

A STUDY OF FRUITING HABITS IN PEAR TREES

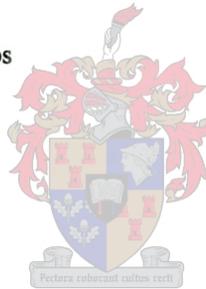
BY
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DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own, original work and has not previously, in its entirety or in part, been submitted at any university for a degree.

Summary

A STUDY OF FRUITING HABITS IN PEAR TREES

The understanding of pear branching and bearing habits is required to optimise management practices. The objective of this study was to quantify the branching and bearing habits of pear cultivars under South African conditions of sub-optimal winter chilling.

Two-year-old branches of *Pyrus communis* L. were classified into groups according to the proleptic (from dormant buds) branching habit. In Winter 1998 upright and flat, two-year-old branches were randomly sampled from trees of seven pear cultivars, i.e., Forelle (on Quince A and BP1 rootstocks), Abaté Fetel, Flamingo, Packham's Triumph, Golden Russet Bosc, Rosemarie and Beurre D'Anjou (all on BP1 rootstock). Laterals were classified according to length (< 1cm, 1-5cm, 5-20cm and >20 cm) and position (distal to proximal quadrants on the two-year-old axis). The number of shoots per cm of quadrant length, per length class for each cultivar was subjected to a cluster analysis, then a canonical and a stepwise discriminant analysis. The cultivars were grouped into four groups from Group 1 (Flamingo) which resembles a spurred growth habit with strong apical control, to Group 4 (Packham's Triumph and Golden Russet Bosc) which resembles a spreading growth habit and weak apical control.

The bearing habits of the same pear cultivars were quantified. In Winter 1998 ten unpruned branches were tagged on trees of each of the seven cultivars. The description started with the development of the main fruiting branch, forming several leaves in the first year of growth (designated year Y), with meristems developing in the leaf axils. In the following season (year Y+1), these axillary meristems have five alternatives: to remain as a latent bud (L), to develop as a vegetative bud (V), to become a flower bud not setting fruit (F), to become a flower bud producing a fruit (P) or to abort and leave a scar (S). Each year the development of these axillary buds were observed and classified anew, giving rise to a sequence. Between 50% ('Forelle/QA') and 75% ('Rosemarie') of buds remained in the growing phase (comprising of V, F or P buds) during the years of monitoring. It was shown that the predominant bud state in the growing phase was V. Although flower formation was low for all cultivars throughout the trial period, 'Packham's Triumph' and 'Rosemarie' displayed a relatively high proportion of F and P buds in year Y+1. The latter two cultivars also displayed the bourse-over-bourse bearing phenomenon (PP), producing flowers and fruit terminally on bourse shoots.

Artificial extinction of reproductive buds was applied in Winter 1999 to individual branches of the pear cultivar Doyenne du Comice. This pear variety bears on spurs and is prone to biennial bearing. The objective was to reduce the number of growing buds, thereby increasing the allocation of assimilates to remaining reproductive structures. Three thinning intensities, i.e. 0%, 33% and 66% removal of reproductive buds and two methods, i.e. removal of proximal reproductive buds and removal of reproductive buds situated distally on spurs (by means of cutting back) were utilised. Autonomy of

fruiting structures was not enhanced, but results warrant the repetition of this trial using whole trees as experimental units.

Opsomming

Dit is belangrik om die vertakkings- en drawyses van pere te verstaan, aangesien bestuurspraktyke hierdeur bepaal word. Die doel van hierdie studie was om die vertakkings- en drawyses van pere onder Suid-Afrikaanse toestande van sub-optimale winterkoue te kwantifiseer.

Tweejaar-oue *Pyrus communis* L. takke is volgens hul proleptiese (vanuit dormante knoppe) vertakkingswyse in groepe geklassifiseer. Regop en plat takke van die peerkultivars Forelle (op Kweper A and BP1 onderstamme), Abaté Fetel, Flamingo, Packham's Triumph, Golden Russet Bosc, Rosemarie en Beurre D'Anjou (almal op BP1 onderstam) is in die winter van 1998 gemonster. Jaarlote is volgens lengte (< 1cm, 1-5cm, 5-20cm and >20 cm) en posisie (distale tot proksimale kwadrante op die tweejaar-oue draer) geklassifiseer. Die getal lote per cm, per lengte klas per kwadrant vir elke kultivar is toe onderwerp aan 'n groep analise en daarna aan 'n kanoniese en 'n stapsgewyse diskriminant analise. Kultivars is in vier groepe gegroepeer vanaf Groep 1 (Flamingo) wat 'n spooragtige vertakkingswyse en sterk apikale kontrole toon, tot Groep 4 (Packham's Triumph en Golden Russet Bosc) met 'n spreidende vertakkingswyse en swak apikale kontrole.

Bogenoemde peerkultivars is ook gebruik vir die kwantifisering van drawyses. In die winter van 1998 is tien ongesnoeide takke per boom gemerk. Die beskrywing van die drawyses het begin met die ontwikkeling van die hoof tak van die dra-eenheid. In die eerste jaar van groei (genoem jaar Y) ontwikkel meristeme in die blaar oksels. In die daaropvolgende seisoen (jaar Y+1) is daar vyf ontwikkelings moontlikhede vir die oksellêre knoppe: om latent te bly (L), om vegetatief te ontwikkel (V), om te blom sonder die set van 'n vrug (F), om te blom en 'n vrug te set (P) of om te aborteer en 'n letsel te los (S). Die ontwikkeling van hierdie oksellêre knoppe is elke jaar gemonitor en opnuut geklassifiseer om sodoende 'n reeks te vorm. Gedurende die moniteringstydperk het tussen 50% ('Forelle/Kweper A') en 75% ('Rosemarie') van die knoppe in die groeifase (G) (bevattende V, F of P knoppe) gebly. Die proporsie knop tipes per jaar vir die onderskeie kultivars het getoon dat die oorheersende knop tipe in die G-fase V-knoppe is. Alhoewel blom inisiasie laag was gedurende die hele proeftydperk, het 'Packham's Triumph' en 'Rosemarie' relatief hoë verhoudings F en P knoppe in jaar Y+1 getoon, wat gepaard gaan met dié kultivars se vermoë om vrugte op een jaar-oue lote te dra. Die beurs-oor-beurs verskynsel (PP) het ook by dié twee kultivars voorgekom.

Reproduktiewe knoppe van die peerkultivar Doyenne du Comice is in die winter van 1999 verwyder (kunsmatige abortering) vanaf individuele takke. Hierdie peerkultivar dra op spore en is geneig tot alternatiewe drag. Die doel was om die hoeveelheid groeiposisies te verminder en sodoende die allokasie van reserwe assimilate na oorblywende reproductiewe strukture te verhoog. Drie uitdun intensiteite (0%, 33% en 66% van reproductiewe knoppe verwyder) en twee metodes (verwydering van proksimale spoorknoppe en verwydering van distale spoorknoppe) is gebruik. Outonomieit van reproductiewe strukture was nie verhoog nie, maar resultate regverdig die herhaling van dié eksperiment. Daar word aanbeveel dat volledige bome dan as eksperimentele eenhede gebruik word.

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1. INTRODUCTION

Knowledge of the development of pear bearing habits and differences between cultivars are very important to all aspects of pear production. An understanding of the development of a cultivar's bearing units will provide guidelines for the use of management practices and decisions such as rootstock, planting density, training, pruning, fruit thinning and so forth.

Studies were done to group apple cultivars into four ideotypes according to the growth and bearing habit of the cultivar (Lespinasse, 1992) and to link the specific ideotype to the phenomenon of biennial bearing (Lauri *et al.*, 1995). Pears were also grouped into five groups based on field observation of their bearing habits and this was used for the proposal of pruning protocols for specific groups (Sansavini and Musacchi, 1994).

The objective of this study was to quantify pear branching and bearing habits under South African conditions. A method to quantify branching habits objectively was developed. Bearing habits were quantified using the method of Lauri *et al.*, 1995. Artificial extinction of buds (by means of pruning) was used in an attempt to increase spur autonomy in the pear cultivar Doyenne D'Comice (spur bearing habit and prone to biennial bearing).

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2. LITERATURE STUDY: ONTOGENY OF POME FRUIT BEARING HABITS.

2.1 Introduction

Knowledge of the development of pome fruit bearing habits and differences between cultivars are very important to all aspects of pome fruit production. An understanding of the development of a cultivar's bearing units will provide guidelines for the use of management practices such as training, pruning, fruit thinning and so forth.

The development of the bearing habit starts the moment a young tree (whip) is planted in the orchard, or in the case of a feathered tree, in the nursery with the development of laterals from the main axis. The development of the scaffold branches and the management of these branches will be determined by the growth habit of the cultivar. This, in turn, will determine the time needed for the tree to fill its allocated space and when a tree will come into bearing. In a bearing tree, the bearing habit of the specific cultivar, amongst other factors, will determine whether a regular, annual crop will be obtained. This is very important from an economic point of view. For example, given a cultivar with a spurred habit, it will determine the planting density, tree training, pruning of mature trees and the inputs required to maintain a regular annual crop (fruit thinning and pruning).

Studies were done to group apple cultivars into four ideotypes according to the growth and bearing habit of the cultivar (Lespinasse, 1992) and to link the specific ideotype to the phenomenon of biennial bearing (Lauri *et al.*, 1995). Pears were also grouped into five groups based on field observation of their bearing habits and this was used for the proposal of pruning protocols for specific groups (Sansavini and Musacchi, 1994).

The ontogeny of pome fruit bearing habits will be reviewed in two parts, vegetative development and reproductive development, for they are closely related. A brief review of biennial bearing and the factors affecting it will follow after which the relationship between bearing habit and biennial bearing will be reviewed.

2.2 Vegetative development (Development of the crown)

2.2.1 Developmental stages

A tree growing from a seed has a juvenile phase, later going into a mature phase. The juvenile phase can be defined as that period within which the tree lacks the ability to flower. In pears the length of this stage varies from 2 to 9 years (Wertheim, 1990). Nursery trees are obtained by budding a specific cultivar onto a rootstock. This budding material is obtained from plant material already in the mature phase, thus the juvenile phase is ruled out. The mature phase also has a young form, which is called a vegetative sub-phase. If one takes the development of the crown in the mature phase independently of

manipulations, one may distinguish the non-fruiting phase (young age), the fruiting phase and the old age (Brunner, 1990).

2.2.2 Factors affecting branching

The development of a fruiting branch starts with the development of a shoot from the main axis, or a secondary axis. This shoot might develop by means of syllepsis or prolepsis.

2.2.2.1 Syllepsis and prolepsis

Two types of lateral branching occur in woody plants: Syllepsis and prolepsis. Syllepsis is the continuous development of a lateral bud to establish a branch, without an evident intervening period of rest of the lateral bud. Prolepsis is the discontinuous development of a lateral bud to establish a branch, with some intervening period of rest of the lateral bud. Prolepsis and syllepsis are, therefore, alternate functional states of the same meristem (Hallé *et al.*, 1978).

Syllepsis is correlated with the rate of shoot extension, i.e., the greater the rate of shoot extension, the greater is the likelihood of its lateral buds developing by syllepsis (Hallé *et al.*, 1978).

2.2.2.2 Apical dominance

With branching in temperate leafy species, for example an apple tree, syllepsis is rare, and only occurs in vigorous shoots. Mostly the axillary buds are inhibited and only the terminal bud actively elongates. The inhibition of the axillary buds by the terminal bud is called apical dominance (Crabbe, 1987; Wertheim, 1990).

Apical dominance is defined by Hallé *et al.* (1978), as the production of growth substances by active terminal buds inhibiting the development of lateral buds. These growth substances are mainly auxins (Crabbe, 1987).

The control of apical dominance, however, is more complex and cytokinins play an important role in overcoming the inhibition of lateral buds. The basipetal auxin and acropetal cytokinin flux are involved. The auxin firstly stimulates root growth and secondly the differentiation of the transport channels. The cytokinin, produced by the young active roots, would then stimulate growth of the axillary buds (Crabbe, 1987).

2.2.3 Branching types

After leaves drop in autumn, the one-year-old shoot sprouting out in spring can produce acrotonic, mesotonic and basitonic branches. Acrotonic branching is the result of strong apical dominance. The other extreme is weak apical dominance resulting in basitonic branching. The longest shoots on the acrotonic branching type are on the apical part of the main axis. On the basitonic branching type they are located on the basal part. In the mesotonic branching type however, the longest shoots are characteristically in the middle part of the shoot axis (Brunner, 1990).

It is generally characteristic of the non-fruiting phase that there is vigorous development of the central leader and of the lateral branches originating from it. The strong acrotonic species (e.g. cherry and pear) maintain their central leader for a longer time. In contrast with this, in less acrotonic species (e.g. sour cherry and apricot) dominance of the central leader is lost early (Brunner, 1990).

2.2.4 Course of development of scaffold branching

According to Brunner (1990), Sitt proposed that the development of branches is always centrifugal, and the branching on them continuously come about towards the periphery of the crown, while they perish successively on the basal limb parts which become bare. This may be connected to the fact that numerous fruit species bear fruit optimally on one- to three-year-old shoot formations. The fruiting on older shoot formations, however, is more periodical and sooner or later these shoot formations die. In consequence of the branch curvature (the weight of the fruit pulling the branch open), the middle part of the branch eludes the apical dominance and grows to form a new branch. The branch eventually bears fruit and bends, repeating the process. This, without intervention of crown shaping, gives the scaffold branches a weeping willow-like form (Brunner, 1990).

On 'Golden Delicious' for example, a fruiting branch growing naturally passes through several phases, rarely longer than for the period of four years. These phases are development, production, progressive bending and total, or more frequently, partial renewal. It is important that the renewal branches formed on the arch reach the fruiting stage before the drooping part is removed (Lespinasse and Delort, 1986).

The branching of other species and varieties, however, only bend down to the horizontal, and in the species which grow erect, it is possible that no fruiting induced curvature comes about. The latter are the acrotonic branching type of species or varieties with strong apical dominance. This is also connected with the fact that their branches are firmer and generally their ability to bear fruit is not high and they tend not to come into bearing early. In this way the scaffold branches have time to become strong and the fruit (of smaller weight) does not induce curvature (Brunner, 1990).

The centrifugal process lasts until the shoot system's growth/death ratio turns to the side of death. In this case the peripheral parts of the branch becomes weak, then die (due to the long and senescent transport supply lines) (Brunner, 1990).

2.2.5 Definition of the term vigour and the relationship between vigour and fruiting

Vigour is an expression of the activity of the cells in the meristem or growing parts of the plant. The more active the cellular division and enlargement, the greater the vigour. The greater the vigour, the greater is the increase in the size of the plant in a stated period of time (Forshey and Elfving, 1989).

While a certain minimum level of vigour is essential, excessive shoot growth reduces fruitfulness by reducing flowering and, may also compete directly with fruit. The relative proportion of shoot and spur leaves is indicative of the shoot growth-fruiting relationship. Total shoot leaf area is closely related to

total shoot growth, and total spur leaf area is related to fruitfulness; and the two are inversely related. Changes in the percent shoot leaves are indicative of changes in the vegetative growth-fruiting relationship (Forshey and Elfving, 1989).

2.2.6 Branch orientation and fruiting

Vigour is represented by the angle of the branch, with vertical branches being the most vigorous. On the basis of Lespinasse and Delort's (1986) observations, there are three distinct zones in a fruit tree: Zone A (0 - 30 degrees): Vigorous shoot growth, particularly where tree volume is being restricted by pruning and training. Zone B (30 - 120 degrees): A balance between fruiting and vigour, with the optimum branch angle between 30 and 45 degrees. Zone C (120 - 180 degrees): Substantial fruiting capacity when light exposure is adequate, but mediocre fruit quality and insufficient skin colour on red varieties (Lespinasse and Delort, 1986).

It is important to specify the conditions under which it will be possible to maintain Zone B on a tree and to promote the optimal development of this ideal zone of equilibrium between vigour and fruiting capacity. This Zone B varies according to the fruiting type and varieties (Lespinasse and Delort, 1986).

2.2.7 Vegetative and generative shoot types

The average length (and generally the average internode length) is larger in the case of vegetative shoots than in the case of generative shoots. The spur is usually accepted to be shorter than 8 -10 cm, the medium long shoot falls in the 10 - 40 cm shoot category. Vegetative shoots are above 40 cm long. Vegetative growth of spurs stops earlier than long shoots, and, therefore, the buds have more time to differentiate into flower buds (Brunner, 1990).

2.2.8 Generative shoot type differences per fruit tree species

The balance of the production, the nutrient withdrawal, the consumption of the shoot formation and in this way the formation of fruiting wood are influenced by the differences in the fruit tree species (Brunner, 1990).

The majority of pome fruits bear on smaller fruiting structures (brindles and spurs), although there are species that produce on long shoots. The flower/fruiting potential of the latter is generally smaller, and the fruit quality poorer, compared to spurs (Brunner, 1990).

The apple, pear and sweet cherry trees producing mostly on brindles and spurs differ considerably in biennial bearing tendency, though the mentioned fruiting woods of all three species are rather long lasting. One of the basic differences between pome and stone fruit is that the former has a greater inclination to biennial bearing. In the pome fruit, both the fruit bud, as well as the fruit developing from the bud, is terminal. That is, the fruit buds of the next year develop proximal to the fruit. The apical position is a dominating position. The fruit in this way is able to withdraw nutrients from proximal parts and, therefore, away from the developing fruit buds. On the other hand the hormones flowing

from the fruit (mainly from the seeds) in a basal direction, are able to counteract the fruit bud formation. The position occupied by the fruit on the bearing formation, therefore, increases its nutrient withdrawal and hormone effect in the case of pome fruit (Brunner, 1990). In stone fruit the fruiting buds are situated laterally. At the apex of the fruiting shoot formation there is a vegetative bud which assures new growth distal to the fruit. In this way it is understandable that biennial bearing in stone fruit is induced by external factors (frost damage, unfavourable weather for pollination) or by general exhaustion of the tree, but this is not decided or developed at the level of the fruiting wood (Brunner, 1990).

Another difference derives from the fruit development and fruit bud differentiation period. The fruit development and fruit bud differentiation of stone fruit do not, or rarely coincide with each other as in the case of pome fruit. There may be a 10-12 weeks' overlap between the nutrient requirements of the fruit and the developing fruit bud in apple and pear. This increases the tendency of alternate bearing of pome fruit (Brunner, 1990).

2.3 Reproductive development

Much work has been done on flower initiation and fruit set, and the factors affecting it. In this review only a few relevant points will be discussed. Flower bud induction is essential for high productivity of orchards (Buban and Faust, 1982). This is true not only for mature trees, but also for getting young (vegetative) trees into early production.

2.3.1 Flower initiation

The process of flower formation can be defined as anything that happens between induction and meiosis. This is followed by differentiation of the flower primordia (Buban and Faust, 1982). The process can be divided into three main stages: When the stimulus triggering flower initiation reaches the apical meristem, RNA and proteins essential for flower initiation are synthesised. This is followed by the mitotic cycle and the morphogenetic cycle when the flower primordia develop.

The major differences between the vegetative and the reproductive apical meristems are, in the case of reproductive meristems, a shortening of the plastochron, an increase in mitotic activity in certain meristematic tissues, an increased size and RNA content of the nuclei in the meristematic cells, and an increased stratification of the growing point (Buban and Faust, 1982).

2.3.2 The role of the vegetative phase of bud development preceding flower initiation

Flower bud formation is attained through transformation of the vegetative apex to a reproductive structure. This transformation only takes place when the structure of the vegetative bud is complete. Flower formation only occurs after 9 bud scales, 3 primordia of transition leaves, 6 true leaflets and 3 bracts have differentiated. Thus, flower initiation occurs only after a critical number of nodes have

developed. This node number is characteristic of the cultivar, for example, in the case of 'Cox's Orange Pippin' it is 20 and with 'Golden Delicious' it is 16 (Buban and Faust, 1982).

The time between the formation of two organ primordia is called the plastochron. A precondition for flower initiation is that the plastochron should not be longer than seven days (Buban and Faust, 1982). Flower initiation is greatly influenced by hormones. The gibberellins produced by the developing seeds of young fruits inhibit flower initiation by extending the plastochron (Buban and Faust, 1982; Crabbé, 1987).

2.3.3 The time of flower initiation

Three to six weeks after bloom is generally considered as the time of flower bud initiation. This period refers to the period of histological differentiation and may last between four to thirteen weeks. Lateral buds on elongated shoots start differentiation later than spur buds, mostly by about three weeks (Buban and Faust, 1982).

2.3.4 Location of flower buds

Flowers may develop on persisting spurs, or on the previous season's shoots. These two types of bloom differ in the time of differentiation and in the factors affecting it. The relative importance of spur and shoot bloom varies with cultivar, tree age and management system (Forshey and Elfving, 1989).

2.3.4.1 Spur bloom

Flower induction on spurs is affected by such factors as nutritional status, soil moisture availability, light exposure but most importantly, fruiting. A heavy crop inhibits flowering for the following year and over-cropping often leads to biennial bearing. Individual spurs tend to alternate and consistent, uniform flowering is possible only when a significant percentage of the spurs do not fruit each year. The seeds in the developing fruitlets inhibit flower induction on fruiting spurs. Gibberellins produced by the seeds are the inhibitors of flower initiation. Flower bud induction of spurs occurs in the three to six weeks after bloom and fruits must be thinned within a month after bloom to ensure a satisfactory return bloom (Forshey and Elfving, 1989).

The effective leaf area per spur is an important factor in flower initiation and partial defoliation, leaf injury, or shading will reduce flowering. Conversely, deblossoming, defruiting and scoring increase flower initiation (Forshey and Elfving, 1989).

2.3.4.2 Shoot bloom

The flowers initiated on the current season's shoots may develop from terminal or lateral buds. Flower initiation on shoots generally does not begin until after extension growth ceases and may continue into autumn. Vegetative growth and fruiting are antagonistic and flowering may be reduced in vigorous trees or trees that grow late in the season. Treatments that stimulate vegetative growth such as pruning,

nitrogen fertilisation and irrigation may reduce flowering. Environmental stress that induces early cessation of shoot growth often results in increased flowering (Forshey and Elfving, 1989).

2.3.5 Fruit set

The influence of branch orientation on shoot growth and fruit set will be discussed, for these aspects are closely related.

The re-orientation of branches from the vertical to the horizontal has been shown to decrease vegetative shoot growth and enhance flower production and fruit set (Wareing and Nasr, 1958; Robbie *et al.*, 1993). On the other hand, orchard management practices, such as fertilisation and pruning, which tends to induce vegetative growth, can reduce flower production and fruit set. These data imply that there is an antagonistic relationship between vegetative growth and fruiting (Robbie *et al.*, 1993).

In a trial done at East Malling, fruit set was examined on branches of 'Cox's Orange Pippen' apple trees that had been re-orientated horizontally or vertically. Within these two treatments, fruit bud formation and flower fertility were quantified in relation to shoot growth. It was clear that branches of 'Cox's Orange Pippen' trees, either on M.9 or MM.109 rootstocks, consistently trained to different angles, set fruit very differently. Orientation from the vertical to the horizontal increased the number of flower buds and the percentage of final fruit set. At the same time shoot extension decreased. The difference in fruit set was maintained through an increase in the length of the effective pollination period. If cessation of vegetative growth were earlier in horizontal branches, then flower initiation might well be advanced. An extended period of flower development might subsequently improve flower bud quality and fruit set (Robbie *et al.*, 1993).

This phenomenon not only plays a role in management practices (i.e. the bending of branches to promote earlier bearing of young trees), but is also of importance due to the fact that different cultivars belonging to different growth habit groups vary in their inherent branching angles. This will determine the amount of management inputs required for early fruit production and control of vigour.

2.4 Classification of cultivars according to fruiting type

Fruit tree cultivars can be grouped according to their fruiting habits (i.e. where the cultivar bears fruit). Lespinasse and Delort (1986) grouped apple tree cultivars into four ideotypes. Sansavini and Musacchi (1994) grouped pears into five groups. The study of pome fruit bearing habits, and the grouping of cultivars according to bearing habits, is important because it plays an integral role in the management of an orchard. Aspects such as orchard training and pruning are determined by the bearing habit of the cultivar. The bearing habit also plays an important role in the tendency of a cultivar to bear a regular, annual crop.

2.4.1 Classification of apple cultivars

This classification by Lespinasse and Delort (1986) took into account both the general form of the tree (i.e. ranging from conical to cylindrical forms), and the distribution of fruiting axes on this structure (Lespinasse, 1992; Lauri and Lespinasse, 1993). Important differences can be observed among apple cultivars in how they develop and bear fruit. There are four distinguishable fruiting types:

Type 1 (Spur-types): In these cultivars, the scaffold branches are conical and have a strong tendency to develop sub-branches on their lower surface. The dominance of the trunk (leader) is not particularly strong, varying among cultivars. The majority of the fruiting spurs are located on branches two years old or older. (Lespinasse and Delort, 1986). Examples: 'McIntosh Wijcik' (Lauri *et al.*, 1995).

Type 2: These cultivars are easy to manage in the free-growing form. The main branches are very solidly attached to the trunk and have strong, wide angles. These trees normally show greater dominance of the central leader than do spur-types. However, basitonic reactions remain strong, enhancing the growth of lower branches (Lespinasse and Delort, 1986). Examples: 'Oregon Spur Delicious' and 'Rein des Reinettes' (Lauri *et al.*, 1995).

Type 3: The trunk dominates the tree's branches. This characteristic makes cultivars of this group particularly suited to the vertical axis management system. Fruiting branches are at a wide angle (60 to 90 degrees) to the trunk, thus facilitating fruiting. There are numerous short shoots. (Lespinasse and Delort, 1986). Examples: 'Braeburn', 'Golden Delicious', 'Jonagold' and 'Royal Gala' (Lauri *et al.*, 1995).

Type 4: These cultivars rarely develop lateral shoots in the lower portion of their wood. This (branching being located on the upper third of the trunk), gives the tree a cylindrical appearance (acrotonic tendency). Main branches become elongated through successive arching. (Lespinasse and Delort, 1986). Examples: 'Fuji' and 'Granny Smith' (Lauri *et al.*, 1995).

Type 4 represents dome-shaped branches with brindles ending in a fruit bud along the main branches (Lauri *et al.*, 1995). The fruiting zone moves towards the outside of the tree, and more rapidly than in the case of Type 3 cultivars (Lespinasse and Delort, 1986).

Cultivars showed an increasing tendency, from type 1 to 4, towards an extended annual growth period and as a result reproductive buds are borne on longer shoots. In type 4 cultivars, where this phenomenon was most marked, the long shoots on which reproductive buds were borne on were typically fruit bearing brindles of approximately 15 cm length. The bourse-over-bourse phenomenon was also noted, with a frequency ranging from 10% in type 1 to 65% in type 4 cultivars. Types 2 and 3 are intermediate (Lauri and Lespinasse, 1993).

The bourse-over-bourse phenomenon, in relation to extended annual growth period and the bearing of fruit buds on long shoots, is of great interest due to its link with the ability of a cultivar to have a regular bearing pattern. To date it is known that the spur-type cultivars are characterised by a biennial bearing habit. On long-branching cultivars leaf-bearing shoots appeared to be able to balance vegetative and reproductive growth and to partition vegetative growth specifically into shoots destined to terminate in a fruiting bud. Such shoots, of moderate vigour, are typically fruit bearing brindles. Fruits developed at sites where vegetative growth had occurred previously. In type 1 cultivars a spatial disjunction between vegetative and reproductive growth was observed, the latter being essentially of the spur-type, inferring insufficient autonomy from the adjacent vegetative parts (Lauri and Lespinasse, 1993).

2.4.2 Classification of pear cultivars

Sansavini and Musacchi (1994) proposed five models of fruiting wood on pear cultivars:

- (1) Brindles or one-year old flowering shoots ('Bartlett').
- (2) Spurs on two- and three-year-old branches as in 'Doyenne du Comice' and 'Abaté Fetel'.
- (3) Spurs on all wood types as in 'Conference'.
- (4) Spurs on old branches as in 'Kaiser' and 'Beurre Bosc'.
- (5) The vegetative sink-controlled spurs as in 'Passe Crassane'.

Sansavini and Musacchi (1994) proposed pruning techniques for each group, based on the bearing habit.

Long pruning is suited only to the first model; the second requires yearly short pruning and cutting back only of the fruiting branches; the third moderate annual pruning to thin shoots and to cut back and renew branches; the fourth a light-moderate cut to stimulate branch renewal and the fifth severe pruning to enhance fruit set.

Group 1 ('Bartlett'): Initial cropping in this group almost always occurs at the apical flower bud of the brindle or along the year-old fruiting shoots. The number of spurs on old wood gradually increases to over 30% of bearing structures with increasing tree age. The pruning of young trees is light, without shortening; thereafter the aim is to promote the formation of new branches and make renewal cuts for old ones. In fruit-loaded trees, the fruits of spurs which set more than one pear need to be hand-thinned to ensure good size and quality of fruit (Sansavini and Musacchi, 1994).

Group 2 ('Doyenne du Comice'): This group's cultivars bear mainly on two-year-old (and partly three-year-old) branches. These branches, well positioned and long (over 50-60 cm) by the second year, form a large number of spurs which, however well nourished, will still have poor chances to set. Hence the need to cut back from one-half to two-thirds of these long and thin fruiting branches, leaving wherever possible at least 8-10 spurs. Each of these branches will thus produce at least 2-4 pears and regenerate flower buds in the remaining vegetative spurs the third year. Thereafter, because of subsequent shortening, the branch is replaced by another beneath it. 'Doyenne du Comice' initially

crops on one-year-old wood and thereafter 60-70% of production occurs on two- and three-year-old branches. The cultivars Concorde and Abaté Fetel have very similar habits. Postponing winter pruning until the appearance of corymbs after bud burst has enhanced the fruit set of the latter. The positive effect appears to be linked to the cultivar's pruning- induced growth stress, which shifts the competition of new shoots onto pollinated flowers, which improve fruit set (Sansavini and Musacchi, 1994).

Group 3 ('Conference'): This very fertile cultivar tends to crop mainly on spurs, which are as productive on two- and three-year-old branches as on older ones. There is, however, a marked difference between young and old branches: the spurs on the young yield large, regular and uniformly ripening fruits whereas the old ones produce smaller, irregular and lower quality fruits. 'Conference' must, therefore, be well pruned each year, eliminating on average about one-third of the fruiting spurs and their branches. In an adult tree, year-old fruiting shoots account for about 20% of the yield and an optimum ratio for the rest would divide half the remaining 80% in two- and three-year-old wood and half in old wood. The latter threshold should not be exceeded so as not to compromise fruit quality (Sansavini and Musacchi, 1994).

Group 4 ('Beurre Bosc'): This cultivar produces over 90% of its crop on spurs on old wood. Pruning is therefore relatively simple, even to the point that it can be done every other year without adversely affecting yield. The fact that over 70% of its initial crop occurs on spurs is further evidence of the marked sink action of the latter as compared to the brindles, vegetative spurs and young branches. Competition is, therefore, not a problem. Fruit set is always high, regardless of pruning method, although the latter must be done to enable the tree to renew its branches over multi-year cycles that are longer than other cultivars. 'Clapp's Favourite' is another cultivar belonging to this group (Sansavini and Musacchi, 1994).

Group 5 ('Passe Crassane'): A transient cropping habit, which is especially evident in young trees, although in very fertile soils it can persist for many years, marks this cultivar. The model is essentially based on the formation of short branches, 20-40 cm long, which in the second year gives rise to an apical shoot and a number of lateral spurs or brindles. To assure a high set of these flowers, the apex of the two-year-old branch must be removed so as to prevent one or more wood buds forming a new shoot that is very competitive with the underlying spurs or brindles. This means that almost all the two- and three-year-old branches have to be headed back. 'Passe Crassane' is the most notable example of a pear genotype whose set is to a certain extent proportional to pruning severity. Yet pruning should not be exaggerated, as depriving the tree of its vegetative renewal capacity will lead to shorter life or alternate bearing (Sansavini and Musacchi, 1994).

2.5 Biennial bearing

It is important to discuss biennial bearing because of the link between the bearing habit of a cultivar and its tendency towards biennial bearing. A brief overview of biennial bearing will follow to get a general idea of the phenomenon and some of the factors affecting it.

Biennial bearing is an economic problem of importance in commercial fruit growing. The incidence of on- and off-years is higher in apples than in pears and as important in late ripening cultivars as in early ripening cultivars. Due to modern rootstocks, better tree forms and maintenance of orchards, the problem of biennial bearing is less than before 1940. Stone fruits do not have a strong biennial bearing pattern (Jonkers, 1979).

A crop that is consistent over many years is the result of the maintenance of equilibrium between many factors, and to achieve this equilibrium fundamental knowledge of the growth and development of the tree is required. Biennial bearing in apples is influenced by the tendency to initiate flower buds and the tendency to set fruit, in which growth of short spurs, growth potential of the tree, the ratio between carbohydrate and nitrogen quantities and the hormonal activity all play a role. In most cultivars young trees are annual and older trees become biennial (Jonkers, 1979).

Flower initiation is very important, and its role in biennial bearing will be discussed in more detail.

Because the tendency to flower changes more than the tendency to set fruit, flower initiation is the decisive phase in the formation of the crop. Vegetative growth and flower initiation is generally seen as counterparts. In biennial bearing cultivars more than 90% of all terminal buds can become generative in one year, in contrast to annual cultivars in which this percentage only amounts to 20%. Biennial bearing behaviour has its base in the separate shoot. Experiments by different authors indicated that 2-5% of the terminal buds initiated flower buds in one year as well as in the following year and 40% remained vegetative in two or more successive years. The key to the correction of biennial bearing is the presence of many resting or non-bearing short shoots on the tree. Fruit bearing of on-year trees of biennial bearers is often combined with poor shoot growth. In an off-year, secondary shoots were formed on more than 20% of all branches, in an on-year this was only on 3.5% of all branches; with 8% in regular bearing trees (Jonkers, 1979).

Overall good maintenance can help to avoid biennial bearing, although this does not apply to specific biennial bearing cultivars such as Benoni and Laxton's Superb apples. Rootstocks can also play a role. The apple cultivars Berlepsch Reinette and Laxton's Superb in Czechoslovakia were biennial bearers on the rootstocks M1, M2 and M11, whereas they showed a regular bearing pattern on M9 as a spindle bush (Jonkers, 1979).

In pear it was found (in the cultivar Doyenne du Comice in particular) that the fruit set in some years is inadequate due to a total or partial infertility of the egg cells. This infertility is influenced by weather conditions, especially spring frosts, and can induce a pattern of biennial bearing (Jonkers, 1979).

According to Jonkers (1979) the disadvantages of biennial bearing are:

- In general, half of the yield of an on-year and an off-year together is less than the yield for one year of a regular bearing cultivar.
- The quality of the fruit in an on-year can sometimes be inferior to the quality of a regular bearing cultivar and more breaking of branches can occur.
- By depletion of the reserves of assimilates in an on-year, the trees can become more sensitive towards frost damage than regular bearing cultivars.
- One of the main disadvantages is the effect on fruit size, i.e., a few large fruits alternating with a mass of small fruit.

The most commonly used index of biennial bearing is the index "I":

$$I = 100 \times (\text{difference between two successive crops} / \text{sum of the two successive crops})$$

The index I can vary between 0, in the case of a regular bearing pattern, and 100 in the case of a pronounced biennial-bearing pattern (Jonkers, 1979).

2.5.1 Flower initiation

In this section only those aspects of flower initiation relevant to the biennial-bearing phenomenon will be discussed. The C/N-ratio plays an important role, despite the fact that it is not a primary cause, and the role of hormones is known to be more important. A high level of starch, inhibitors such as several auxin-resembling regulators and a low level of gibberellins appear to be most favourable for flower initiation. In a biennial bearer such as 'Miller's seedling', it is clearly shown that in alternating years lack of fruit buds is the cause of the off-year and not lack of fruit set. Biennial bearing behaviour can thus be reduced to the incidence of repeated flowering of the shoots (Jonkers, 1979). It was shown in 'Glockenapfel' that:

- 2% of the shoots flower two years in succession,
- 59% of the shoots flower with one-year interruption,
- 39% of the shoots flower with several years' interruption (Jonkers, 1979).

2.5.2 The influence of the leaves

A certain quantity of leaves are necessary for flower initiation, not less than 30 leaves per fruit, and preferably 40 leaves per fruit in old trees. In dwarfed trees very often 10-20 leaves per fruit are sufficient. The leaf accounts for the formation of carbohydrates and maintains an active transpiration flow to ensure that the buds are supplied with mineral nutrients and hormones (such as cytokinins) (Jonkers, 1979).

2.5.3 The effect of seeds

It was shown that a strong relationship exists between the seed content of the fruits in one year and the quantity of flowering shoots in the next year. Seeds produce relatively large amounts of gibberellins that stimulate growth and diminish flower initiation. This points to the fact that the development of seeds is the main factor in biennial bearing behaviour, more so than the competition of fruits for nutrients (Jonkers, 1979).

2.6 The relationship between bearing habit and biennial bearing

Much work has been done to gain a better understanding of fruiting and, in particular, the relationship between vegetative growth and fruiting. However, little has been done to investigate the initiation and development of fruiting organs as a function of time. Similarly, in breeding programs, ramification and fruiting of the tree have rarely been considered. The research carried out at the INRA Research Centre at Bordeaux allowed Lespinasse and co-workers to describe and classify, in a precise manner, the ramification and fruiting of known apple cultivars. A study of 44 apple cultivars provided evidence of a link between certain morphological characters of the tree and agronomic performance (Lespinasse and Delort, 1993). They have shown, on unmanaged trees, a relation between the volume of the bourse that terminate the fruiting branch and biennial bearing. Acropetal cultivars with large bourse rarely alternated, while basipetal cultivars, with short spurs, tended to alternate. The bourse appeared to play a major role at the level of the growth distribution on the young fruiting branch (autonomy of lateral shoots), and consequently in the balance between fruiting and vegetative development of each fruiting site (Lespinasse and Delort, 1993).

It was found that basipetal cultivars such as 'Wijcik', which carry numerous short spurs and terminal bourses of small volume, do not naturally have a regular production from the one year to the next. In contrast to this, acropetal cultivars with large drooping terminal bourse have a regular production. This is the case with the 'Rome Beauty' group and, to a lesser extent, with 'Granny Smith'. The terminal bourse appears to have an important role, first at the level of growth partitioning on the young fruiting branch, that is to say, cessation of orthotropic development and of lateral crowned brindles, and second, concerning the equilibrium between fruiting and the growth of each fruiting site. Therefore, depending on the cultivar, annual growth can, either be totally separated from the fruiting site (as in spur types), or integrate itself into the fruiting site with the crowned brindles. From this observation it can be appreciated why some varieties such as Granny Smith can adapt to light pruning. In this case it is sufficient to avoid excessive crowding of the crowned brindles which, at the end of bent branches would become too weak (Lespinasse and Delort, 1993).

In the following section the development of the fruiting site and its relevance to biennial bearing will be discussed in some detail, referring to an article published by Lauri *et al.* (1995), thereby linking the plant ideotype to biennial bearing. It is of further importance because the experimental procedure

described by Lauri *et al.* (1995) to study the bearing habits of apple cultivars, was used in this study to quantify the bearing habits of pears.

2.7 Genotypic differences in the axillary bud growth and fruiting pattern of apple fruiting branches over several years

Only a few studies have tried to link the plant ideotype and the ability of the cultivar to bear regularly. It was shown that spur-type cultivars (columnar such as 'McIntosh Wijcik' or Type 2 such as 'Oregon Spur Delicious') have a strong alternate-bearing tendency. On the other hand, cultivars belonging to Type 4, e.g. 'Granny Smith' or 'Rome Beauty', are known to have regular fruiting patterns, which may be related to the ability of these cultivars to produce a significant proportion of their crop terminally on shoots.

Ten cultivars belonging to the Types 2 ('Oregon Spur Delicious', 'Reine des Reinettes'), Type 3 ('Braeburn', 'Golden Delicious', 'Melrose', 'Jonagold', 'Royal Gala') and Type 4 ('Fuji', 'Granny Smith', 'Red Winter') were studied. They started the description of the growth and fruiting pattern with the development of the main shoot of the fruiting branch. This shoot grows forming several leaves during the first year of the experiment, designated as Y, with meristems developing at each leaf axil. These axillary meristems have five alternatives for the following season (in year Y+1): to develop as a vegetative bud (V); to become a flower bud producing a fruit (A); to become a flower bud without fruit (F); to remain as a latent bud (L); or, to abort and leave a scar (S). The following year the development of each of these axillary buds was observed and classified anew, giving rise to a sequence of two letters. This was continued for year Y+2, Y+3 and so on (Lauri *et al.*, 1995).

2.7.1 Definition of functional stages

The analysis of the sequences revealed several functional stages and the following conventions were proposed:

- 1) Latent stage (L);
- 2) Growing stage (G), which begins with the first V, F or A, ending with S. It includes all V, F and A, and sometimes L. This stage is divided into two sub-stages:
 - a) A vegetative sub-stage (V), comprising only V, and
 - b) A reproductive sub-stage (R), beginning with the first F or A, and sometimes comprising V but rarely L.
- 3) Ending state or scar (S).

Each stage, or sub-stage, is of variable duration and may be absent. This functional sequence corresponds to ontogenetic movement, beginning with the undetermined bud in the axil of the subtending leaf, and ending in a scar (S). Generally, this ending state is observed after flowering and corresponds to the abortion of all potential bourse shoots (Lauri *et al.*, 1995).

2.7.2 Description of bud types during the growing stage and the functional equilibrium within the reproductive sub-stage

The second step involved the description of bud types during the growing stage (G). This was done by determining the proportion of V, F and A within each growing sequence (without L or S) (Lauri *et al.*, 1995).

The third step focussed on the functional equilibrium between F, A or V within the reproductive sub-stage (R), i.e. after the first F or A in the growing stage (G). Three indices were then developed:

1) The fruit-richness index (p):

$$p = N(A) / N(R)$$

In which N(A) denoted the total number of A's and N(R) denoted the total number of A's, F's, V's and L's in the reproductive sub-stages of all observed sequences. The fruit-richness index ranges from zero (no fruit) to one (every type in the reproductive sub-stage is A).

2) The alternation-to-fruit index (a):

$$a = N(AA') / N(AA) + N(AA')$$

In which N(AA) denoted the total number of A followed in the sequence by another A, and N(AA') the total number of A which were not followed by another A in the sequence. The index ranges from zero (every A is followed by another A) to one (no A is followed by another A).

3) The alternation synchronism (t):

$$t = [E(AA') - O(AA')] / N(AA')$$

In which E(AA') denoted the total number of AA' successions fruiting the even years, O(AA') the number of AA' successions fruiting the odd years, and N(AA') the total number of AA' successions. This index ranges from zero (as many even as odd A's) to one (all A's occur during years of the same parity, i.e. either even or odd) (Lauri *et al.*, 1995).

One general trait, common to all cultivars, was the general ontogenetic movement (L > G > S) that the initial axillary bud underwent after it was first formed on the current-year wood, until its death. Some traits discriminated between cultivars. The first one was the proportion of G > S change, characterising 'Red Winter', 'Granny Smith' and 'Fuji', all these belonging to Type 4. It was shown that the sequence ending (occurrence of a S) occurred in highest proportion after F. This corresponded to the abortion of potential bourse shoots on non-bearing inflorescences. A possible explanation of this behaviour should consider the nutritional and hormonal status of the flower bud as it develops after the cessation of the visible growth of the subtending axis during summer and autumn. Thus stronger proximal sinks may interfere negatively with the development of the more distal flower bud. Consequently, the

development of the first primordia of the bourse shoot may then be compromised. They propose the use of the term extinction to denote the ability of certain growing points, essentially flowering ones, to abort all further growth potential. Their previous work showed that the extinction mechanism develops during the second or third year of growth (Lauri *et al.*, 1995).

The second discriminating trait concerned the higher relative proportion of A in the reproductive sub-stage for 'Red Winter', 'Jonagold' and 'Royal Gala', as apposed to the higher proportion of V for the other cultivars. The balance between A and V in the reproductive sub-stage is more accurately shown by the relationship between the two indices p and t. The variation range was narrower for p than for t. This suggests that apple genotypes have been selected more for their intrinsic ability to bear fruits than for their non-alternation-to-fruit pattern. Moreover, the inherent ability of some cultivars to produce terminal fruit on bourse shoots is critical in the search for sustainable fruit production from year to year. This trait suggests that, for the cultivars concerned, the sequences have a certain functional autonomy that allows the bourse-over-bourse phenomenon to occur (Lauri *et al.*, 1995).

Within the range of cultivars studied here, the two extreme ideotypes represented two opposing architectural organisation patterns, which is either hierarchic (highly integrated branching system with a strong central leader and branches and flowering on lateral spurs) or polyarchic (in which axis tend to become rapidly equivalent). The spur-type and compact trees are characterised by abundant spurring with nearly all axillary buds growing into spurs. 'Oregon Spur Delicious', characterised by strong vegetative erect scaffold branches and numerous lateral flowering, short spurs with little extinction phenomenon, is an example of such an integrated architecture. On the other hand, Type 4 cultivars show a polyarchic pattern, where the axes rapidly become morphologically similar, and functionally more independent. They appeared to be able to balance vegetative and reproductive growth by reducing the number of growing buds through an extinction mechanism, and to distribute vegetative growth amongst shoots destined to terminate in a fruit bud. Hierarchic patterned cultivars appear to be unable to autonomously maintain a regular year-to-year fruiting pattern on short spurs with insufficient growth potential. This leads to a poor overall fruit-richness and an alternate-bearing habit. Polyarchic cultivars do not show such a separation between vegetative and reproductive growth, and their autonomous shoots seem to be able to crop terminally each year (Lauri *et al.*, 1995).

According to Dickman *et al.* (in Lauri *et al.*, 1995), an ideotypic apple grown in a high-density orchard should present, among other traits, spurred habit, fruits on lateral spurs not on branch terminals and no biennial bearing. This does not correspond to the optimal branching and fruiting pattern that, as shown here, establish an intrinsic discrepancy between the strict non-alternating pattern and the spurred habit (Lauri *et al.*, 1995).

According to earlier work done by the authors, it appears that the ability of a cultivar to crop annually on a non-alternating-to-fruit sequence (bourse-over-bourse phenomenon) is associated with a minimum length of bourse shoots or of the bourse itself. These considerations are consistent with other studies

that have shown that threshold vigour is necessary for flower bud initiation, leading to high spur quality. It therefore appears that rather than to consider vegetative growth and flower initiation as counterparts, it would be more suitable to look for a better partitioning of growth, favouring vegetative growth on shoots destined to fruit terminally. These linked traits, extinction and autonomy might be considered as part of the biological yield potential (Lauri *et al.*, 1995).

2.8 Discussion

When a young tree is planted in an orchard, the tree must fill its allocated space, and at the same time develop efficient bearing units on which the fruit will be borne eventually. When this is accomplished, the tree must start to bear fruit. The sooner this is accomplished, the more profitable it is to the producer. After the young tree comes into bearing, it is important to obtain a regular, annual crop, without biennial bearing.

Cultivars can be classified into groups that exhibit similar growth habits. The growth habit of a cultivar will determine to a great extent the way a tree will develop vegetatively. Thus, it will play an important role in the planning of an orchard, from the rootstock being used to the tree spacing and the training system. Further more, it will determine the management inputs required for obtaining the optimum tree form and a regular, annual crop.

Lauri and Lespinasse (1993), grouped apple cultivars into four ideotypes, taking into account the tree form and distribution of bearing axis on this structure. They quantified the different stages of development a bearing unit undergoes (Lauri *et al.*, 1995). They also quantified the fruitfulness of a cultivar and the tendency of the cultivar to produce a regular, annual crop. This work is of tremendous importance for the understanding of a cultivar's vegetative development, its reproductive development and the regularity of its crop (i.e. the tendency towards biennial bearing). This information plays an important role in all aspects of fruit production, from the breeding of new cultivars (taking into account the tendency of the selection towards a regular, annual crop and not just the inherent fruitfulness of the selection), to the management practices required for the training of young trees, the pruning of trees in production and the inputs required to obtain a regular, economic crop from year to year.

Based on field observations, Sansavini and Musacchi (1994) have grouped pears into five groups according to bearing habit. They then proposed pruning protocols for each group, taking into account the bearing sites and fertility of cultivars in the different groups. Such detailed work as Lespinasse *et al.* (1995) did on apples, however, has not been done on pears. Since pears are inherently less fruitful than apples and are more difficult to manage, similar work must be done on pears to aid us in management. This information will also help us with the development of new cultivars.

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PAPER 1: Branching Habit of Two-year-old Pear Branches Classified on the Basis of Length and Position of One Year-Old Laterals.

Additional index words. *Pyrus communis* L., proleptic branching, apical control

Abstract. Two-year-old branches of *Pyrus communis* L. were classified into groups according to the proleptic (from dormant buds) branching habit, indirectly quantifying the degree of apical control. In Winter 1998 upright and flat, two-year-old branches were randomly sampled from trees of seven pear cultivars, i.e., Forelle (on Quince A and BP1 rootstocks), Abaté Fetel, Flamingo, Packham's Triumph, Golden Russet Bosc, Rosemarie and Beurre D'Anjou on BP1 rootstock. For each branch the length and position of the one-year-old shoots on the two-year-old axis was determined. Laterals were classified according to length (< 1cm, 1-5cm, 5-20cm and >20 cm) and position (distal to proximal quadrants on the two-year-old axis); sixteen classes in total. The number of shoots per length class per cm quadrant length for each cultivar was subjected to a cluster analysis, then a canonical and a stepwise discriminant analysis. The cultivars were grouped into four groups from Group 1 ('Flamingo') which resembles a spurred growth habit with strong apical control, to Group 4 ('Packham's Triumph' and 'Golden Russet Bosc') which resembles a spreading growth habit and weak apical control. Groups 2 and 3 were intermediate. The gravimorphic influences on the branching habit were investigated.

To understand the ontogenic development of fruiting structures or fruiting habit in pear at the cultivar level, it is important to understand cultivar differences in branch development. The branching habit determines the characteristics of the bearing-structures, i.e., spur, short or long shoot. In apple two opposing tendencies are observed (Lespinasse, 1992; Lauri and Lespinasse, 1993; Lauri *et al.*, 1995). In upright growing cultivars the terminal vegetative growth is dominant for a long time, resulting in fruiting on numerous spurs from the base to the top of the branch. Bearing in these cultivars often alternates since many of the spurs develop simultaneously. Another group of cultivars also initially grows erect, however, the early appearance of terminal fruiting and bourse shoot development induces rapid bending of these branches and a resultant spreading habit. Growth and fruiting are located at the same site and bearing is more regular (Lespinasse and Lauri, 1996).

Branching in pear is proleptic (from dormant buds) and acrotonic (from distal buds), and is at least partially controlled by the degree of apical control exerted by the terminal extension growth over the growth of lateral shoots in terms of length and orientation. Apical control is understood to be strong when the terminal extension growth checks the growth of the lateral shoots such that only spurs develop. Weak apical control occurs when lateral shoots successfully compete with the terminal extension growth, resulting in numerous equally strong distal extension shoots (Brown *et al.*, 1967; Cline, 1997; Cook *et al.*, 1999). Among branching habits in upright growing pear branches a continuum from strong to weak apical control is observed between cultivars.

Lespinasse (1992) summarised the classification of apple cultivars into four fruiting types or ideotypes, on the basis of growth and fruiting habit. In pear, Sansavini and Musacchi (1994), based on field observations, have proposed five fruiting wood management strategies. The objective of this study was to quantify and classify varietal differences in pear branching habits. This will provide a basis for understanding pear fruiting habits. The influence of gravimorphic responses on branching habit was considered.

Materials and methods

Two-year-old branches from seven pear cultivars, i.e. Forelle, Abaté Fetel, Flamingo, Packham's Triumph, Golden Russet Bosc, Rosemarie and Beurre D'Anjou (on BP1 rootstock) were used in this investigation, representing a continuum of growth habits ranging from strongly upright to almost weeping (Fig.1). 'Forelle' branches were included separately from trees on vigorous BP1 and dwarfing Quince A (QA) rootstocks. All trees were planted in an evaluation orchard on the Bien Donné Experimental Farm, Western Cape (34 °S, 138 m), South Africa between 1990 and 1993. Due to insufficient winter chilling, dinitro-*o*-cresol (DNOC) oil (4%) was applied at terminal bud swell in spring to break rest.

Upright and flat, two-year-old branches were randomly selected from each cultivar in Winter 1998 (ten branches per orientation for each cultivar). For each branch, the length (excluding the terminal bud) and position of the one-year-old shoots on the two-year-old wood (axis), and the length of the axis was determined. Shoot position was measured as the distance from the distal end (zero position) of the axis.

All one-year-old shoots were classified according to four length classes, i.e., <1cm (A), 1-5 cm (B), 5-20 cm (C) and >20 cm (D). Shoot position was classified by dividing each two-year-old axis into four equal quadrants [Q1 (distal), Q2, Q3 and Q4 (proximal)]. For each branch, the shoot density (number of shoots per cm of quadrant length) was determined for each of the sixteen classes (e.g. Q1A, Q1B, etc.). The mean shoot density per class for the upright branches of each cultivar was submitted to a cluster analysis to determine which groups could be distinguished (PROC CLUSTER, SAS[®] release 6.12, SAS Institute Inc., Cary, NC.). Thereafter the shoot density per class of each upright branch was submitted to canonical and stepwise discriminant analyses in order to establish group membership (PROC DISCRIM).

To test the models developed for upright branches in 1998, upright branches from the cultivars Packham's Triumph, Flamingo and selections 15C-2-3 and 15B-5-2 were sampled from the same orchard in Winter 2000. The shoot density per class for each branch was determined as before. The branching habit of these cultivars was classified and tested against the discriminant function obtained for the 1998 data.

To determine the gravimorphic influence on branching habit the shoot density per class on horizontal branches of each cultivar sampled in 1998 was tested against the models developed for the upright (natural) branching habits, again using discriminant analysis (PROC DISCRIM).

Results and Discussion

The cultivar means of the two-year-old axis length, one-year-old shoot length and the one-year-old shoot density for the upright and flat branches (ignoring position) are shown in Table 1. The meaningful classification of upright branching habits into cultivar groups via cluster analysis of only these data failed (data not presented). Branching habit is a function of lateral length relative to position on the axis (Rauh, 1939). Cluster analysis of the cultivar mean shoot density per class (shoot length by position) on upright shoots resulted in the logical grouping of cultivars into four branching habit groupings (Fig. 1 and 2).

Canonical discriminant analysis of the upright, branch shoot density per class was then used to classify the individual branches into the four branching habit groups as determined by cluster analysis of the cultivar means. Table 2 shows the results of this reclassification. For groups 1 to 4 respectively, 100%, 65%, 77% and 76% of the branches were reclassified into the original groups identified with the cluster analysis. Variation between branches within a cultivar with regards to branching habit is expected (Hallé, 1978). In the case of 'Forelle' branches, 35% were not classified into group 2, but into groups 1 and 3. The branching habit of 'Forelle' (group 2) is less rigidly controlled than say 'Flamingo' (100% classification into group 1). 'Forelle' branches from trees on both rootstocks showed similar grouping (Fig. 2), clearly displaying the hereditary character of branching.

A stepwise discriminant analysis selected, in order of importance, the quadrant x length variables Q1A, Q1D, Q4A, Q4B, Q2C, Q1C and Q1B to discriminate between the four groups (Table 3). Together they accounted for 42.5% of the correlation between branches and their groups. Varietal expression of apical control between cultivars is primarily restricted to the distal quadrant (Q1) of the axis in terms of the number of short shoots (<1cm; A) and long shoots (>20cm; D).

The mean value for each quadrant x length variable was plotted for each group as identified by the canonical discriminant analysis (Fig. 3). This data profiles the branching habit of each group. Group 1, consisting only of 'Flamingo', displays a spurred branching habit (Fig. 1). Strong apical control is apparent from the dominance exerted by the terminal extension growth over the numerous spurs observed on the full length of the two-year-old axes. Group 4, consisting of 'Packham's Triumph' and 'Golden Russet Bosc', on the other extreme exhibit the weakest apical control. Numerous distally situated lateral buds develop into long shoots, their growth apparently not as strongly checked by the terminal extension growth (Fig. 1). Groups 2 and 3 fall within the continuum between these two extremes with apical control weaker in group 3 than in group 2.

Upright, two-year-old branches from the cultivars Packham's Triumph, Flamingo, and new selections 15C-2-3 and 15B-5-2 were sampled after growth cessation in 2000. These cultivars were classified according to the previously determined discriminant functions (1998 data), using canonical discriminant analysis. Results are shown in Table 4. 'Packham's Triumph' was again classified into group 4 (60% of branches) and 'Flamingo' into group 1 (70% of branches), confirming the model developed using the 1998 data. The selections '15C-2-3' and '15B-5-2' were classified into group 2 (60% and 58.33% of branches, respectively).

Data from horizontal branches were tested, using canonical discriminant analysis, against the discriminant functions developed for the upright branches to determine the effects of gravimorphic response on the upright (natural) branching habit. 'Abaté Fetel', 'Forelle/QA', 'Forelle/BP1', and 'Rosemarie' were classified into their original branching habit groups (Table 5). Except for a slight reduction in vigor (less long shoots, more spurs), the gravimorphic response did not alter the hereditary branching habit displayed by upright shoots of these cultivars. The gravimorphic effect was more pronounced in the cultivars Beurre D'Anjou, Flamingo, Golden Russet Bosc, and Packham's Triumph, where the branching habits were altered to such a degree that many branches were classified into other groups (Table 5). Flat 'Packham's Triumph' branches displayed reduced vigour and a higher occurrence of long shoots proximal to the distal quadrant. Vigour was reduced in 'Golden Russet Bosc' and 'Beurre D'Anjou' to the extent that flat branches were classified into branching habit groups 3 and 2, respectively (Table 5). Flat 'Flamingo' branches showed reduced branching (less short shoots), with 80% classified into group 3 (Table 5). Bending is known to reduce vegetative growth (Wareing and Nasr, 1958).

It was possible to classify the pear cultivars used in this investigation into four branching habit groups, on the basis of length and position of one-year-old laterals on the two-year-old axes of upright branches. The expression of apical control by the terminal extension growth diminished from group 1 to 4. 'Flamingo' (group 1) display strong apical control with clear dominance of the terminal extension growth over lateral spurs. 'Packham's Triumph' and 'Golden Russet Bosc' (group 4), exhibit the weak apical control. Numerous distally situated lateral buds develop into long shoots, apparently not checked by the terminal extension growth. Pear cultivars not included in this investigation will probably adhere to a branching habit within the continuum observed between group 1 through 4. The hereditary branching habit of 'Abaté Fetel', 'Forelle', and 'Rosemarie', as determined by the degree of apical control, is strongly expressed and was not influenced by rootstock or gravimorphic effects. In 'Beurre D'Anjou', 'Flamingo', 'Golden Russet Bosc', and 'Packham's Triumph', the upright branching habit was significantly altered by gravimorphic effects, mainly due to a reduction in vegetative growth and branching.

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Table 1: Cultivar mean two-year-old axis length, one-year-old shoot length, and one-year-old shoot density.

Cultivar	n		Axis length (cm)			Mean shoot length (cm)			Shoot density ^z (shoots/cm)		
	Upright	Flat	Upright	Flat	Pr>f ^y	Upright	Flat	Pr>f	Upright	Flat	Pr>f
Abaté Fetel	10	8	58	51	0.3924	4.6	3.3	0.0232	1.19	1.33	0.0894
Beurre D'Anjou	10	10	42	35	0.0356	5.3	3.0	0.0388	1.13	0.19	0.0001
Flamingo	10	10	66	76	0.4116	3.0	1.6	0.0179	1.34	0.51	0.0004
Forelle/QA	10	10	40	27	0.0075	3.9	3.9	0.9505	1.13	1.01	0.1869
Forelle/BP1	10	10	53	48	0.6281	9.2	2.9	0.0041	0.92	1.05	0.1328
Golden Russet Bosc	7	7	42	22	0.0095	8.6	4.4	0.0053	1.12	1.38	0.0576
Packham's Triumph	10	10	41	44	0.7543	11.1	9.3	0.4307	1.09	1.19	0.4820
Rosemarie	10	10	49	58	0.2241	9.4	4.4	0.0277	0.98	1.10	0.1061

^y Each time the probability refers to the difference between upright and flat branches for a given cultivar and variable.

^zShoot density as determined over the full axis length

Table 2: Reclassification of individual upright branches by discriminant analysis into branching habit groups identified by cluster analysis of length by position classes on a cultivar basis.

From Group ^x	Into group				Total
	1	2	3	4	
1	10 ^y	0	0	0	10
	100 ^z	0	0	0	100
2	2	13	5	0	20
	10	65	25	0	100
3	0	4	23	3	30
	0	13	77	10	100
4	0	2	2	13	17
	0	12	12	76	100

^x Groups as in Figure 2 determined by cluster analysis of the cultivar means

^y Number of branches

^z % of total

Table 3: Discriminant variables selected, in order of importance, by the stepwise analysis of discrimination of branches between groups.

Step	Variable	ASCC ^z	Pr>ASCC
1	Q1A	0.1910	0.0001
2	Q1D	0.2836	0.0001
3	Q4A	0.3398	0.0001
4	Q4B	0.3665	0.0001
5	Q2C	0.3836	0.0001
6	Q1C	0.4008	0.0001
7	Q1B	0.4247	0.0001

^z Average squared canonical correlation

Table 4: Classification of individual upright branches sampled from 'Packham's Triumph', 'Flamingo', '15C-2-3' and '15B-5-2' in 2000 by discriminant analysis into branching habit groups identified by cluster analysis on a cultivar basis.

Cultivar	Branching habit group ^x				Total
	1	2	3	4	
Packham's Triumph	2 ^y	0	2	6	10
	20 ^z	0	20	60	100
Flamingo	7	2	0	1	10
	70	20	0	10	100
15C-2-3	0	6	2	2	10
	0	60	20	20	10
15B-5-2	0	7	3	2	12
	0	58	25	17	100

^x Groups as in Figure 2 determined by cluster analysis of the cultivar means in 1998

^y Number of branches

^z % of total

Table 5: Classification of individual flat branches by discriminant analysis into branching habit groups identified by cluster analysis of upright branches on a cultivar basis.

Cultivar	Branching habit group ^x				Total
	1	2	3	4	
Abaté Fetel	1 ^y	0	6	1	8
	13	0	75	13	100
Beurre D'Anjou	0	10	0	0	10
	0	100	0	0	100
Flamingo	2	8	0	0	10
	20	80	0	0	100
Forelle/QA	2	8	0	0	10
	20	80	0	0	100
Forelle/BP1	1	7	1	1	10
	10	70	10	10	100
Golden Russet Bosc	0	1	6	0	7
	0	14	86	0	100
Packham's Triumph	3	1	2	4	10
	30	10	20	40	100
Rosemarie	1	3	6	0	10
	10	30	60	0	100

^x Groups as in Figure 2 determined by cluster analysis of the cultivar means

^y Number of branches

^z Percentage of total

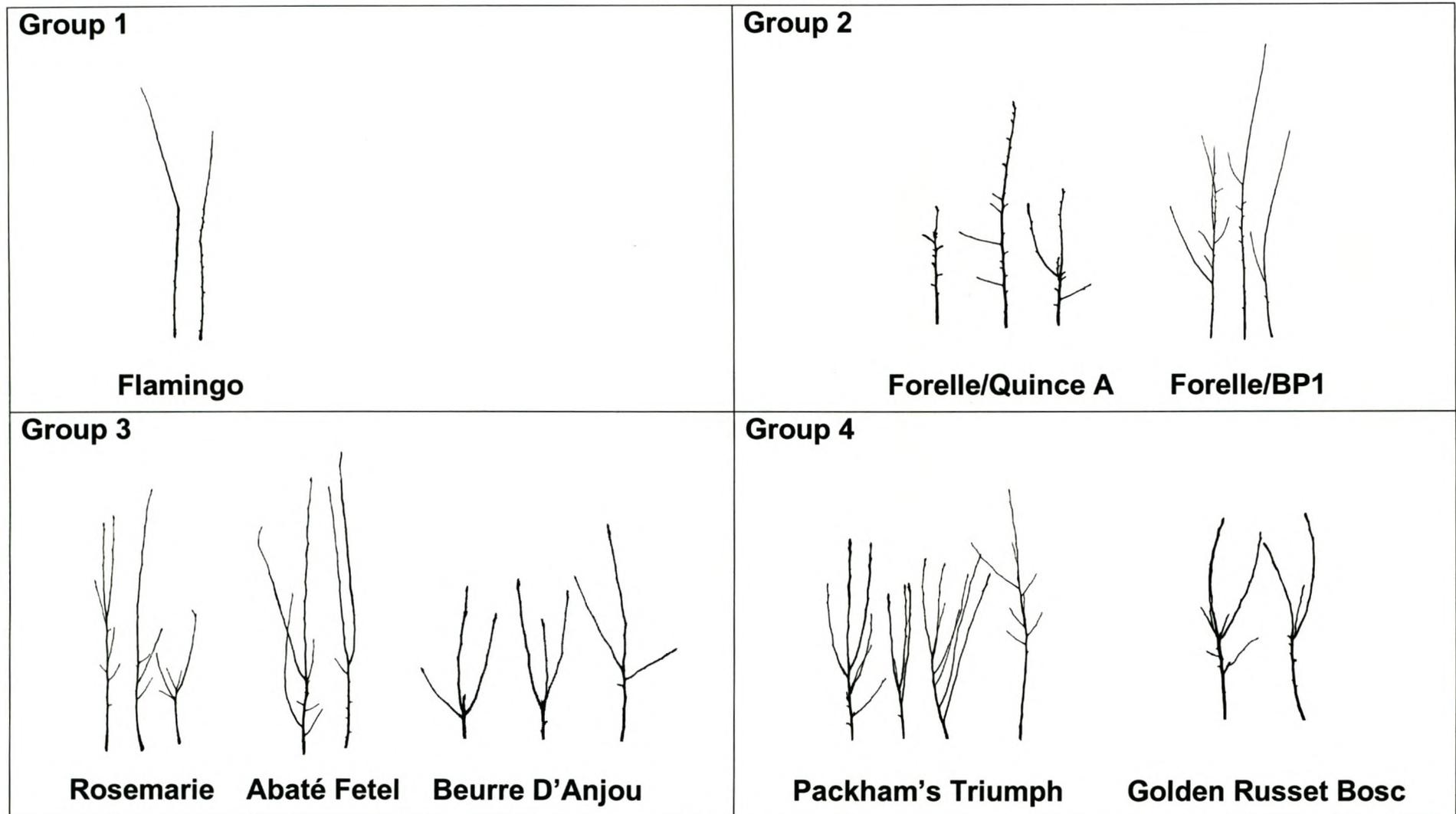


Fig. 1. Examples of upright, two-year-old pear branches showing cultivar differences in branching habit (cultivars in Group 1, 3 and 4 on BP1 rootstock).

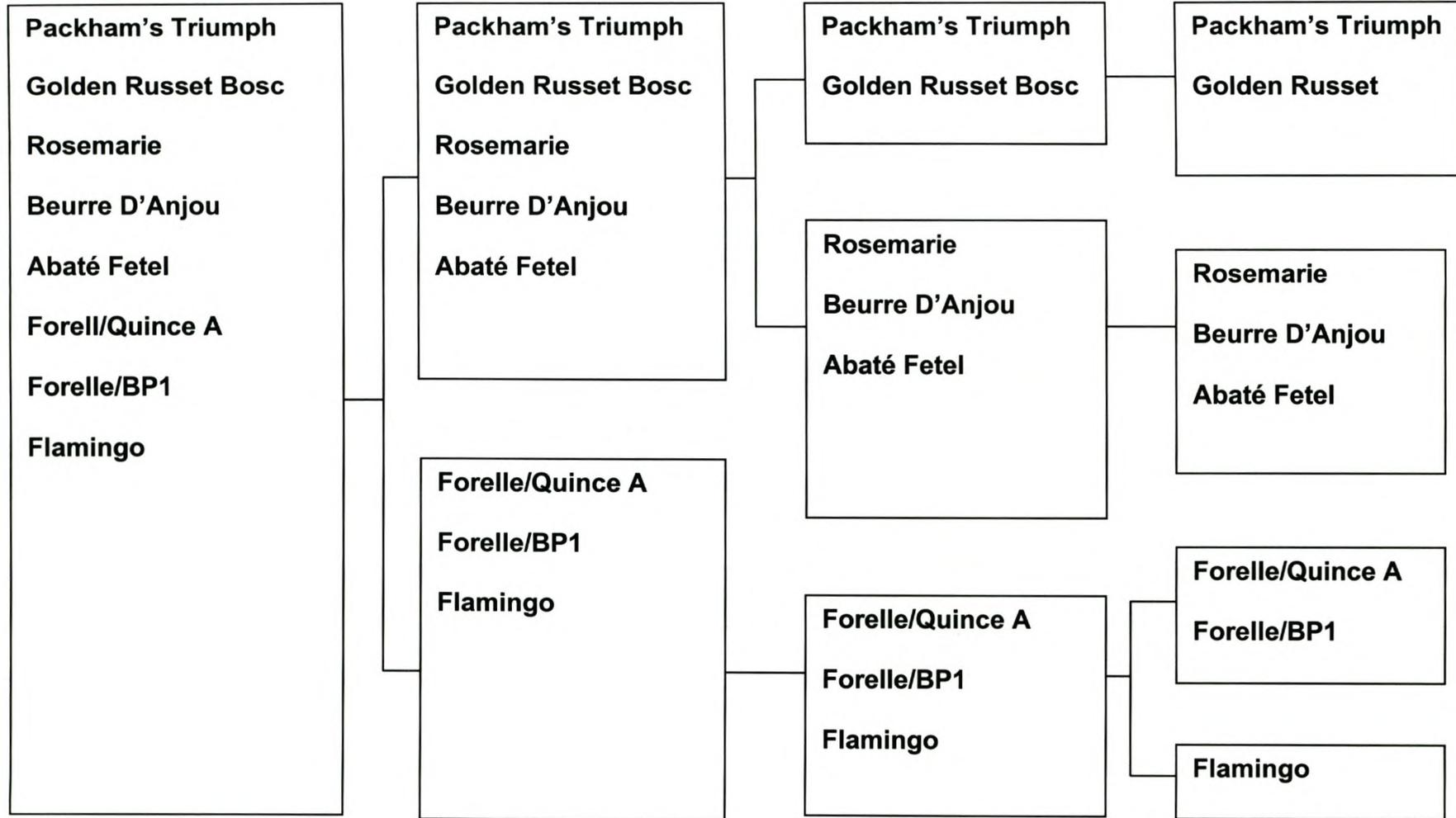


Fig. 2. Classification of pear cultivars into four branching habit groups by cluster analysis of the cultivar mean shoot density per length by position class, using only data from upright branches. (All cultivars not specified on BP1 rootstock.)

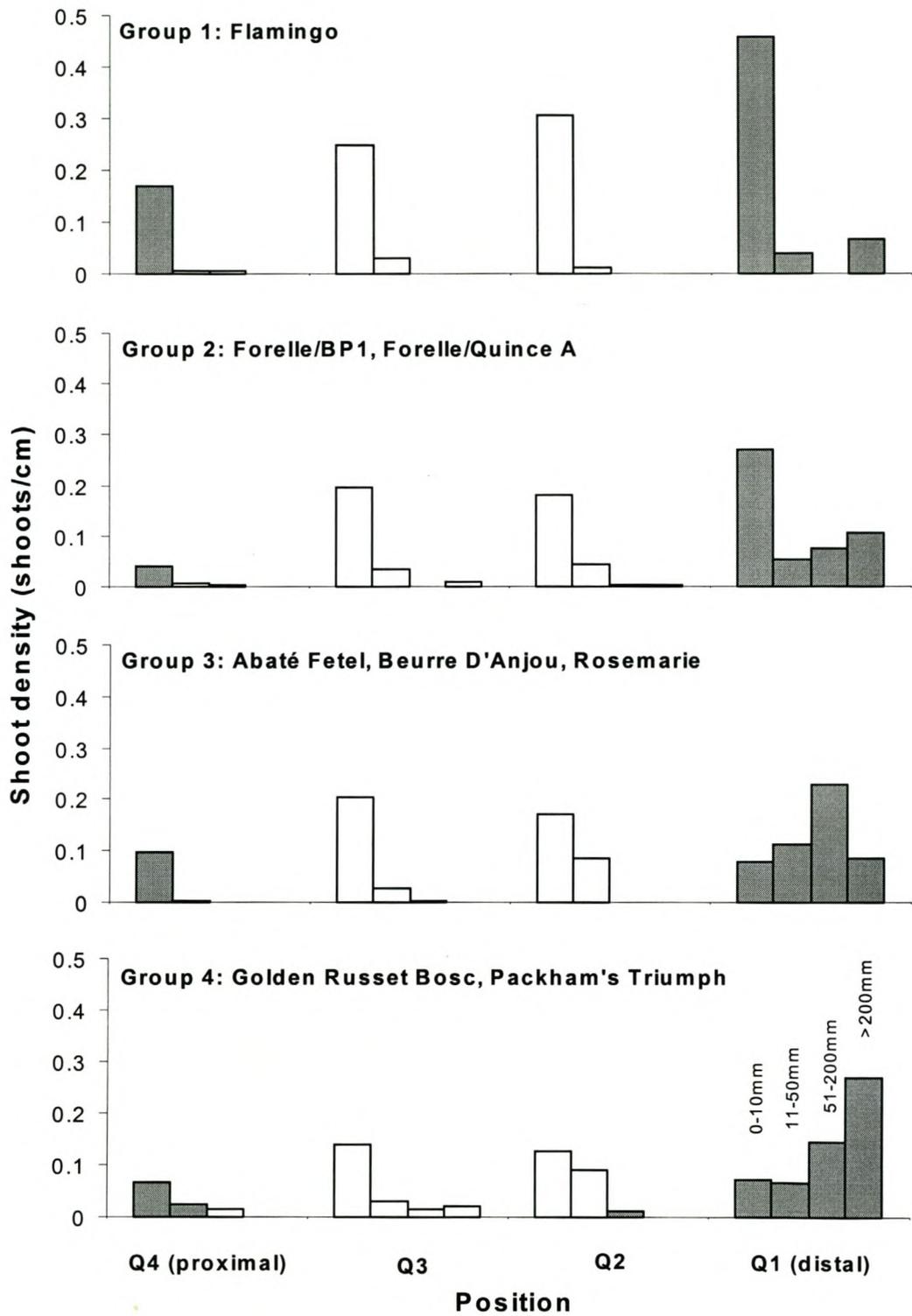


Fig. 3. Shoot density of each length by position class for the four branching habit groups. Shaded parameters account for 42.5% of the correlation between branches and their grouping.

PAPER 2: Quantification of the Bearing Habits of Seven Pear Cultivars Under South African Conditions Based on the Lateral Bud Growth.

Additional index words. *Pyrus communis* L., bearing habit, vigour, flower initiation

Abstract. The bearing habit of seven pear cultivars was quantified according to the ontogenetic development from axillary buds. In Winter 1998 ten unpruned branches were tagged on trees of seven pear cultivars, i.e., Forelle (on Quince A and BP1 rootstocks), Abaté Fetel, Flamingo, Packham's Triumph, Golden Russet Bosc, Rosemarie and Beurre D'Anjou (all on BP1 rootstock). The description started with the development of the main fruiting branch, forming several leaves in the first year of growth (designated Year Y), with meristems developing in the leaf axils. In the following season (Year Y+1), these axillary meristems had five developmental alternatives: to remain as a latent bud (L), to develop as a vegetative bud (V), to become a flower bud without fruit (F), to become a flower bud setting a fruit (P) or to abort and leave a scar (S). Each year the development of these axillary meristems was observed and classified anew, giving rise to a sequence. Between 50% ('Forelle/QA') and 75% ('Rosemarie') of buds remained in the growing stage (comprising of V, F or A buds) during the years of monitoring. This coincided with relatively low proportions of buds remaining in the latent phase (L) or moving to the ending state (S). A relatively large proportion of buds went from the growing phase back to the latent phase (up to 20% in the case of 'Beurre D'Anjou'), probably due to inadequate winter chilling. Considering the proportion of bud types within each year for a given cultivar, it was shown that the predominant bud type in the growing stage was V. This was again apparent considering the year to year transitions within the growing stage (mostly VV sequences). Although flower initiation was low for all cultivars throughout the trial period, 'Flamingo' and 'Abaté Fetel' went into the reproductive phase (F or P) in year Y+3. 'Packham's Triumph' and 'Rosemarie' displayed a relatively high proportion of F and P buds in year Y+1, corresponding to the ability of these cultivars to bear fruit on one-year-old shoots. These cultivars also displayed the bourse-over-bourse phenomenon (PP), producing flowers and fruit terminally on bourse shoots. The extinction mechanism (abortion of mainly F buds to form an S in the case of apple) occurred to some extent in the cultivars 'Packham's Triumph' and 'Rosemarie'. In the other cultivars, V mostly preceded S, possibly due to damage resulting from DNOC-winter oil applied to break rest.

The leaves, through photosynthesis, produce the carbohydrates used in growth. Growth includes development of the tree and production of fruit. Vegetative growth is essential to maintain leaf area and develop new bearing sites (Forshey and Elfing, 1989). Woody tissues of the tree, however, compete with the fruit for assimilates from the leaves (Forshey and Elfing, 1989), resulting in an inverse relationship between cropping and vegetative growth (Crabbe, 1987; Forshey and Elfing, 1989). To obtain an optimum vegetative growth to fruiting relationship, development of excessive vegetative

growth should be prevented, preferably by means of cropping (Forshey *et al.*, 1992). The coexistence of these two functions (vegetative growth and cropping) are ensured in trees by a temporal and spatial separation of the two functions (Crabbe, 1987).

The development of the bearing structure in different pear cultivars was the subject of a previous study (Paper 1). Two-year-old branches of seven pear cultivars were classified into groups according to the proleptic (from dormant buds) branching habit, indirectly quantifying the degree of apical control. The branching habit determines the characteristics of the bearing-structures, i.e., spur, brindle or long shoot. The spurs and brindles (short shoots) are the preferred sites for flower development in pear trees (Crabbe, 1987; Brunner, 1990).

Lespinasse (1992) summarised the classification of apple varieties into four fruiting types or ideotypes, on the basis of growth and fruiting habit. Lauri *et al.* (1995) quantified the bearing habits of apple trees belonging to these ideotypes, with emphasis on the phenomenon of biennial bearing. The objective of this study was to quantify the ontogenetic development of bearing structures in seven pear cultivars grown under South African conditions of sub-optimal winter chilling, using the methods of Lauri *et al.* (1995).

Materials and methods

Seven pear cultivars, i.e. Forelle, Abaté Fetel, Flamingo, Packham's Triumph, Golden Russet Bosc, Rosemarie and Beurre D'Anjou were used in this investigation. Trees were grafted on semi-vigorous BP1 rootstock. 'Forelle' trees on dwarfing Quince A rootstock were also included in the study. All trees were planted in a cultivar evaluation orchard on the Bien Donné Experimental Farm, Western Cape (34 °S, 138 m), South Africa between 1990 and 1993. Due to insufficient winter chilling, dinitro-*o*-cresol (DNOC) winter oil (4%) was applied at terminal bud swell in spring to break rest. There were ample cross-pollinators available and conditions were conducive to fruit set. Fruit were not thinned during this trial.

Ten unpruned fruiting branches, orientated between 45⁰ and 90⁰ from the vertical, were randomly selected per cultivar. The fruiting habit of the pear cultivars was quantified using the methods of Lauri *et al.* (1995) developed for apple branches. The description started with the development of the primary axis of the branch, in the first year of growth (designated year Y), comprising of an unbranched shoot with leaves and axillary buds. In the following seasons, these axillary buds had five developmental alternatives: remain dormant as a latent bud (L), grow and develop a vegetative bud (V), become a flower bud without fruit (F), become a flower bud setting a fruit (P) or to abort and leave a scar (S). Each year the development of each axillary meristem was observed and classified anew, giving rise to a sequence.

If the axillary production in any year was an inflorescence (F or P), the behaviour of the terminal bud of the longest bourse-shoot was determined the following year. Developmental transitions such as FV or PV correspond to sympodial growth by substitution (with the bourse-shoot being a relay axis). A VV transition corresponds to monopodial growth (compare Hallé *et al.*, 1978). The transition PP arises where a flower bud produces fruit and is followed by a fruit borne terminally on the bourse-shoot the following year, a phenomenon called bourse-over-bourse bearing (Lauri *et al.*, 1995).

In winter 1998 the history of each axillary meristem on the fruiting branches was recorded (working backwards), giving rise to one, two or three letter sequences. The behaviour of these axillary meristems were observed and classified in the winters of 1999 and 2000. This resulted in three, four or five-year-old sequences for each of the cultivars studied.

Lauri *et al.* (1995) proposed three functional phases in apples, i.e., the latent phase (L), the growing phase (G) including V, F or P and the ending phase (scar, S). We started our analysis of the sequences by determining the transition between these phases from Year Y+1 to Y+2, Y+2 to Y+3 etc., occurring within each individual sequence. The phase changes observed were LL, LG, LS, GG, GL, GS, GS_V, SS and SS_V. S_V denotes a phenomenon observed in our data where a bud aborted, but a rudimentary bud subtending the scar on the same position developed, usually into a vegetative shoot. The phase changes per cultivar were calculated for each individual branch, summed and expressed as proportions.

The second step was to determine the proportion of bud types or states (L, V, F, P, S and S_V) per year per cultivar. Thirdly, the transition between bud states (V, F and P) within the growing phase of each sequence, was determined. Nine different transitional combinations (transitions) were possible, i.e., VV, VF, VP, FV, FF, FP, PV, PF and PP. The proportion of each transition for each subsequent year (Y+1 to Y+2 etc.) for each cultivar was calculated. Lastly, the bud state preceding the S phase was determined. The possible transitions LS, VS, FS and PS were determined and expressed proportionally.

Results and discussion

The first step in the quantification of the bearing habits was to determine the phase changes undergone in successive years for each cultivar (Lauri *et al.*, 1995). The three functional phases (L, G and S) for apple were observed in pear, with an additional phenomenon observed where a rudimentary bud subtending an aborted bud (S) resumed vegetative growth of the axis at that position (S_V).

Fig. 1 shows that between 50% ('Forelle/QA') and 75% ('Rosemarie') of buds remained in the growing phase (G) during the years of monitoring. This coincided with relatively low proportions of buds remaining in the latent phase (L) or moving to the ending phase (S). The re-awakening of vegetative growth at the site of aborted buds (S_V) further reduced the number of sequences going to the ending phase. Comparing 'Forelle/QA' and 'Forelle/BP1', it is interesting to note that a larger

proportion of buds remained in the latent phase in the case of the dwarfing QA rootstock. Growth on QA rootstock is significantly less vigorous than on BP1 rootstock (Du Plooy and Van Huyssteen, 2000), possibly explaining this phenomenon.

A relatively large proportion of buds went from the growing phase back to the latent phase (up to 20% in the case of 'Beurre D'Anjou') (Fig. 1). In apple, the GL transition never exceeded 1.4% for any cultivar (Lauri *et al.*, 1995). The relative high occurrence of the GL transition could possibly be ascribed to inadequate winter chilling. The trial site is in one of the warmer production areas in South Africa, receiving 579, 584, 664, 588 and 301 Utah chill units from May to July for the years 1995 through to 1999. The occurrence of the GL transition tended to be higher in cultivars generally accepted to have a higher chilling requirement like 'Beurre D'Anjou' and 'Golden Russet Bosc'. In cultivars with lower chilling requirements (Flamingo, Forelle and Rosemarie) the occurrence of the GL transition was certainly lower. A symptom of delayed foliation is delayed and protracted bud-break in spring with many buds not developing at all (Wertheim, 1990).

Fig. 2 shows the proportion of bud states (L, V, F, P, S_v and S) per year for each cultivar. The relatively low proportion of the L and S bud states are again apparent. The predominant bud type in the growing phase is V, especially in the case of 'Golden Russet Bosc', 'Beurre D'Anjou' and 'Forelle/BP1' (Fig.2). Although flowering was generally low for all cultivars throughout the trial, 'Flamingo' and 'Abaté Fetel' went into the reproductive phase (F and P) in year Y+3. 'Packham's Triumph' and 'Rosemarie' displayed a relatively high proportion of F and P buds in year Y+1. This may be explained by the fact that most pear cultivars bear primarily on spurs, but some cultivars ('Packham's Triumph' and 'Rosemarie') have the ability to also bear fruit on one-year-old shoots. The occurrence of some P buds in year Y+1, but mostly from year Y+2, in the case of 'Forelle/QA', is probably due to the dwarfing Quince A rootstock, enhancing the precocity of 'Forelle' pears (Du Plooy and Van Huyssteen, 2000).

Fig. 3 displays bud state transitions observed between successive years within the growing phase (G). The transition most frequently observed was VV. This corresponds to results in Fig. 1 and 2, displaying the vegetative nature of the cultivars in this study. The combination PP denotes the bourse-over-bourse bearing phenomenon. This phenomenon was observed in the cultivars Packham's Triumph, Rosemarie and to a lesser extent in Forelle/QA and corresponds to the ability of these cultivars to bear fruit terminally on bourse shoots. For these cultivars the sequences have a certain functional autonomy which allows this phenomenon to occur (Lauri *et al.*, 1995).

Functional autonomy of fruiting structures is observed in the apple cultivars Red Winter and Granny Smith, and corresponds to their ability to balance vegetative and reproductive development by reducing the number of growing buds. This is accomplished, in apple, primarily by an extinction mechanism (abortion of weak reproductive structures), and enhanced allocation to more autonomous reproductive

structures (Lauri *et al.*, 1995). In the studied pear cultivars, the occurrence of this extinction mechanism was low compared to apple, possibly due to lower functional autonomy of sequences (lower occurrence of PP, Fig. 3). In the pear cultivars 'Packham's Triumph' and 'Rosemarie' where some degree of bearing structure autonomy was observed (Fig. 3), the relative high proportion of latent buds may aid in reducing the number of growing buds, thereby increasing the allocation of assimilates to fruiting structures. In apple, abortion (S) was mostly preceded by a non-fruiting inflorescence (F) (Lauri *et al.*, 1995). In these pear sequences, vegetative development (V) mostly preceded S (Fig. 4). This might be due to damage caused by the application of DNOC-winter oil to break rest, rather than extinction.

Most cultivars in this study were predominantly in a vegetative state (Fig. 1, 2 and 3) under prevalent conditions, due to a lack of flower formation. There may be two explanations for this. Firstly, the use of semi-vigorous BP1 rootstocks might delay flowering. The rootstock effect is clearly shown when 'Forelle/BP1' and 'Forelle/QA' are compared in this study. Du Plooy and Van Huyssteen (2000) also showed the positive effect of Quince A rootstock on precocity of 'Forelle' pears in the same site. The negative effect of excessive shoot growth on flowering and fruit set in apple is reviewed by Forshey and Elfing (1989). The second factor may be related to the high proportion of active buds (low proportion of buds in latent or ending state, Fig. 1 and 2), possibly resulting in increased competition for assimilates. The control of flower bud induction in apple trees has been reviewed by Buban and Faust (1982), who concluded that reproductive development in apple is most sensitive to hormonal, nutritional and physiological effects. This is also true for pears (Wertheim, 1990). The large proportion of developing buds (mostly vegetative) produces large amounts of hormones such as gibberellins and auxins, possibly having a negative effect on flower induction.

The vegetative growth to fruiting balance for the seven pear cultivars in this study needs to be shifted in favour of fruiting. There was a general lack of flowering, resulting in low productivity. It became clear that cultivars such as Packham's Triumph and Rosemarie are more precocious under prevalent conditions. The effect of dwarfing Quince A rootstock on the precocity of 'Forelle' has also been shown. Although the occurrence of the extinction mechanism was generally low, the high proportion of latent buds may aid in reducing the number of growing buds, thereby increasing the allocation of assimilates to fruiting structures. This, in combination with the tendency of cultivars such as Packham's Triumph and Rosemarie to develop longer and possibly more autonomous shoots (Paper 1), may explain their higher productivity and the occurrence of bourse-over-bourse bearing. Cultural practices such as training branches to the horizontal, ringing and scoring, regulated deficit irrigation and application of plant growth regulators such as chlormequat (CCC, Cycocel) may enhance flowering and lead to a more favorable vegetative growth to fruiting relationship.

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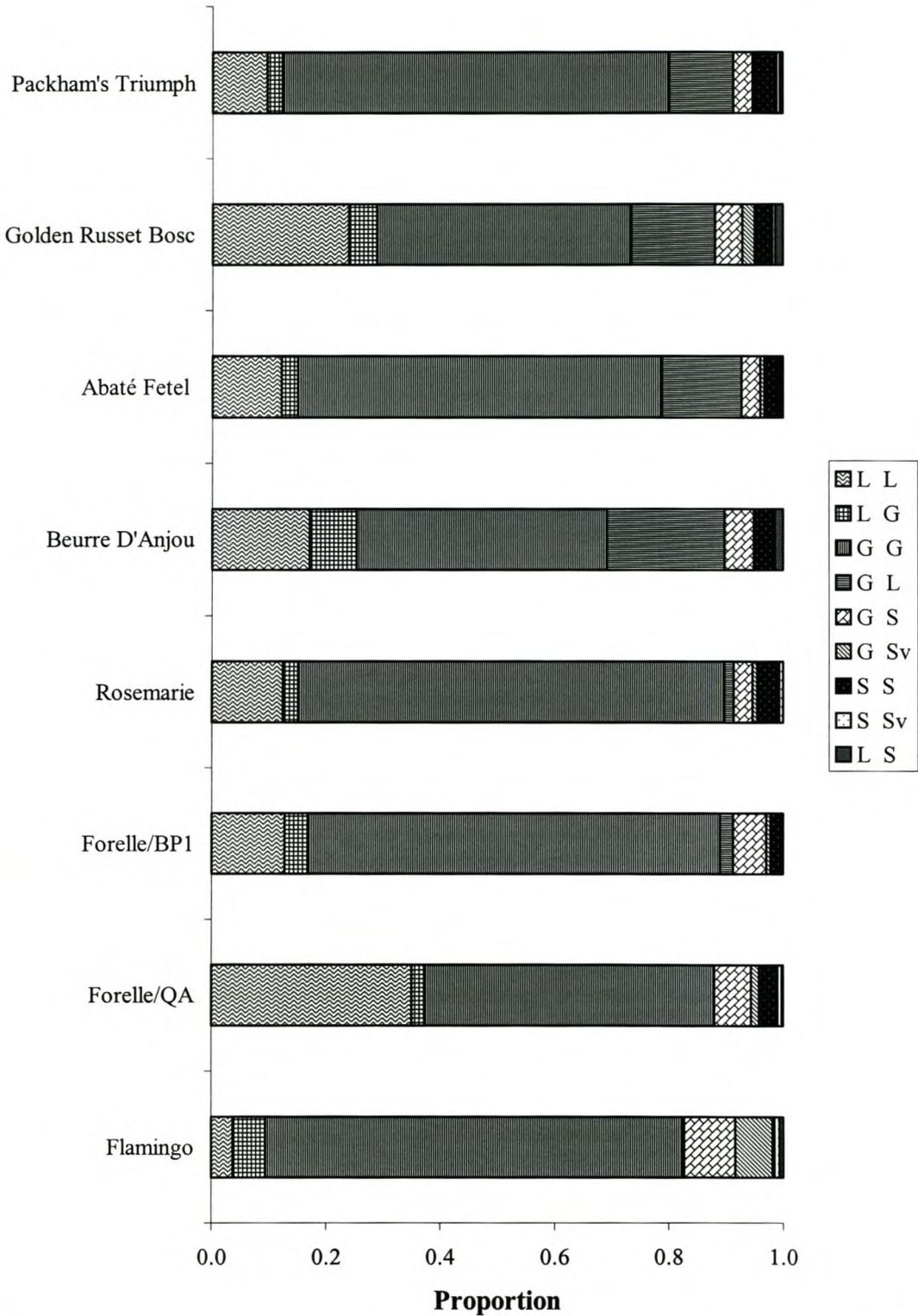


Fig. 1. Average proportions of phase changes observed for each cultivar. Phase changes observed were transitions between the latent phase (L), the growing phase (G), the ending state (S) and the phenomenon where a rudimentary bud subtending an aborted bud resumed vegetative growth of the axis at that position (S_v).

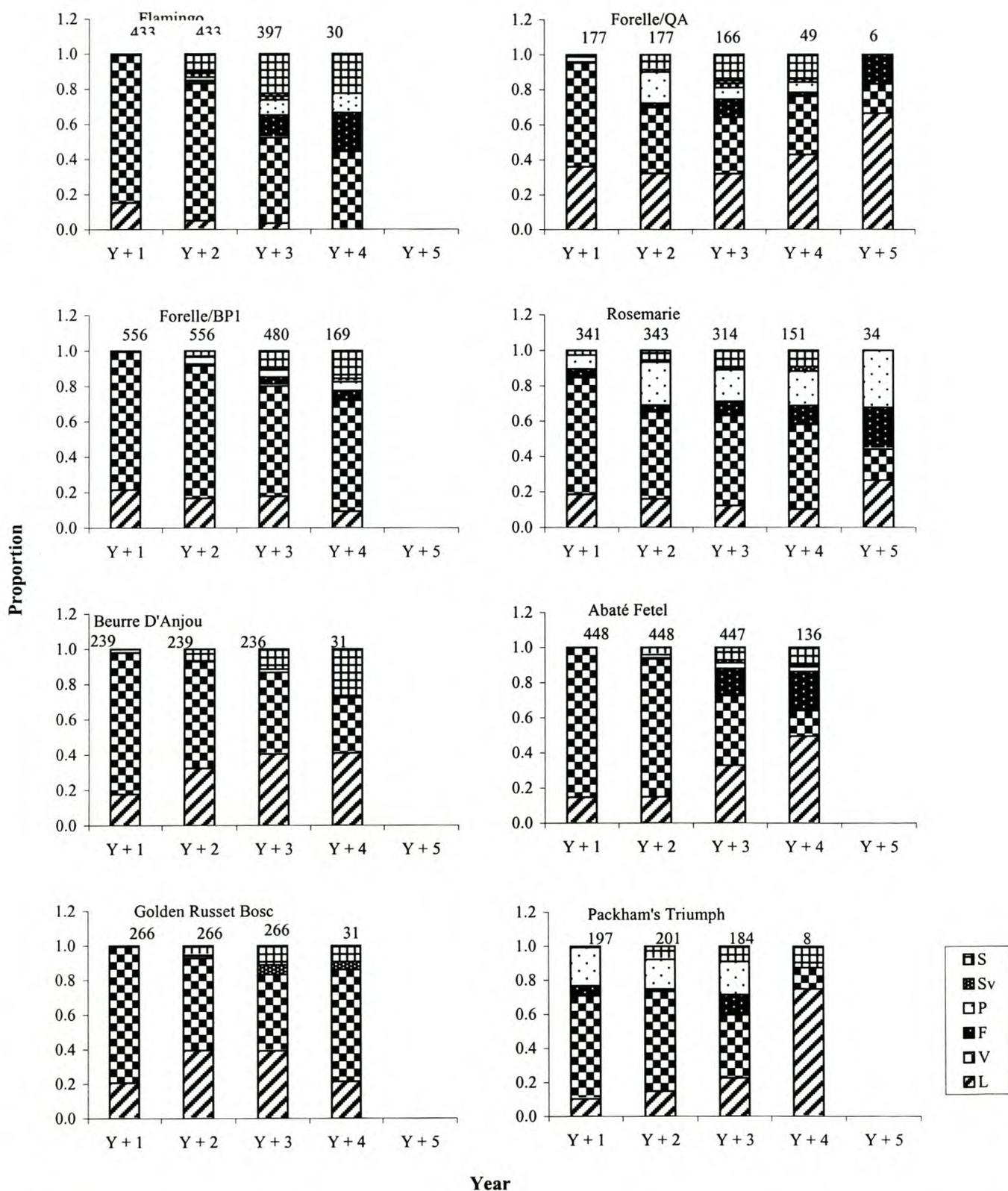


Fig. 2. Proportion of bud states per year for each cultivar. The bud states observed were latent buds (L), vegetative buds (V), flower buds without fruit (F), flower buds producing fruit (P), rudimentary buds subtending aborted buds, resuming vegetative growth of the axis at that positions (Sv) and aborted buds (S). The total number of sequences (n) in each year is indicated above the bars.

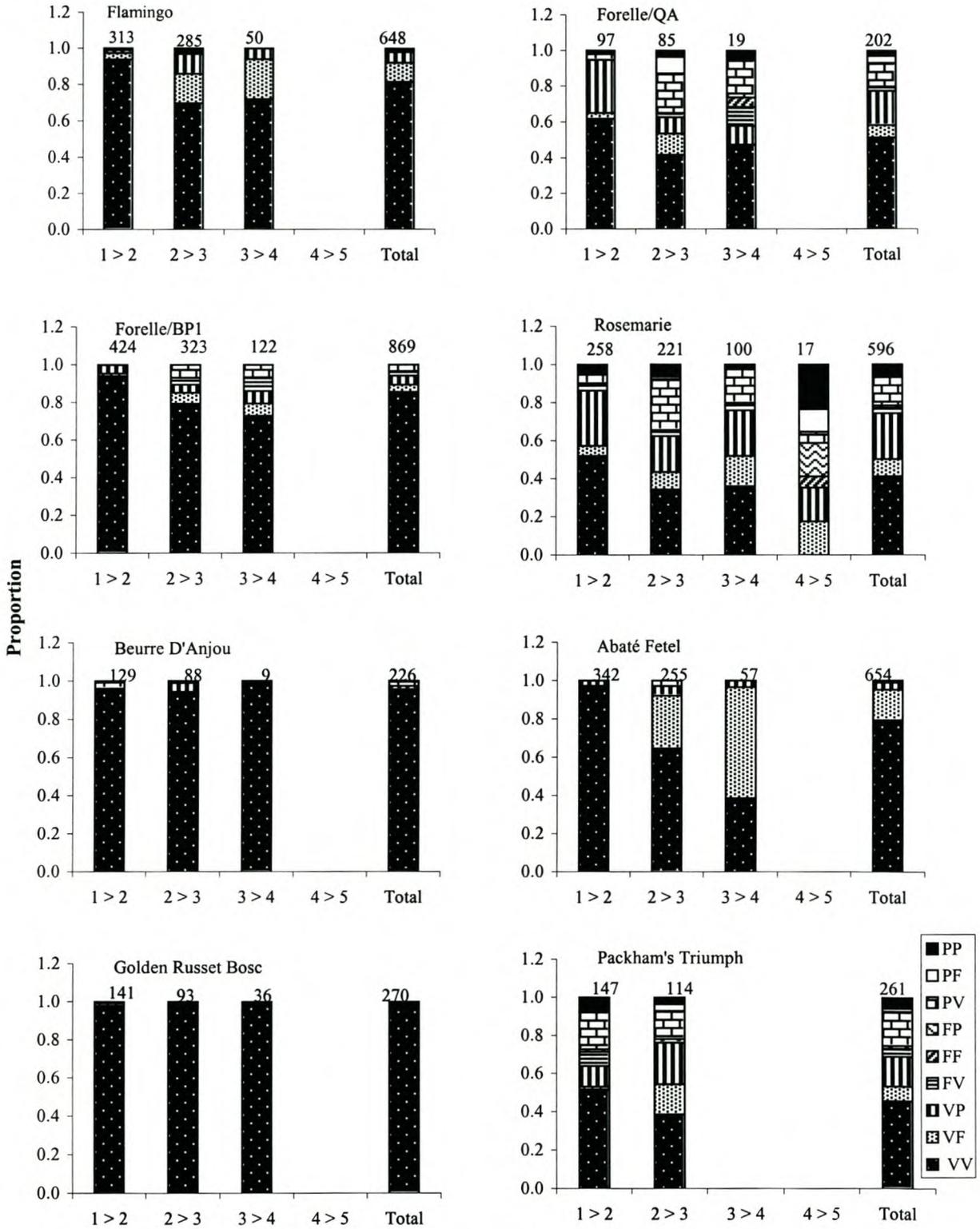


Fig. 3. Proportion of the different possible axillary bud year to year transitions observed in the growing phase for each cultivar. All combinations of vegetative buds (V), flower buds without fruit (F) and flower buds producing fruit (P) occurring in the growing phase are shown. The total number of sequences (n) for each age transition is indicated above the bars.

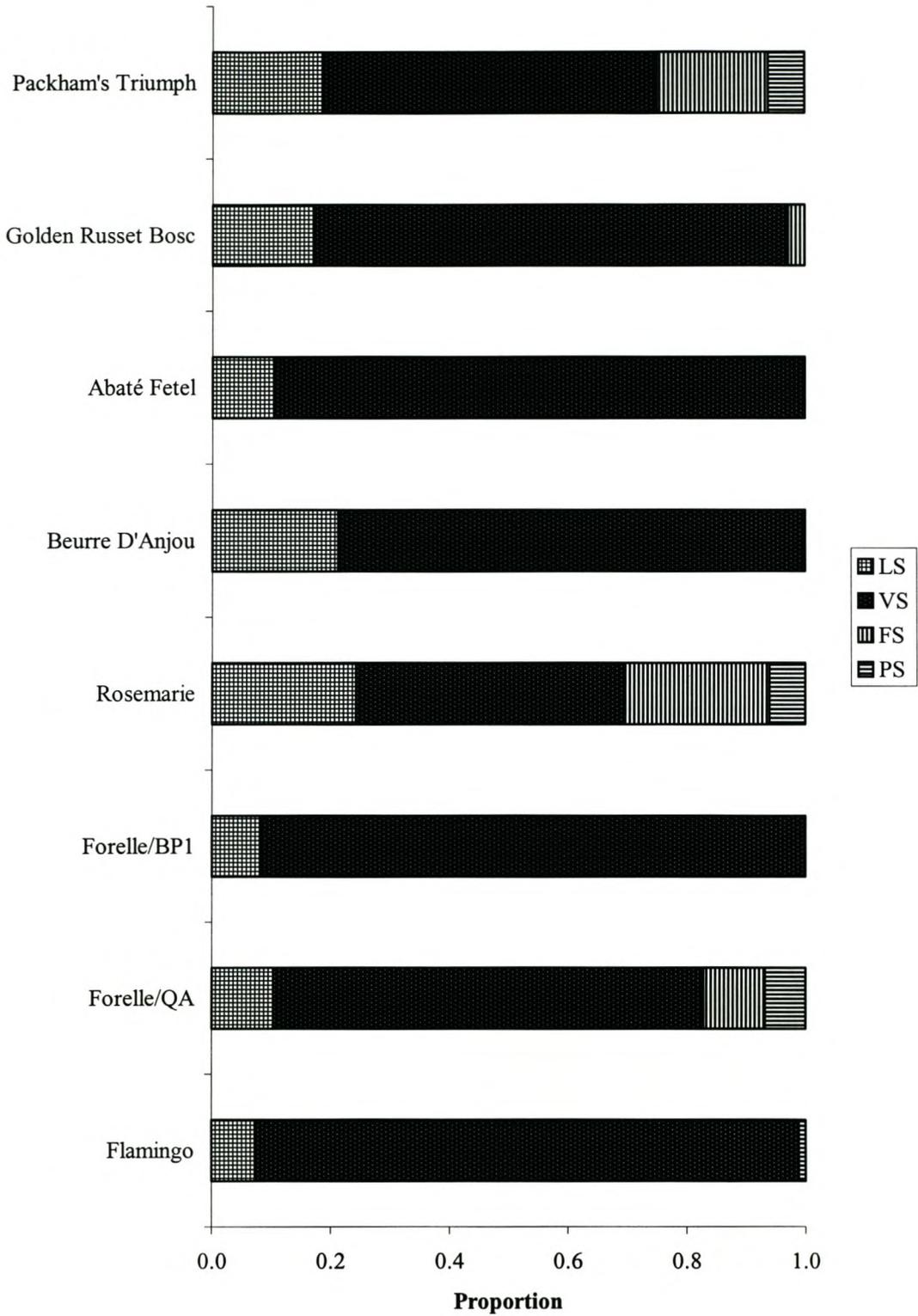


Fig. 4. Proportion of the different bud states preceding the ending state (S) for each cultivar. Possible bud types preceding S are latent buds (L), vegetative buds (V), flower buds without fruit (F) and flower buds producing fruit (P). The transitions LS, VS, FS and PS are shown.

PAPER 3: The Effect of Intensity and Method of Reproductive Bud Thinning in Winter on Fruit Set and Vegetative Development of 'Doyenne du Comice' Pear Branches.

Additional index words. *Pyrus communis* L., fruit set, bourse shoot, pruning

Abstract. Artificial extinction (removal) of reproductive buds was applied in Winter 1999 to the pear cultivar Doyenne du Comice. This pear cultivar bears on spurs and is prone to biennial bearing. The objective was to reduce the number of growing buds, thereby increasing the allocation of assimilates to remaining reproductive structures. Two reproductive bud thinning methods, i.e. removal of proximal reproductive buds and removal of reproductive buds situated distally on spurs (by means of cutting back), and three thinning intensities, i.e., 0%, 33% and 66% removal of reproductive buds were utilised. The experimental design was a two by three factorial design with 16 blocks, using individual branches, orientated at approximately 45⁰ to the vertical, as experimental units. The data showed that thinning of reproductive buds (decreasing the number of flowers) resulted in less competition during fruit set, thereby increasing the percentage fruit set in Spring 1999. There were also indications that reproductive buds on distal positions on spurs were larger and might be of better quality, expressed by the mean number of flowers, leaves (in the case of 66% thinning intensity) and bourse shoots per reproductive bud. Removal of 66% reproductive buds increased the number of vegetative shoots, but decreased the number of bourse shoots (due to reduced competition and sites, respectively). In Spring 2000 almost no treatment effect was observed. It is concluded that autonomy of fruiting structures was not enhanced, but that results warrant the repetition of this trial using whole trees as experimental units.

The pear cultivar Doyenne du Comice bears fruit primarily on spurs (Sansavini and Musacchi, 1994) and is prone to biennial bearing (Jonkers, 1979). Lauri *et al.* (1995) linked the bearing habit of apple cultivars to their tendency towards biennial bearing. They showed that cultivars with spurred bearing habits were more inclined towards biennial bearing than cultivars bearing terminally on long shoots and brindles. Cultivars like Granny Smith and Rome Beauty have the ability to balance vegetative and reproductive development by reducing the number of growing buds. This is accomplished primarily by an extinction mechanism (abortion of weak reproductive structures), and enhanced allocation to more autonomous reproductive structures (Lauri *et al.*, 1995). In Paper 2 it was shown that the extinction mechanism in pear is less pronounced than in apple. The objective of this trial was to determine whether spur autonomy could be enhanced by artificial extinction of buds, i.e., by means of bud thinning.

Materials and methods

This trial was conducted in the 'Koue Bokkeveld', the coldest production area in the Western Cape. The pear cultivar Doyenne du Comice on BP3 rootstock, planted in 1989 at a spacing of 4 x 1.5 m, in a North-South orientation, was used in the investigation.

In Winter 1999 sixteen branches orientated approximately 45° to the vertical were randomly tagged for each treatment combination. The experiment was a completely randomised design with two factors. Two methods of thinning consisted of the removal of proximal reproductive buds near the base of spurs and cutting back into spurs to remove the distal reproductive buds. Three intensities of bud thinning consisted of 0%, 33% and 66% removal of reproductive buds. All long, vegetative shoots were cut back to a stub of one centimetre. The total number of reproductive buds, number of reproductive buds removed, number of vegetative buds and number of shoots removed were recorded. The length and width (across two plains) of ten randomly sampled remaining reproductive buds were recorded.

In Spring 1999 the number of reproductive buds and the number of flowers and leaves in the reproductive structures were recorded. From this data the mean number of flowers and leaves per reproductive bud, as well as percentage fruit set was calculated. In Winter 2000 the number of shoots, number of bourse shoots, mean length of bourse shoots, number of extinct (aborted) and reawakened (S_V) buds were recorded. In Spring 2000 the number of reproductive buds, the number of flowers, fruit and leaves on reproductive structures, and the number of vegetative buds were recorded. From this data the mean number of flowers and leaves per reproductive bud, as well as percentage fruit set were calculated again.

Analyses of variance were performed using the GLM (General linear models) procedure of SAS® release 6.12 (SAS Institute, Inc., Cary, NC.).

Results and discussion

The spur bearing pear cultivar Doyenne du Comice is prone to biennial bearing (Jonkers, 1979). Lauri *et al.* (1995) linked the bearing habit of apple cultivars to their tendency towards biennial bearing. Regular bearing apple cultivars like Granny Smith have the ability to balance vegetative and reproductive development by reducing the number of growing buds. This is accomplished primarily by an extinction mechanism (abortion of weak reproductive structures), and enhanced allocation to more autonomous reproductive structures (Lauri *et al.*, 1995).

Artificial extinction by means of reproductive bud removal was applied in Winter 1999 with the aim to enhance allocation of assimilates to remaining reproductive structures and increase their autonomy. The removal of proximal reproductive buds and cutting back into spurs were done to determine whether distal reproductive buds were larger and possibly of better quality (T. Deckers, 1999, Pers.

comm.). It was shown in this trial that distal reproductive spur buds were indeed larger than the proximal buds and that their size increased with intensity of thinning (Table 1 and 2).

In Spring 1999 following the removal of 66% reproductive buds from proximal positions, the number of flowers and expanded leaves was greater in the remaining reproductive buds, indicating better quality of the distal buds (Table 3). A thinning intensity of 66% significantly increased the percentage fruit set in spring 1999 (Table 4), probably due to the reduced competition between flowers.

Removal of proximal reproductive buds resulted in less vegetative shoots and more bourse shoots (Table 5). The increased number of bourse shoots may be a further indication of better bud quality. Removal of 66% reproductive buds increased the number of vegetative shoots, but decreased the number of bourse shoots (Table 5). The first result could be due to reduced competition, resulting in more assimilates available for vegetative growth. The reduction in number of bourse shoots may be due to the reduction in possible sites. The removal of 66% reproductive buds from proximal positions resulted in an increased abortion of buds (extinction) as shown in Table 6. In Spring 2000 no treatment effect on flowering, fruit set and leaf formation was observed (Table 7), except for the increased number of vegetative buds in the case of 0% reproductive bud removal (Table 8).

There is an indication in this data that reducing the number of reproductive buds (thereby decreasing the number of flowers) reduced competition during fruit set, resulting in increased fruit set. There are also indications that reproductive buds situated in distal positions on spurs are of better quality in terms of more flowers and leaves per bud. However, autonomy of fruiting structures was not induced, possibly due to the fact that individual branches were used as experimental units and not whole trees. It is suggested that this trial be repeated on whole trees.

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Table 1: Description of bud types before and after reproductive bud thinning treatments applied to individual branches of the pear cultivar Doyenne du Comice during Winter 1999. Average width (mm) was calculated for ten randomly sampled remaining reproductive buds. Number of shoots removed is also shown.

Treatment	Tot. rep. buds	Rep. buds removed	% Rep. buds removed	Rep. buds remaining	Rep. bud width (mm)	No. of shoots removed	No. of veg. buds
Method							
Remove proximal	27 a	9 a	34 a	18 a	4.3 a	1 a	13 a
Cut back distal	28 a	9 a	33 a	18 a	4.2 b	1 a	12 a
Intensity							
0% removed	28 a	0 c	0 c	28 a	4.2 c	2 a	15 a
33% removed	25 a	8 b	34 b	16 b	4.3 b	1 a	11 b
66% removed	29 a	19 a	67 a	10 c	4.4 a	1 a	11 b
Pr > f							
Method	0.7631	0.5164	0.8277	0.9809	0.0264	0.7505	0.3066
Intensity	0.2834	0.0001	0.0001	0.0001	0.0001	0.3106	0.0255
Method x intensity	0.7619	0.8438	0.1886	0.7954	0.5826	0.8604	0.1985

Means separation within columns by LSD (5%)

Table 2: Mean bud length (mm) of ten remaining reproductive buds following reproductive bud thinning treatments applied to individual branches of the pear cultivar Doyenne du Comice in Winter 1999.

Treatment combination		
Method	Intensity	Bud length (mm)
Remove proximal	0% removed	10.3 c
Cut back distal	0% removed	10.4 c
Remove proximal	33% removed	10.9 b
Cut back distal	33% removed	10.3 c
Remove proximal	66% removed	11.7 a
Cut back distal	66% removed	10.8 b
Pr > f		
Method		0.0001
Intensity		0.0001
Method x intensity		0.0003

Means separation within columns by LSD (5%)

Table 3: Mean number of flowers and leaves per reproductive bud resulting from reproductive bud thinning treatments applied to individual branches of the pear cultivar Doyenne du Comice in Winter 1999. Data recorded in Spring 1999.

Treatment combination		No. of flowers/bud	No. of leaves/bud
Method	Intensity		
Remove proximal	0% removed	10.0 b	7.8 c
Cut back distal	0% removed	10.5 ab	8.2 b
Remove proximal	33% removed	10.9 a	8.8 b
Cut back distal	33% removed	10.3 ab	7.5 c
Remove proximal	66% removed	10.9 a	9.7 a
Cut back distal	66% removed	9.9 b	7.9 bc
Pr > f			
Method		0.1307	0.0001
Intensity		0.6182	0.0007
Method x intensity		0.0447	0.0001
Means separation within columns by LSD (5%)			

Table 4: Number of reproductive buds, flowers, fruit, leaves and percentage fruit set (per branch) resulting from reproductive bud thinning treatments applied to individual branches of the pear cultivar Doyenne du Comice in Winter 1999. Data recorded in Spring 1999.

Treatment	No. of rep. buds/branch	No. of flowers/branch	No. of fruit/branch	% Fruit set (Fruit/100 flowers)	No. of leaves/branch
Method					
Remove proximal	15 a	158 a	6 a	4.1 a	123 a
Cut back distal	15 a	152 a	5 a	3.8 a	114 a
Intensity					
0% removed	22 a	235 a	7 a	3.1 b	174 a
33% removed	13 b	141 b	6 a	4.0 ab	108 b
66% removed	8 c	89 c	5 a	4.7 a	73 c
Pr > f					
Method	0.8392	0.7306	0.2251	0.5000	0.4802
Intensity	0.0001	0.0001	0.2281	0.0346	0.0001
Method x intensity	0.7654	0.9563	0.8278	0.6023	0.9050

Means separation within columns by LSD (5%)

Table 5: Vegetative development following reproductive bud thinning treatments applied to individual branches of the pear cultivar Doyenne du Comice in Winter 1999. The total number of shoots and bourse shoots, mean length (mm) of bourse shoots and number of reawakened buds (S_V) are shown. Data recorded after the 1999/2000 growth season.

Treatment	No. of shoots/branch	No. of bourse shoots/branch	Mean bourse shoot length	No. of re-awakened buds/branch
Method				
Remove proximal	0.3 b	3.4 a	75 a	0.19 a
Cut back distal	0.7 a	1.8 b	59 a	0.17 a
Intensity				
0% removed	0.4 ab	3.9 a	62 a	0.31 a
33% removed	0.3 b	1.7 b	71 a	0.16 ab
66% removed	0.8 a	2.1 b	69 a	0.06 b
Pr > f				
Method	0.0150	0.0001	0.2814	0.8118
Intensity	0.0456	0.0005	0.8853	0.0664
Method x intensity	0.7825	0.5257	0.3005	0.2457

Means separation within columns by LSD (5%)

Table 6: Total number of aborted (S) buds observed following reproductive bud thinning treatments applied to individual branches of the pear cultivar Doyenne du Comice in Winter 1999. Data recorded after the 1999/2000 growth season.

Treatment combination		
Method	Intensity	No. of aborted buds/branch
Remove proximal	0% removed	0.8 c
Cut back distal	0% removed	0.8 c
Remove proximal	33% removed	1.4 bc
Cut back distal	33% removed	0.6 c
Remove proximal	66% removed	4.0 a
Cut back distal	66% removed	1.8 b
Pr > f		
Method		0.0001
Intensity		0.0001
Method x intensity		0.0033

Means separation within columns by LSD (5%)

Table 7: Number of flowers (per branch and per bud), fruit, fruit set percentage and number of leaves (per branch and per bud) resulting from reproductive bud thinning treatments applied to individual branches of the pear cultivar Doyenne du Comice in Winter 1999. Data recorded in Spring 2000.

Treatment	No. of flowers/branch	No. of flowers/bud	No. of fruit/branch	% Fruit set (fruit/100 flowers)	No. of leaves/branch	No. of leaves/bud
Method						
Remove proximal	144 a	9.9 a	10 a	5.9 a	102 a	7.4 a
Cut back distal	141 a	9.5 a	8 a	5.0 a	102 a	7.2 a
Intensity						
0% removed	165 a	9.5 a	9 a	4.7 a	113 a	6.9 a
33% removed	124 a	9.8 a	8 a	5.9 a	91 a	7.5 a
66% removed	137 a	9.9 a	10 a	5.7 a	102 a	7.6 a
Pr > f						
Method	0.8898	0.4065	0.2362	0.4264	0.9520	0.5290
Intensity	0.2725	0.7638	0.8711	0.6249	0.4487	0.1853
Method x intensity	0.2837	0.1272	0.1523	0.1065	0.2184	0.9145

Means separation within columns by LSD (5%)

Table 8: Number of vegetative buds per branch resulting from reproductive bud thinning treatments applied to individual branches of the pear cultivar Doyenne du Comice in Winter 1999. Data recorded in Spring 2000.

Treatment combination		
Method	Intensity	No. of vegetative buds/branch
Remove proximal	0% removed	38 a
Cut back distal	0% removed	25 b
Remove proximal	33% removed	23 b
Cut back distal	33% removed	21 b
Remove proximal	66% removed	21 b
Cut back distal	66% removed	23 b
Pr > f		
Method		0.0768
Intensity		0.0027
Method x intensity		0.0468
Means separation within columns by LSD (5%)		

6. CONCLUSION

Studies were conducted in order to group apple cultivars into four ideotypes according to the growth and bearing habit of the cultivar (Lespinasse, 1992) and to link the specific ideotype to the phenomenon of biennial bearing (Lauri *et al.*, 1995). Lauri *et al.* (1995) showed that cultivars belonging to Type 1 and 2 (for example 'McIntosh Wijkik' and 'Oregon Spur Delicious', respectively) were more prone to biennial bearing than those belonging to Type 4 ('Granny Smith'). Regular bearing in Type 4 cultivars corresponds to their ability to balance vegetative and reproductive development by reducing the number of growing buds. This is accomplished in apple primarily by an extinction mechanism (abortion of weak reproductive structures), and enhanced allocation to more autonomous reproductive structures (Lauri *et al.*, 1995).

This information was applied for instance in pruning 'Granny Smith' trees, where light pruning is done and crowding of crowned brindles are avoided (Lespinasse and Delort, 1993). The Solen training system was specially developed for this type of management (Lespinasse and Delort, 1993). This information was also applied in the apple breeding program at the INRA Research Centre (France). They selected cultivars that bare fruit on crowned brindles and have regular fruiting patterns (Lespinasse and Delort, 1993).

To our knowledge, the only attempt to classify pear cultivars was made by Sansavini and Musacchi (1994). This classification was based on field observations. Branching and bearing habits of pear cultivars are influenced by factors such as branch orientation (training), rootstock and climatic factors such as amount of winter chilling received (Papers 1 and 2). The classification of Sansavini and Musacchi (1994) will, therefore, not necessarily be applicable under South African conditions. Furthermore, certain cultivars grown in South Africa were not included in the classification of Sansavini and Musacchi (1994).

The objective of this study was, therefore, to quantify pear branching and bearing habits under South African conditions. The first part of the study entailed the quantification of pear branching habits, which was important because the branching habit determines the characteristics of the bearing structures, i.e., spur, brindle or long shoot. Two-year-old branches of *Pyrus communis* L. were classified into groups according to the proleptic (from dormant buds) branching habit, indirectly quantifying the degree of apical control. The cultivars were grouped into four groups from Group 1 ('Flamingo') which resembles a spurred growth habit with strong apical control, to Group 4 ('Packham's Triumph' and 'Golden Russet Bosc') which resembles a spreading growth habit and weak apical control. Groups 2 and 3 are intermediate. The hereditary branching habit of 'Abaté Fetel', 'Forelle', and 'Rosemarie', as determined by the degree of apical control, is strongly expressed and not influenced by rootstock or gravimorphic effects. In 'Beurre D'Anjou', 'Flamingo', 'Golden Russet Bosc', and 'Packham's Triumph', the upright branching habit was significantly altered by gravimorphic effects, mainly due to the reduction in vegetative growth and branching.

The bearing habit of the pear cultivars was quantified next, using the method of Lauri *et al.* (1995). It was shown that between 50% ('Forelle/QA') and 75% ('Rosemarie') of buds remained in the growing phase (comprising of V, F or A buds) during the years of monitoring. This coincided with relatively low proportions of buds remaining in the latent phase (L) and moving to the ending state (S). A relatively large proportion of buds went from the growing phase back to the latent phase (up to 20% in the case of 'Beurre D'Anjou'), probably due to inadequate winter chilling. Considering the proportion of bud states within each year for a given cultivar, it was shown that the predominant bud state in the growing stage was V. This was again apparent considering the year to year transitions within the growing stage (mostly VV transitions). Although flower initiation was low for all cultivars throughout the trial period, 'Flamingo' and 'Abaté Fetel' went into the reproductive phase (F or P) in year Y+3. 'Packham's Triumph' and 'Rosemarie' displayed a relatively high proportion of F and P buds in year Y+1, corresponding to the ability of these cultivars to bear fruit on one-year-old shoots. The latter two cultivars also displayed the bourse-over-bourse phenomenon (PP), producing flowers and fruit terminally on bourse shoots. The extinction mechanism (abortion of mainly F buds to form an S in the case of apple) occurred to some extent in the cultivars Packham's Triumph and Rosemarie. In the rest of the cultivars, V mostly preceded S, possibly due to damage from DNOC-winter oil applied to break rest. The positive effect of the dwarfing Quince A rootstock on precocity of 'Forelle' was also shown.

There was succeeded in developing an objective method of quantifying branching habits of two-year-old pear branches into groups according to the proleptic (from dormant buds) branching habit, indirectly quantifying the degree of apical control. Bearing habits of pear cultivars were then quantified according to the method of Lauri *et al.* (1995). Knowledge obtained from above studies led to a further trial. Artificial extinction of reproductive buds was applied in Winter 1999 to individual branches of the pear cultivar 'Doyenne du Comice'. This pear cultivar bears on spurs and is prone to biennial bearing. The objective was to reduce the number of growing buds, thereby increasing the allocation of assimilates to remaining reproductive structures. Autonomy of reproductive structures was, however, not enhanced. Results warrant the replication of this trial, using whole trees as experimental units.

Further studies are needed to apply the results obtained in this study in developing management strategies for individual pear cultivars or groups. The results might also be of value in pear breeding programs, similar to what is done in the apple breeding program at INRA Research Centre (France).

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