.9}$ | $21.3_{23}$ | $5.6_{0.8}$ |
| | Cane | $26.9_{2.3}$ | $25.8_{2.4}$ | $20.1_{2.8}$ | $5.2_{1.1}$ | $35.4_{2.9}$ | $33.4_{1.7}$ | $24.7_{2.4}$ | $6.3_{1.0}$ |
| | Hedge | $26.0_{2.3}$ | $25.2_{2.8}$ | $18.5_{2.2}$ | $6.1_{1.1}$ | $34.7_{3.0}$ | $32.5_{3.1}$ | $24.2_{2.6}$ | $8.6_{1.7}$ |
| **Plain** | | | | | | | | | |
| 1989/90 | Spur | $73.3_{6.6}$ | $62.9_{5.3}$ | $34.5_{2.4}$ | $4.2_{0.7}$ | $40.3_{2.7}$ | $35.2_{1.4}$ | $21.9_{2.6}$ | $2.5_{0.4}$ |
| | Cane | $58.7_{7.8}$ | $60.1_{3.7}$ | $46.4_{4.9}$ | $5.8_{1.2}$ | $33.8_{6.6}$ | $35.5_{1.7}$ | $27.3_{2.7}$ | $3.5_{0.7}$ |
| | Hedge | $38.2_{5.2}$ | $38.6_{2.4}$ | $26.2_{3.8}$ | $3.8_{1.1}$ | $35.0_{4.1}$ | $36.5_{1.3}$ | $24.8_{3.6}$ | $3.6_{1.0}$ |
| 1990/91 | Spur | $46.0_{4.7}$ | $45.1_{4.5}$ | $42.1_{6.9}$ | $15.8_{2.6}$ | $32.4_{2.3}$ | $30.8_{1.1}$ | $26.5_{1.7}$ | $10.4_{1.3}$ |
| | Cane | $43.9_{4.9}$ | $42.0_{3.5}$ | $40.4_{2.7}$ | $25.3_{1.3}$ | $27.9_{1.7}$ | $27.5_{1.3}$ | $28.3_{1.5}$ | $16.3_{1.5}$ |
| | Hedge | $30.2_{2.2}$ | $25.0_{2.4}$ | $21.7_{2.0}$ | $10.7_{1.6}$ | $34.9_{1.9}$ | $27.9_{1.6}$ | $24.9_{1.5}$ | $12.3_{1.4}$ |

*Berry distribution along the bunch rachis*

The distribution of berries over the bunch frame (Figures 12 and 13) was assessed by combining data for successive berry size classes and bunch branches, averaged over the three pruning treatments as they showed similar trends. The grape inflorescence being a panicle, the number of berries became less along the acropetal sequence of branches, as was the case with flower numbers.

The data in Figure 12, for each site × season lot, represent the mean number of berries per branch pair 1/2 to 11/12 in size classes 1/2, 3/4 and 5/6, expressed for each size class pair as the percentage of all berries within the class. When the percentages of the three pruning treatments were averaged, the logarithms of the means gave highly significant negative linear regressions with the numbers 1 to 6 representing the six branch pairs. Fourteen of these regressions had $R^2$ values greater than 95%, seven between 85% and 95% and three between 78% and 85%. The intercepts a, retransformed to antilogs, varied between 17 and 44, and the retransformed regression coefficients b varied between –1.184 and –1.652. Both a and b were bigger for size class 3/4 than for the other two, while b was the smallest for size class 1/2. Thus, while there were differences between the various lots their main trend was similar—a regular and exponential decrease in berry number along the bunch rachis.

In contrast to Figure 12 where histograms are shown in which values for the six pairs of branches are combined for each size class pair, Figure 13 contains histograms combining the values of the three pairs of size classes for each pair of branches. There was remarkable uniformity in the proportion of berries in the three pairs of size classes right along the rachis in all site × season lots despite large differences in their overall values.

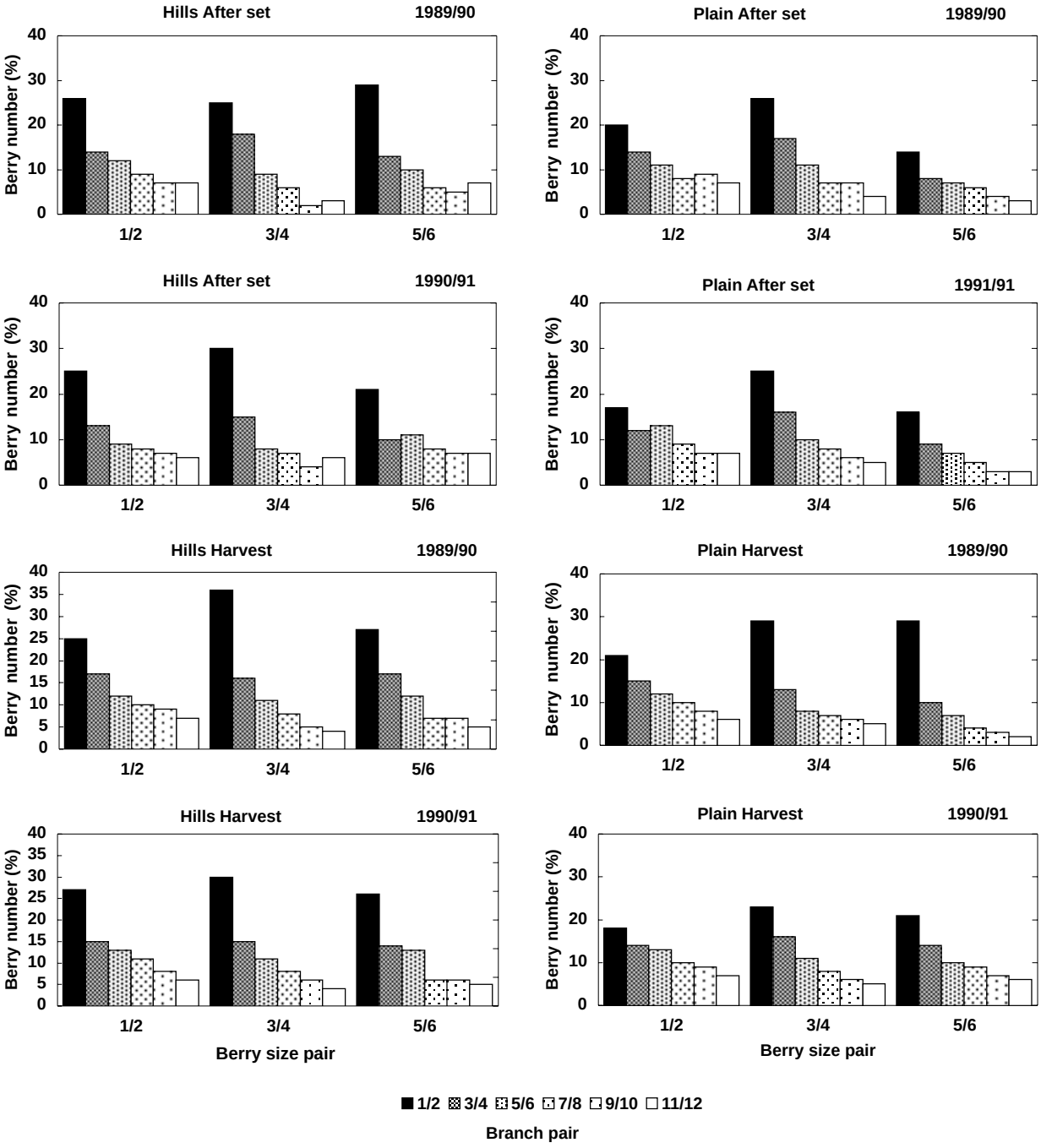



**Figure 12**. Number of berries of size classes 1/2, 3/4 and 5/6 on branch pairs 1/2 to 11/12 expressed, for each branch pair, as percentage of all berries per class pairs. Chardonnay bunches were sampled at random after set and at harvest in two seasons from vines pruned to spurs, canes or hedge in two vineyards (Hills, Plain). For berry weights of the size classes see Table 4.

## Concluding remarks

One purpose of this paper was to comment on some of the events which impinge on the morphological development of a grapevine's reproductive apparatus. The confusing, multi-worded description of the bud system should be replaced by a clear and unequivocal numerical system as proposed earlier and again supported here. Likewise, refining the description of phenological stages is recommended by taking into account varietal differences in bud appearance during budburst. In this context, a review of the method of describing anthesis may also be appropriate because it is difficult to visually integrate the variation in flower opening that exists within inflorescences and between inflorescences, whether on single vines or between vines. As acceptance of the modified E–L system (Coombe 1995) is important for executing on time many of the essential vineyard operations, refinement of key observations appears appropriate. This applies especially to their use in modelling vine response to environmental conditions. For modelling purposes it is also important to recheck the problem of flower initiation, as opposed to inflorescence initiation and differentiation. With respect to preventing the formation of 'second crop', especially where machine harvesting is practised, the relationship between the timing of shoot tipping and bunch formation has to be recognised.

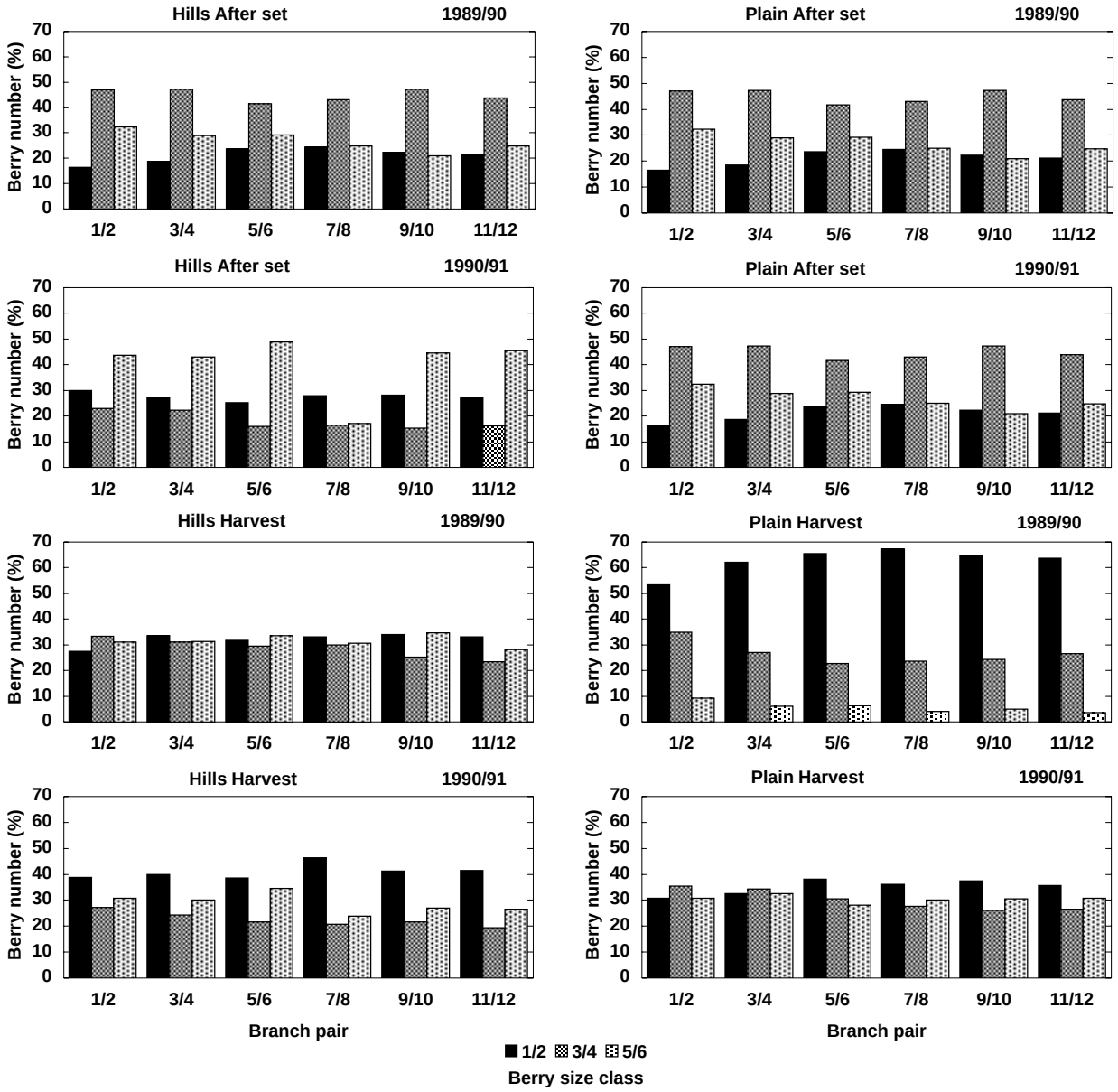



**Figure 13**. Number of berries in size class pairs 1/2, 3/4 and 5/6 on branch pairs 1/2 to 11/12 expressed, for each size class pair, as percentage of all berries per branch pair. Chardonnay bunches were sampled at random after set and at harvest in two seasons from vines pruned to spurs, canes or hedge in two vineyards (Hills, Plain). For berry weights of the size classes see Table 4.

Teratological forms are likely to be due to abnormal levels of metabolic activity and are thus useful for identifying such activity unrecognised when at normal levels. This appears to be the case with the here-described occurrence of intracarpellary ovaries. Further studies would be needed to show whether this phenomenon is as frequent as shown for cultivars in Burgundy. If this were the case, it would be of practical importance when unfavourable conditions, may they be nutritional or climatic, result in poor set ('*coulure*').

A second intention of this paper was to describe the distribution of flowers and berries on inflorescences and bunches. It was somewhat surprising to see reasonable consistency in mean data, considering the large variability in inflorescence size introduced by the technique of predetermined random sampling. In one site × season lot, there was a 22-fold difference in flower number between the largest and smallest inflorescence, in the other three lots this ratio varied between 6 and 10. The use of number of bunches as a factor in yield analysis seems therefore to be of little value unless bunch size is also taken into account. After all, crop per vine consists of the number of berries, even though these berries are attached to bunches. This may appear a trivial point, but bunch number per se is determined in most viticultural experiments without regard to berry number, and may thus lead to quite erroneous conclusions.

The fact that the complement of berries per bunch, and presumably also per vine, consists of four classes of quite differently sized berries may have major implications for berry sampling, and estimation of berry quality. Especially in coloured grape varieties a close relationship between berry size and berry quality exists because of the change in the ratio between skin (location of coloured metabolites) and pulp. Unfortunately it was not possible to complement the observations on distribution

of berry size with parallel measurements of berry composition, but such a study may establish the achievable limit for quality uniformity among the crop which may be affected by inherent berry variability within bunches.

Bunches of tight-bunched cultivars such as Chardonnay and Pinot Noir develop into almost solid bodies as berries enlarge. Most berries collected in this experiment at Plain, and to a lesser extent at Hills, were deformed due to lack of space within the bunch, being pear-shaped rather than roundish-oval. The tightness of such bunches must affect berry illumination (even after removal of shading leaves), disease susceptibility and, on thin-skinned varieties, may even lead to berry splitting. Relatively few berries will be fully exposed to sunlight, and exposure effects on berry composition may be due more to changes in temperature than to light per se (Coombe 1987). This has important implications for canopy manipulation in climates were summer temperatures are often excessive. On the other hand, measures to reduce bunch compactness may be as important as measures to increase bunch exposure in regions with comparatively low summer temperatures. In general, viticultural practices aimed at producing more but smaller bunches without altering cropping potential may well bring important improvements in fruit quality.

Results presented here have clear implications for techniques used for crop sampling. While sampling of single berries may be appropriate for cultivars with loose bunches—as recommended e.g. by Rankine et al. (1962)—this may not be possible or even advisable for cultivars with tight bunches such as Chardonnay. In those cases, the single berries will be taken from the outside of the bunches and will not be representative of the whole population. Sampling whole bunches is a better solution for commercial samples. Such a procedure may, however, reduce crop load significantly in experiments, and thus distort vine physiology and alter final yield, so that collecting single branches, preferably from the proximal third of the bunch, may be the best compromise. Such a sample will include berries of all size classes.

Finally, results such as those presented here on bunch morphology add to our appreciation of inherent variability between the berries which make up a grape crop. Further research along these lines may show whether similar relationships exist for other cultivars, especially those with less compact bunches, and how this variability in berry size relates to berry composition

## Materials and methods

Observations reported here all relate to cultivars of *Vitis vinifera* L. For the experiment on inflorescence and bunch morphology, sampling was done on two sites, 'Hills' at Piccadilly in the Adelaide Hills, altitude 500 m, and 'Plain' at Willunga, south of Adelaide, near sea level and about 10 km from the coast. Both experiments consisted of 12-times replicated randomised blocks, each block with three single-vine plots of three pruning treatments, 18 or 24 spurs (Hills/Plain), 3 or 4 canes, and hand-cut hedges with uncontrolled bud numbers, imitating machine-hedging. Two inflorescences were chosen at random on each vine by matching random numbers with numbers obtained from inflorescence counts started at one end of each vine. These bunches, dusted with insecticide (to avoid the damage from earwigs (order Dermoptera) and thrips (order Thysanoptera) encountered in the preceding season which made results unusable) were enclosed in brown paper bags just before anthesis commenced. They were collected after set and held frozen for later counts of flowers (from counts of the dry calyptra), abscinded berries, and for determining the number and distribution over the bunch rachis of set berries. All berries of every bunch were allotted visually to one of seven size classes, classes 1-4 being, in descending order of size, the berries making up the crop, class 5 being small berries without viable seeds, class 6 'shot', undeveloped but green ovaries, and class 7 dead, black ovaries. Ten-berry samples from size classes 1-4 of each lot were used to determine mean berry weight, seed number and berry weight per seed. Similar observations on berries were made during harvest on randomly chosen bunches.

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