

Seasonal effects of light exposure, temperature, trunk growth and plant carbohydrate status on the initiation and growth of epicormic shoots in *Prunus persica*

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SUMMARY

Understanding the physiology of epicormic sprout initiation and growth is economically important for arboricultural management. In this experiment, factors influencing the initiation and growth of epicormic sprouts, including light exposure, temperature, trunk growth, date of green pruning, and tissue concentrations of non-structural carbohydrate, were investigated in *Prunus persica*. Field trials were conducted in Rome, Italy, during the 2004 growing season, using transparent, silver or black cage treatments to manipulate the light and temperature environment experienced by topped trees. Each month, non-structural carbohydrate (NSC) concentrations were measured in bark, wood and root tissues, and the number of epicormic sprouts produced per tree and the dry weight (DW) per sprout was recorded for a fresh group of topped trees. Date of pruning, light exposure, node number present in the stump, estimated bark NSC, and estimated xylem NSC were significantly related to the number of sprouts formed. Cage temperature, trunk volume, and trunk diameter growth did not significantly affect the number of sprouts formed. Date of pruning, light exposure, and estimated bark NSC were significantly related to the DW per sprout. Temperature, trunk volume, trunk diameter growth, and estimated wood NSC did not significantly affect the DW per sprout. Date of green pruning appeared to be the most important factor to explain sprouting behaviour, leading to the conclusion that correct timing of Summer pruning may reduce subsequent epicormic sprouting.

In most angiosperm and a few gymnosperm tree species, dormant axillary buds may become embedded in the stem as the bark tissue forms around them. These buds of exogenous origin can remain latent inside the trunk for many years. They elongate only enough to keep pace with the radial growth of the cambium, maintaining their vascular connection. This type of bud has been known variously as dormant (Fernow, 1911; Chandler, 1925), preventitious (Büsgen and Münch, 1929), epicormic or latent (Stone and Stone, 1943), trace (Aaron, 1946), or suppressed (Zimmermann and Brown, 1974). The term 'epicormic' will be used throughout this paper.

The size of the epicormic bud population fluctuates throughout the life of a tree. The population increases by 'branching' as meristematic tissue in the scale axils of latent buds develops into secondary latent buds that may form clusters of buds along the stem (Hahne, 1926; Fontaine *et al.*, 2001). Another way in which the epicormic bud bank grows is through the inclusion of collar buds of lateral shoots, as the shoot bases are engulfed by radial growth of the parent stem (MacDaniels, 1952; Kormanik and Brown, 1969). In some species, the number of epicormic buds may increase through the initiation of adventitious meristems. The number of viable epicormic buds in the bud bank can also decrease, due to bud mortality or release as buds grow into epicormic shoots (Fontaine *et al.*, 2001). Although older trees have more buds per trunk area

than do younger trees, due to forking and inclusion (Kormanik and Brown, 1969), it has been widely observed that buds in older trees tend to sprout less. Also, within a single tree, younger epicormic buds sprout more readily than older ones (Wilson and Kelty, 1993). This may be due to the mechanical barrier of thicker older bark, or to weakened vascular connections (Büsgen and Münch, 1929).

Many observations have been made regarding the distinctive physical characteristics of released epicormic shoots compared to non-epicormic growth. Epicormic shoots, also known as sprouts (Chandler, 1925), sucker shoots (MacDaniels, 1952), agony branches (Büsgen and Münch, 1929), coppice shoots, and water-sprouts (Fernow, 1911), typically have one of two forms. In intensively pruned plantings, such as orchards, epicormic sprouts may form long vertical shoots in the centre of the canopy, arising from the trunk and main scaffolds. These dominant vigorous sprouts are characterised by a thick stem diameter, large leaves, long internodes, a high rate of sylleptic release of lateral axial buds, and fewer flower buds per length relative to non-epicormic shoots (Büsgen and Münch, 1929; Yamashita, 1971). In unpruned plantings, such as unmanaged forests, however, epicormic sprouts may be short rosette shoots with one or a few leaves that barely protrude from the bark (Kormanik and Brown, 1969). Although the sprouts typically arise in a disordered pattern, seemingly outside normal phyllotaxy, in some species they are strictly preventitious (MacDaniels, 1952; Roussel, 1978; Fontaine *et al.*, 1998).

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The ecological role of epicormic sprouting is several-fold. Epicormic sprouting allows canopy rejuvenation in suppressed trees (Nicolini *et al.*, 2001) and maintenance of crown productivity in older trees (Remphrey and Davidson, 1992; Ishii *et al.*, 2002). The epicormic budbank allows rapid regrowth in response to canopy damage due to herbivory, coppicing (Baker, 1934), storm damage (Quine, 2004), insect damage (Batzer, 1973), fire (Johnson, 1977), or pruning (Kerr and Harmer, 2001). The presence of latent buds throughout the stem system permits plasticity in the face of environmental change such as increased light exposure (Kramer and Kozlowski, 1979) or raised water-tables (Evans, 1987).

It is generally agreed that hormones mediate the epicormic sprouting response (Wignall *et al.*, 1985), and that trees vary greatly in their predisposition to sprouting among species and, to a lesser extent, among individuals within a species (Blum, 1963; Ward, 1966; Evans, 1987; Remphrey and Davidson, 1992). However, the environmental and physiological cues that stimulate buds in the bud bank to emerge from latency and to produce epicormic shoots have long been a subject of conjecture for foresters and orchardists alike. The frequency and size of sprouts are said to be affected by light exposure (Trimble and Seegrist, 1973; Wignall and Browning, 1988a), temperature (Baker, 1934), severity of Winter (Mauget, 1984), orientation of the trunk (Della Bianca, 1972), water availability (Jemison and Schumacher, 1948), fertiliser (Auchmoody, 1972), mycorrhizal inoculation (Fournier *et al.*, 2003), root carbohydrate reserves (Baker, 1934), root damage (Evans, 1987), tree age (Fontaine *et al.*, 2001), trunk diameter (O'Hara and Valappil, 2000), annual growth increment (Nicolini *et al.*, 2003), girdling (Wignall *et al.*, 1987), pruning or other canopy damage (Berntsen, 1961), and by season (Wignall and Browning, 1988b).

Much of the information in the literature regarding epicormic sprouting is contradictory. Della Bianca (1972) observed more sprouts on the southern-exposed side of the trunks of poplar, but Ward (1966) noted no difference in the number of sprouts on different faces of the trunks of oak. Evans (1982) noted that trees with a large increase in diameter at breast height generally produced more sprouts, while other workers (Bachelard, 1969; O'Hara and Valappil, 2000; Nicolini *et al.*, 2003) noted the occurrence of sprouts predominantly in trees with small annual growth increments. Wignall and Browning (1988b) found that the timing of partial girdling during the season affected the amount of epicormic re-sprouting, but Kerr and Harmer (2001) found that varying the time of pruning did not affect epicormic shoot control. These issues have yet to be clarified.

In managed ecosystems, with tree crops, the presence of epicormic sprouts is generally undesirable because they cause economic loss. In lumber trees, the increased presence of knots and blemishes due to epicormic sprouting reduces the quality and value of the harvested wood. In fruit trees, vigorous epicormic sprouting can congest the canopy, blocking light and preventing fruit from gaining colour (Tymoszyk *et al.*, 1980; Day *et al.*, 1989; Myers, 1993) and contributing little carbohydrate to fruit growth (Tymoszyk, 1984). The only commercial uses for epicormic sprouts are as propagation material

for certain species due to their superior rooting ability (Hackett, 1985; Harmer, 1988; Chalupa, 2002), and as coppice shoots in some forestry management systems (Smith *et al.*, 1997). Consequently, prevention, control and removal of epicormic sprouts are priorities in the management of many cultivated tree crops.

Epicormic sprout removal on forest trees has traditionally been accomplished in Britain with pruning chisels (Evans, 1982). Currently, the most common approach to managing epicormic sprouting in vigorous fruit trees, such as peaches and walnuts, is removal by heavy semi-annual pruning. Preventive treatments that have been tested in various species include herbicides (Holmes, 1962; Patch *et al.*, 1986), plastic wrappings (Roussel, 1978; Evans, 1987), partial girdling (Wignall *et al.*, 1987), and mechanical disbudding (Chandler, 1965; Smith *et al.*, 1997; Smith and Erdogan, 2000). However, none of these treatments are practical and effective from environmental, labour and/or cost perspectives. A better alternative, proposed by many, is to select for genotypes with less tendency to produce epicormic sprouts (Kormanik and Brown, 1969; Wignall *et al.*, 1985; Evans, 1987). This may lessen the severity of the epicormic sprouting problem in the long-term, but studying the physiology of epicormic sprouting remains important to improve management strategies for extant orchards and forests.

The objective of this research was to investigate some of the contradictions in the literature regarding epicormic sprouting in *P. persica*, an orchard species capable of vigorous epicormic sprouting. Anatomical studies of peach-wood confirmed the apparently preventitious origin of most or all epicormic sprouts in this species, and preliminary field studies indicated that *P. persica* is suitable for sprouting research (unpublished data). The specific goals of this research were to examine the effects of light exposure, temperature, orientation, trunk diameter growth, date of green pruning, and non-structural carbohydrate content on epicormic shoot emergence and growth.

MATERIALS AND METHODS

Plant material and field design

In March 2004, 185 2 year-old peach trees ('Cardinal' grafted on rootstock of 'Montclar' peach seedlings) were planted in four rows in the fields of the Istituto Sperimentale per la Frutticoltura, Rome, Italy. Trees were planted at 1 m × 3 m spacing and drip irrigation was installed. Trees were watered each week throughout the growing season. Initial measurements of trunk diameter were made 50 cm above the graft union.

Every 4 weeks throughout the 2004 growing season, a fresh group of trees were topped to 50 cm above the graft union. All pre-existing sprouts below 50 cm height were removed, and their number recorded, so that a bare-topped trunk remained. The number of nodes present in the remaining 50 cm of trunk was recorded to estimate the epicormic bud bank present. Trunk diameter was measured at 5 cm and at 50 cm above the graft union and the current-year increases in trunk cross-sectional area (TCSA) and trunk volume were calculated. Cylindrical wire cages (120 cm high × 50 cm diameter) were then placed over the individual stumps

of freshly-topped trees, covered with either transparent, black opaque, or silver reflective plastic to alter the light and temperature environment inside the cage. Control trees were not caged. Five trees were randomly assigned to each treatment (transparent cage, black cage, silver cage, non-caged control) on each treatment date (19 March, 15 April, 13 May, 9 June, 7 July, 5 August, 2 September).

Transparent plastic was intended to create a high temperature with high light environment, black plastic to create high temperature with low light environment, and reflective silver foil/plastic to create a low temperature with low light environment, while the plastic-free control treatment represented low temperature with high light. Cage temperatures were recorded periodically with minimum-maximum thermometers placed along the North side of the bark of one tree in each treatment, and meteorological data were obtained from a nearby weather station from 8 April to 30 September 2004. Cages were vented top and bottom with light-excluding vents to encourage airflow and minimise plant damage due to overheating. Light penetration (photon flux density, in $\mu\text{moles m}^{-2} \text{s}^{-1}$) through the cage materials was measured in four of the five cages of each type at solar noon on a clear day in July with a quantum sensor (LI-190; LICOR Inc., Lincoln, NE, USA).

After the 4-week treatment period, the cages were removed. Sprouts originating from the North and South sides of the trunk of each tree were counted separately, removed, dried at 60°C to constant weight and weighed. Sprouts emerging below the graft union were counted, but were not dried.

Carbohydrate content

Since carbohydrate sampling is destructive, carbohydrate contents were estimated on each sampling date using five additional trees. Two 1 cm-wide cross-sectional disks were collected from the trunks at ~ 25 cm above the graft union. The bark was carefully separated from the wood at the cambium. Root samples were collected from a depth of 10–30 cm, within 0.5 m of the trunk. Four 10 cm lengths of young roots, 0.5–1.0 cm in diameter, were taken per tree. Bark, xylem and root samples were dried at 60°C to constant weight then weighed and ground to pass through a No. 40 mesh sieve.

Samples were analysed at the analytical laboratory of the Department of Agriculture and Natural Resources, University of California, Davis by standard methods (Smith, 1969). Starch was hydrolysed with

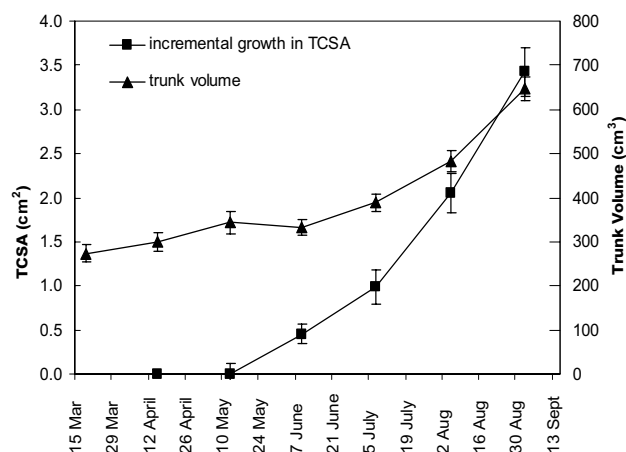


FIG. 1

Tree growth over the season. Increments in trunk cross-sectional area (TCSA) and trunk volume. Bars represent \pm SE.

amyloglucosidase, and high performance liquid chromatography (HPLC) was performed for glucose, sucrose and fructose using a fast carbohydrate column (HPAP, Bio-Rad Laboratories, Hercules, CA, USA). Concentrations of glucose, sucrose and fructose were summed to give non-structural carbohydrate (NSC) levels, and should reflect a large percentage of the total NSC. NSC data from sampled trees were used to calculate a 'predicted carbohydrate content' for bark and xylem of treated trees at the time of treatment, based on treatment date and calculated trunk volume.

Statistical analysis

Analysis of variance was performed separately for numbers of sprouts and sprout DW, with appropriate weighting and winsorising of the data as necessary to fit the assumptions of the ANOVA model (Sachs, 1984). Statistical Analysis Systems software version 9.1 (SAS Institute Inc., Cary, NC, USA) was used for all statistical analyses.

RESULTS

Trunks grew steadily, adding an average of 3 cm² to TCSAs from May to September (Figure 1). Trees sprouted abundantly after topping, with 97% of trees producing at least one epicormic sprout within 4 weeks of pruning and caging treatments. The number of sprouts per tree ranged from zero to 23. The total DW of sprouts collected per tree ranged from zero to 10.0 g.

TABLE I
Analysis of variance of factors affecting the number of epicormic sprouts and dry weight per sprout

Source	df	Number of sprouts		Dry weight per sprout	
		Mean Square	F value	Mean Square	F value
Light	1	226.85	11.15**	52.71	5.98*
Temperature	1	33.08	1.63	0.99	0.11
Light \times temperature	1	15.78	0.78	10.13	1.15
Date	6	80.64	3.96**	45.67	5.18**
Light \times date	6	6.03	0.30	9.63	1.09
Temperature \times date	6	4.68	0.23	6.15	0.7
Trunk volume	1	27.06	1.33	2.81	0.32
TCSA increase	1	31.11	1.53	1.64	0.19
Node number	1	157.63	7.75**	3.84	0.44
Error (number of sprouts)	94	20.34	—	—	—
Error (dry weight of sprouts)	92	—	—	8.82	—

*, and **: *P* values at 0.05 and 0.01 levels of significance, respectively.

Excluding data collected from the transparent treatment in June, July, August and September.

Factors affecting sprouting

Because there was no significant difference between the number of sprouts initiated, or the DW per sprout on the North and South sides of each tree, the 'side' variable was removed from the model, and the North and South data were summed to analyse other effects on numbers of sprouts and DW per sprout (Table I). Light exposure increased both the number of sprouts and the DW per sprout ($P = 0.001$; $P = 0.016$). Cage temperature did not affect either the number of sprouts or the DW per sprout. The date of topping significantly affected both the number of sprouts and the DW per sprout ($P = 0.001$; $P = 0.0001$). None of the two-way interactions between light, and temperature, and date of topping were significant. Neither trunk volume nor increase in TCSA significantly affected the number of sprouts or the DW per sprout. The number of nodes present in 50 cm of trunk was significantly related to the number of sprouts initiated per tree ($P = 0.007$), but was not significantly related to the DW per sprout.

Control

Mean daily ambient temperatures during each of the 4-week growing periods increased from March through July, levelled-off in August, and declined slightly in September (Figure 2A). The number of sprouts produced decreased from March through May, then returned to March levels in June, with a peak in August

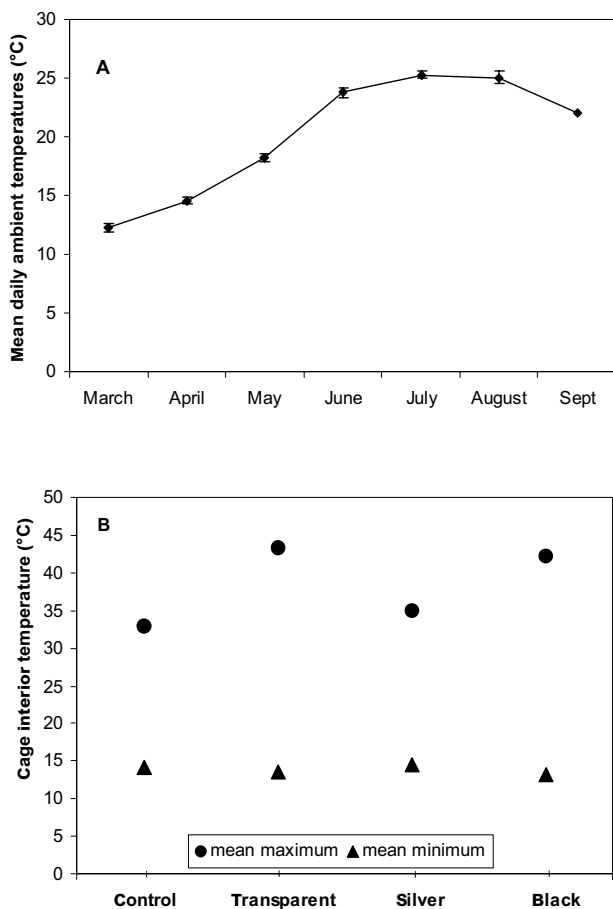


FIG. 2

Four-week average of mean daily ambient air temperatures [maximum + minimum)/2] in Rome from weather station (Panel A). Mean maximum and minimum temperatures inside the three types of treatment cage and uncaged controls (Panel B).

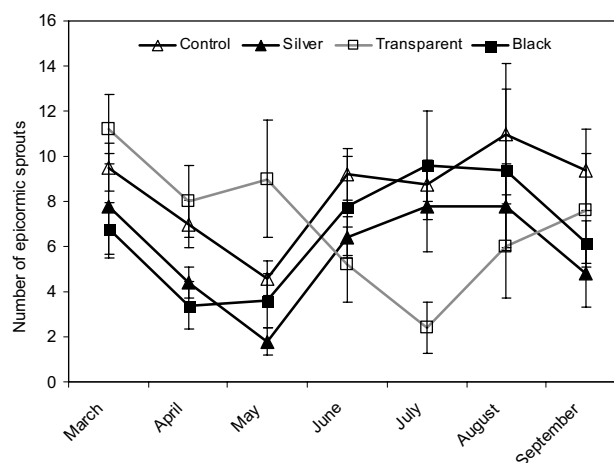


FIG. 3

Mean number of epicormic sprouts initiated per tree over the 4-week period following severe pruning in uncaged control, and silver, transparent or black caged treatments (5-tree means). Bars represent \pm SE.

(Figure 3A). Dry weight per sprout was low in March, April and May, increasing dramatically in June and in August, before decreasing in September (Figure 4A).

Transparent

The average light penetration through the clear plastic cages was approx. 50% of the ambient light experienced by the uncovered control treatment ($> 800 \mu\text{moles m}^{-2} \text{s}^{-1}$ c.f. an ambient $1,600 \mu\text{moles m}^{-2} \text{s}^{-1}$ on the measurement date). The mean maximum cage temperature was about 10.5°C higher in the transparent treatment than in the control treatment (Figure 2B). There was evidence that trunks overheated and bark was damaged on some very hot days in June, July, and August, so data points from these treatment periods were excluded from the ANOVA. In the first three treatment periods, sprouting behaviour in the transparent treatment was similar to the control treatment (Figure 3; Figure 4).

Silver

The foil-and-plastic construction of the silver cages was an effective light barrier. The average light penetration through the silver cages was $< 10 \mu\text{moles m}^{-2} \text{s}^{-1}$. The mean maximum cage temperature was about

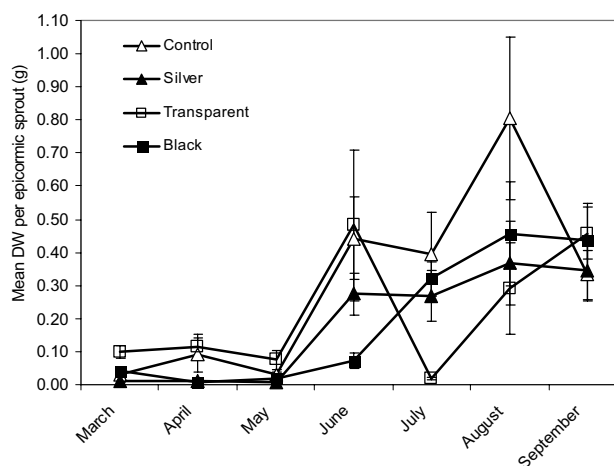


FIG. 4

Mean dry weight (g) per epicormic sprout in uncaged control, and silver, transparent or black caged treatments at each 4-week sampling period. Bars represent \pm SE.

2.0°C higher in the silver treatment than in the control treatment (Figure 2B). The mean number of sprouts per tree followed a similar pattern to the control treatment (Figure 3B). The mean DW per sprout was more than ten-times higher in the last four treatment periods than in the first three (Figure 4B).

Black

The heavy black plastic used in the construction of the black cages was an effective light barrier. The average light penetration through the black cages was $< 10 \mu\text{moles m}^{-2} \text{s}^{-1}$. The mean maximum cage temperature was about 9.2°C higher in the black treatment than in the control treatment (Figure 2B). The mean number of sprouts in the black cages followed the same general pattern as the control and silver cages (Figure 3C). As in the silver and control treatments, the DW per sprout was relatively higher in Summer than in Spring (Figure 4C).

Non-structural carbohydrate

In bark, xylem and root tissue, glucose was by far the most abundant of the three sugars quantified, partly because the starch fraction was hydrolysed and included in the glucose fraction. The NSC content of bark tissue was constant from March to May, increased from May to July, and levelled-off from July to September (Figure 5A). The NSC of xylem tissue decreased from March through May, increased from May through July, and stayed level from July through September (Figure 5B). The NSC of root tissue decreased from March through June, and fluctuated only slightly from June through September (Figure 5C). Sprout number per tree was significantly related to the estimated bark and wood NSC concentrations of individual trees ($P = 0.026$; $P = 0.009$, respectively). Dry weight per sprout was significantly related to bark NSC ($P < 0.0001$), but was not significantly related to wood NSC.

DISCUSSION

Peach trees responded vigorously to topping and existing sprout removal by the production of epicormic shoots. The date of green pruning was the most important factor affecting both sprout initiation and sprout growth. The seasonal pattern of sprouting noted in this experiment contrasted with previous literature. Harmer (1988) observed that sprouting during the 2 months following partial girdling, took place in oak trees cut in March, April, May and June (peaking in April), but no sprouts formed after cutting in July through January. Wignall *et al.* (1987), with data similar to Harmer (1988), concluded that “epicormic buds enter dormancy early in the season.” In our experiment with peach, early season sprouting was followed by a decline in late Spring as noted by Wignall *et al.* (1987) and by Harmer (1988), but there was an additional sprouting period in Summer prior to a decrease in the Autumn. The difference may have been that epicormic buds on vigorous and well-irrigated young peaches in Rome entered dormancy months later (October) than epicormic buds on the mature forest trees used in previous studies in Britain.

This experiment studied only the immediate sprouting

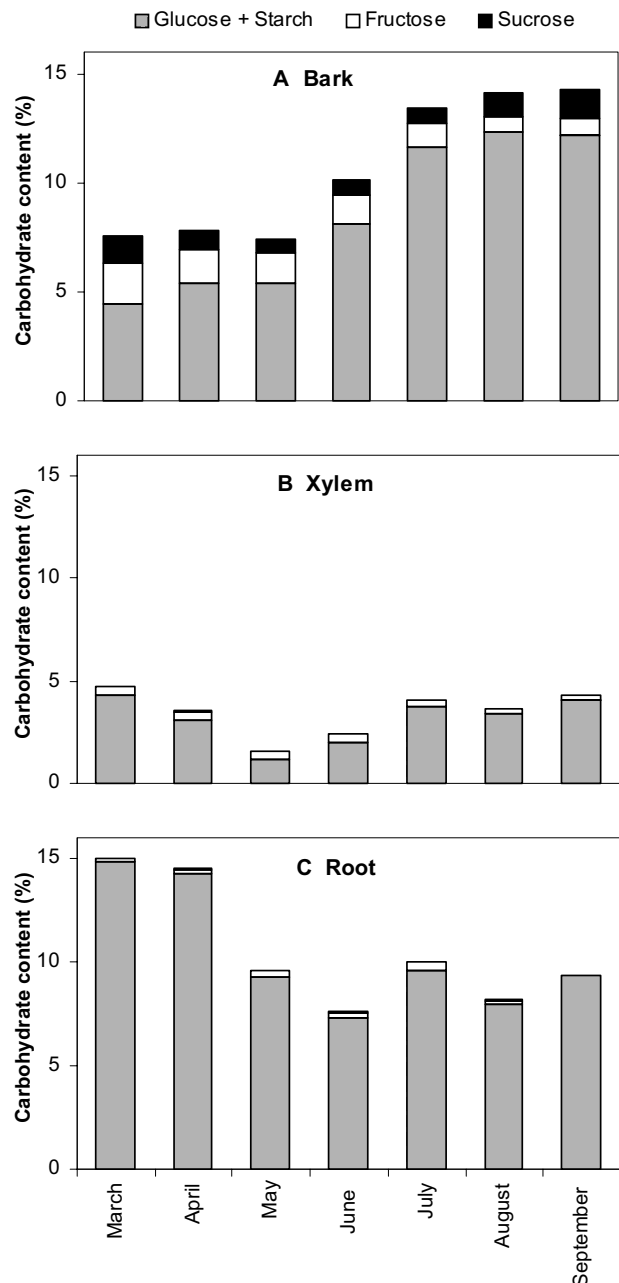


FIG. 5 Non-structural carbohydrate (glucose, fructose and sucrose) contents (%) of bark (Panel A), xylem (Panel B), and root (Panel C) tissues throughout the growing season.

response to date of green pruning, but the longer-term effects of dormant and green pruning are also of interest for foresters and orchardists. Baker (1934) commented that most epicormic sprouts are produced from trees in the Spring following topping during dormancy. Data on oak trees indicate that green pruning during the period when there was the least immediate re-sprouting (Summer, in the case of oak in Britain) also decreased re-sprouting in the following season (Wignall *et al.*, 1985). No studies have looked at the long-term effect of timing of dormant or green pruning specifically on epicormic re-sprouting in orchard crops, and this may be an interesting avenue for future research.

In this study with peach, there was a significant positive relationship between the amount of light exposure and sprout initiation. Wignall *et al.* (1985) first

hypothesised that light exposure is a “permissive” factor in epicormic bud emergence; “both exposure to light and the specific thinning stimulus being necessary” for sprouting, but later concluded that light did not play a major role in epicormic bud emergence (Wignall and Browning, 1988a). In the present peach experiments, light exposure significantly affected the emergence of epicormic buds (Table I), although light was not necessary for sprouts to emerge. Topped trunks totally in the dark produced about 75% of the number of sprouts produced by trunks with full light exposure (Figure 4). The significant positive effect of bark temperature on the emergence of epicormic buds noted by Wignall *et al.* (1988a) was not supported by our data, although the extreme temperatures experienced by plants in the transparent treatment during June, July and August resulted in overheated bark and reduced sprout emergence.

The general consensus in the literature is that light influences epicormic sprout growth by affecting sprout photosynthesis, and thus their contribution to their own carbohydrate requirements. Our data support this concept. The significant difference between the DWs of light- and dark-grown epicormic sprouts indicates that they had apparently produced a significant quantity of their own carbohydrate within the 4-week treatment period.

No evidence was found, in this experiment, to support the observation that the South-exposed sides of trunks produced more and larger epicormic sprouts than the North-exposed sides of trunks (Della Bianca, 1972). If greater light exposure, or greater temperature resulting from direct light exposure of the southern face was a factor, North-South differences would have been expected in the transparent and control treatments in these experiments, and not in the dark treatment. No significant differences were detected in either case. However a North-South difference in light exposure would probably be greater in larger trees than were used in our experiment, and/or in trees with full canopies, where self-shading would decrease the incident light on the northern trunk face. North-South sprouting differences may also be more pronounced at higher latitudes where the angle of the sun is lower, and the difference in exposure between North- and South-facing bark is larger.

The significant relationship noted here between the number of nodes in 50 cm of trunk and the number of epicormic sprouts produced, supports previous hypotheses in the literature. Blum (1963) and Fontaine *et al.* (2001) reported that in species with only preventitious epicormic buds [as is apparently the case in peach, (unpublished data)], the epicormic potential of an individual is related to the original number of epicormic buds. In this study with young peach trees, individuals that produced fewer lateral buds in the first year (i.e., by producing longer internodes and thus fewer nodes per stem length) produced fewer epicormic sprouts per trunk length when stimulated by topping in their third year. This information may be useful for the manipulation of nursery and field growing conditions during the early years, when a tree establishes its main trunk, in order to encourage long internodes and to reduce long-term epicormic sprout production. It should

be noted that this reduction would, at best, be slight and that the best method to control epicormic sprouts is probably the selection of varieties with a genetic tendency to produce fewer epicormic sprouts, as recognised in other species (Kormanik and Brown, 1969; Wignall *et al.*, 1985; Evans, 1987).

An incremental change in trunk diameter has been associated with the initiation of epicormic sprouts (Bachelard, 1969; Evans, 1982; O'Hara and Valappil, 2000; Nicolini *et al.*, 2003). In our experiment, neither trend was detected; but it is possible that these trees were too similar in size and vigour to detect such differences.

During the period of the year when sprouting occurs in response to the removal of apical dominance by topping (i.e., when epicormic buds were sensitive to auxin), it also appeared that tree carbohydrate reserves were very important in influencing epicormic sprouting. The number of epicormic sprouts produced in response to topping roughly mirrored the fluctuations in tree carbohydrate reserves. That is, depletion of root carbohydrate reserves by the growing canopy until reaching the annual minimum, then subsequent accumulation of carbohydrates as the mature canopy became a net producer. Maurel *et al.* (2004) found that increases in hexose and sucrose concentrations in xylem sap, and of hexose concentration in meristematic tissue, were positively correlated with the bud-break capacity of lateral peach buds in the Spring. The significant positive relationship, found in the present study, between estimated bark and xylem concentrations of NSC and the number of epicormic sprouts produced over the season, indicates that similar processes may be involved in epicormic and lateral bud-break in peach. Sprout size also appeared to be very sensitive to tree carbohydrate status. Early season sprouts, produced during the period of carbohydrate depletion, tended to remain much smaller than late season sprouts, produced during the period of carbohydrate replenishment. The significant positive relationship between estimated bark concentration of NSC and the DW per sprout of epicormic sprouts produced over the season may indicate that, although they all photosynthesised, young epicormic shoots were nourished in part by carbohydrates present in bark tissue.

In summary, the date of green pruning was the most important factor affecting epicormic sprout number and DW following tree topping. Correct timing of green pruning may reduce subsequent epicormic sprouting. Light exposure was also important for both sprout number and DW, but temperature did not appear to be significant. The number of sprouts formed was influenced by the number of nodes present in the length of trunk. There was some evidence that carbohydrate availability was related to sprout number and DW, but more work is needed to further elucidate this relationship.

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