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Anatomical Changes in Cells and Chalazal Haustorium of Endosperm with Respect to Physiological Fruit Drop in 'Shimizu Hakuto' Peach

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We investigated the morphology of seed, particularly of the endosperm of intact and abscising 'Shimizu Hakuto' peach (*Prunus persica* Batsch) subjected to different fruit thinning levels for four years. The objective was to study the anatomical basis for physiological fruit drop which occurs from end of Stage 2 to beginning of Stage 3 of fruit growth. The percentage of physiological fruit drop was significantly higher ($P = 0.05$) in trees subjected to heavy fruit thinning (HFT) than in those subjected to light fruit thinning (LFT) or standard fruit thinning (SFT). The mean endosperm length in fruit which dropped at the peak of physiological fruit drop from trees under HFT was equal to that of intact fruit collected at 65 days after full bloom (DAFB); the mean embryo length in dropped fruit was shorter than that in the intact fruit collected at the same time. Endosperm and embryo cells in dropped fruit showed typical necrotic symptoms, such as cells with shrunken cytoplasm and collapsing cell nucleus. Collapsing cell nucleus in the endosperm of the intact fruit collected from trees under HFT began at 66 DAFB that corresponded with the time when the endosperm stopped growing. Morphology of chalazal haustorium was observed in the on-tree fruit collected from the beginning to the middle of Growth Stage 2 in trees under HFT and SFT. Although most chalazal haustoria had reached the chalaza at the beginning of Growth Stage 2 in both fruit thinning levels, those in most of HFT fruit exhibited abnormal shrinking at 54 DAFB. These results indicate that a series of events take place in the seeds predestined to drop. That is, after certain factor(s) that cause shrinking of the chalazal haustorium and retardation of embryo growth to occur, assimilated reserves in the endosperm cannot be translocated to the embryo because of shrinkage of the chalazal haustorium. Finally, necrosis of embryo is induced.

Key Words: cell nucleus, chalazal haustorium, endosperm, peach, physiological fruit drop.

Introduction

Among the developing peaches on the tree, some fruit drop occurs after final fruit thinning. This is one of the most serious problems that affect fruit production and is cultivar-dependent. Previous studies on the causes of increased rate of physiological fruit drop have included tree vigor and pollination (Kubota et al., 1993), levels of reserve nutrients (Matsukawa et al., 1981), and shading (Kuroda, 1975). Seed abortion has been suggested as a trigger for individual fruit drop (Tukey, 1936). Previously, we reported that in peach cultivars, such as 'Shimizu Hakuto' that show high rate of physiological fruit drop, the growth of seed, especially of the embryo is more likely to stop as compared to other cultivars that show a low rate of physiological fruit drop (Fukuda et al., 2001). Wanaka (2001) has recommended that final fruit thinning should be done after embryo length is more than 5 mm in order to decrease physiological fruit drop in 'Shimizu Hakuto' peach. Although anatomical studies on the process of physiological fruit drop in peach, including the formation of abscission zone have been made (Rascio et al., 1985), the histological process leading to inferior embryo growth has not been investigated yet.

Prunus species, including the peach, possess non-albuminous seeds enclosed in the pit (endocarp) of fruit (Powell and Pratt, 1966; Schauz and Stösser, 1992). The peach endosperm grows rapidly after double fertilization as it absorbs stored carbohydrates and mineral nutrients from the nucellus or translocated from chalaza after the beginning of Growth Stage 2. The embryo then grows in the endosperm rapidly by consuming substances stored in the endosperm (Dute and Peterson, 1992; Rudall, 1992; Van Dongen et al., 2003). Since the endosperm is able to produce some plant growth regulators, such as auxin, gibberellin and cytokinin, it may affect embryo growth and fruit development (Graebe et al., 1965; Powell and Pratt, 1966). This implies that quality rather than the size of the endosperm is important for

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maintaining normal embryo growth. Chalazal haustorium of endosperm has been regarded as the tissue through which translocation of assimilates in and out of the seed occurs (Jacobsen et al., 1994; Rudall, 1992). In recent years, studies on the relationships between endosperm/embryo growth and premature fruit drop that occurs until the end of Growth Stage 1 have been undertaken in *Prunus* species (Dittmann and Stösser, 1999; Nakano et al., 1999; Schauz and Stösser, 1992). However, there is little information available to explain the physiological fruit drop in peach that occurs after mid June.

The objective of this study was to investigate the anatomical changes in the endosperm during seed development that lead to physiological fruit drop in 'Shimizu Hakuto' peach trees after heavy fruit thinning (HFT).

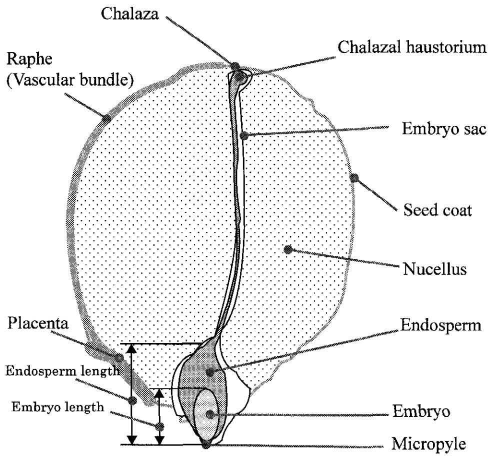

Fig. 1. Diagram of longitudinal cross section of peach seed.

Materials and Methods

Plant materials and treatments

Six mature 'Shimizu Hakuto' peach (*Prunus persica* Batsch) trees growing in the Research Farm of the Faculty of Agriculture, Okayama University, were used for experiments from 2000 to 2003. The dates of full bloom were April 10 in 2000 and 2001 and April 8 in 2002 and 2003. Three HFT trees were thinned annually in early May and adjusted to a final crop load of about 70 leaves per fruit at harvest. A set of three trees was subjected to light fruit thinning (LFT), in early June 2000, to 1.5-fold of final crop load, or subjected to standard fruit thinning (SFT), in which the first thinning was done in early May to 2, 3-fold of final crop load and the second thinning was done in early June to final crop load from 2001 to 2003. After fruit thinning in early June, all fruit were covered with orange colored paper bag.

Rate of physiological fruit drop and lengths of endosperm and embryo in dropped fruit

The number of dropped fruit from each tree during the period of physiological fruit drop was counted, and their percentage was calculated. In HFT trees, dropped fruit were collected at the peak of physiological fruit drop and seeds were taken out of the fruit. The presence of crack in the suture line of the pit was used to separate split- from non-split-pit fruit when seeds were removed from abscised and intact fruit. After measuring the size and fresh weight of the seeds, the endosperms, which contained the embryos, were excised, and their lengths from the apices of the endosperm and embryo to the micropyle (Fig. 1) were measured. Sections of the endosperm and immature embryo cotyledon were prepared by microslicer (DTK-1000, D.S.K., Japan) to a thickness of 200 to 300 μm with more than one layer of unbroken cells. These sections were then stained by Giemsa stain solution for 15 min. and photographed with a CCD camera adapted to a light microscope to study the cell morphology of the endosperm and embryo.

Quantitative determination of cell nucleus collapsed in the endosperm and embryo

Six to nine seeds collected from June 9 to July 7, 2000, and from June 2 to June 23, 2001 were fixed with formalin–acetic acid–alcohol (FAA) fixative to assess the condition of the cell nuclei in the sections. Preparation and staining of the endosperm and embryo sections were performed as described for above dropped fruit. In 2000, the degree of cells with collapsed cell nuclei of endosperm and embryo in HFT and LFT was classified into three grades based on appearance as follows; 0: no collapse in almost the whole cell nuclei, 1: collapse in a part of the cell nuclei and 2: collapse in almost the whole cell nuclei. In 2001, occurrence of collapsed cell nuclei was investigated in 40 endosperm cells in HFT and SFT and the percentages of cells with collapsed nuclei were calculated. The percentage of collapsed cell nuclei was divided into four grades; less than 20%, 20–50%, 50–90% and more than 90%. The percentage of the distribution in these grades in HFT was compared with that in LFT or SFT. The relationship between the percentage of cells with collapsed cell nucleus and endosperm length was investigated in the seeds collected from HFT and SFT trees at 66 days after full bloom (DAFB) in 2001, one week before physiological fruit drop began.

Examination of abnormal symptoms in chalazal haustorium

The morphology of chalazal haustorium in the endosperm in 15 seeds collected in each treatment from June 2 to June 16 in 2003 was examined. Chalazal haustorium is formed at the apex of the endosperm in the embryo sac when the endosperm apex reaches the chalaza at the end of Growth Stage 1 (Fig. 1). To expose the chalazal haustorium, the seed coat near the chalaza was chipped off from both cheek sides of the seed using a razor and the nucellus underneath was removed without damaging the embryo sac. The morphology of haustorium was observed under a light microscope. Cross sections at the micropyle ends of seeds collected at May 29 (50 DAFB) were prepared by paraffin sectioning and observed under a light microscope after stained with 0.1% toluidin blue O.

Results and Discussion

In 'Shimizu Hakuto' peach under normal cultivation, fruit drop occurs during fruit growth, between 70–90 DAFB, the phenomenon referred to as the third phase of physiological fruit drop. Its degree depends on the environmental conditions and tree vigor (Wanaka, 2001). Furthermore, physiological fruit drop is significantly increased by HFT in which the number of fruit is adjusted by thinning to the level of final crop load as early as the middle of Growth Stage 1 (Fukuda et al., 2001). We investigated the relationship between physiological fruit drop which occurs from end of Growth Stage 2 to the beginning of Growth Stage 3 and seed development and used 'Shimizu Hakuto' peach trees subjected to different fruit thinning levels.

Rate of physiological fruit drop and change in the percentage of dropped fruit

The change in the percentage of dropped fruit in trees under HFT and SFT in 2003 (Fig. 2) shows that under both treatments, fruit drop began at 71 DAFB and continued until 90 DAFB. The final percentage of physiological fruit drop in HFT of 20 to 30% was significantly higher ($P = 0.05$) than the 5 to 10% in LFT or SFT in all four years.

Lengths and cell morphology of endosperm and embryo in dropped fruit

To investigate the time when endosperm and embryo growth in dropped fruit stops, lengths of seed, endosperm and embryo in fruit which dropped at the peak of physiological fruit drop in HFT were measured (Table 1). There was no significant difference ($P = 0.05$) in endosperm and embryo lengths among the years. Regardless of years tested, the endosperm ceased growth after reaching 12 mm or 50% of seed length while the embryo grew to less than 1 mm or 5% of seed length.

The cross sectional appearance of cells in the endosperm and embryo in on-tree and dropped fruit (Fig. 3) reveal that their cell walls appear normal but the plasmalemma and cytoplasm have shrunk, and the cell nuclei has collapsed. Such symptoms were not observed in on-tree fruit which showed normal growths of endosperm and embryo at that time. A shrunken cytoplasm and collapsed cell nuclei are considered as a typical symptom of necrosis (Hooper and Wiese, 1972).

The growth curves of mean lengths of seeds, endosperms and embryos in the trees under HFT are compared to those of trees under SFT (Fig. 4) show no difference in growth of endosperm in both treatments until 70 DAFB at which time the endosperm in HFT was a little smaller than in SFT. However, embryo length in SFT increased rapidly after 65 DAFB, whereas that in HFT did not. These results agree well with those obtained in our previous report (Fukuda et al., 2001). When the mean endosperm length in fruit dropped in 2003 were superimposed to growth curve of endosperm in on-tree fruit, we observed that the time when endosperm stopped growing was approximately at 65 DAFB. Thereafter the difference in endosperm length between HFT and SFT increased. But when the mean length (0.9 mm) of embryo in dropped fruit is compared to mean embryo length (2.5 mm) of on-tree fruit collected at 65 DAFB, the difference is significantly different. That embryo growth was inferior compared to endosperm growth in the fruit destined to drop indicates that embryo growth is not mutually linked with endosperm growth. In this study the endosperm continued to grow even though embryo length was very small in the fruit destined to drop. This observation suggests that substances which are essential for

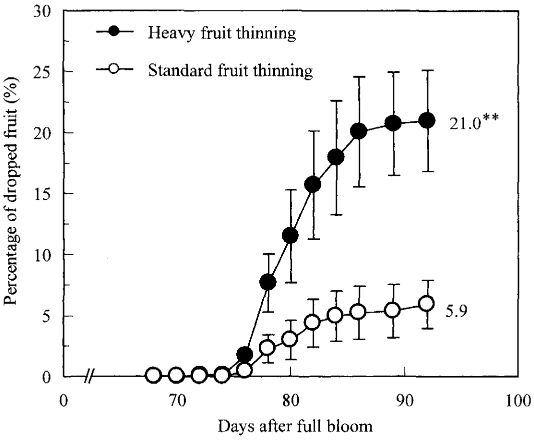

Fig. 2. Changes in the percentage of dropped fruit in 'Shimizu Hakuto' peach trees under heavy fruit thinning (HFT) and standard fruit thinning (SFT) (2003). * indicates significant difference in the percentage of dropped fruit between trees under HFT and SFT at $P = 0.05$ by t-test (n = 3). Vertical bars indicate SE.

Table 1. Lengths of seed, endosperm and embryo in fruit dropped from 'Shimizu Hakuto' peach tree under heavy fruit thinning.

Year	Number of investigated fruit[z]	Length (mm)		
		Seed	Endosperm	Embryo
2000	9	21.1 ± 0.3[y]	12.8 ± 0.8	0.2 ± 0.2
2001	21	21.0 ± 0.2	11.5 ± 0.6	0.9 ± 0.2
2002	20	21.3 ± 0.2	10.1 ± 0.8	0.8 ± 0.2
2003	20	21.7 ± 0.1	12.2 ± 0.6	0.9 ± 0.1
Significance		NS[x]	NS	NS

[z] Collected date: 73 days after full bloom (DAFB) in 2000, 76–81 DAFB in 2001, 73–78 DAFB in 2002, 73–77 DAFB in 2003.

[y] Average ± SD.

[x] NS indicates not significant by Tukey's multiple range test at $P < 0.05$ among the years.

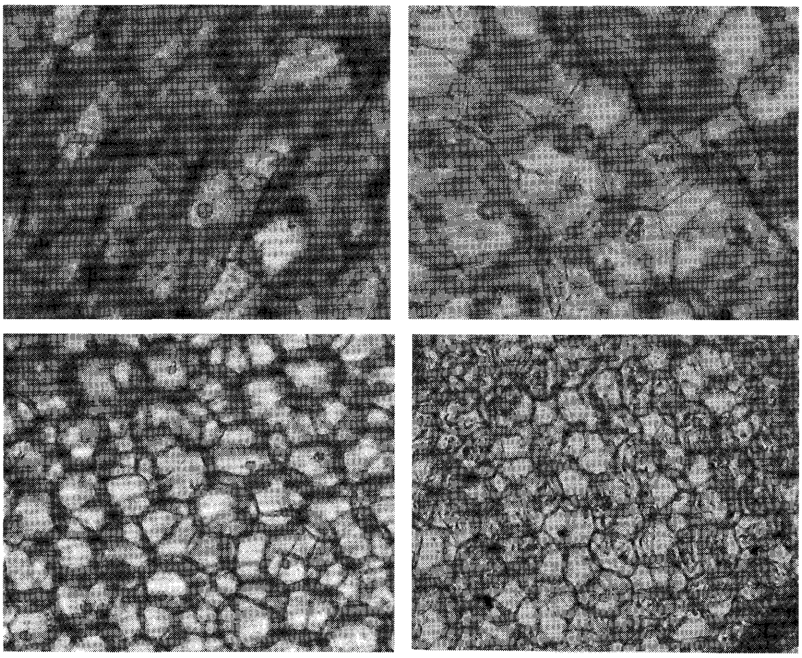

Fig. 3. Longitudinal cross section of apex of endosperm (upper) and embryo (lower) in on-tree (left series) and dropped fruit (right series) (2000). On-tree and dropped fruit were collected at the peak of physiological fruit drop.

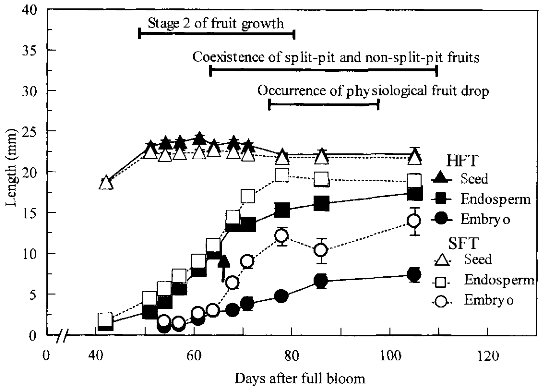

Fig. 4. Growth curves of endosperm and embryo in 'Shimizu Hakuto' peach trees under heavy fruit thinning (HFT) and standard fruit thinning (SFT) (2003). Arrow indicate the time when endosperm reached to mean lengths (12.2 mm) (refer to Table 1) in dropped fruits on the growth curve of endosperm in growing fruit on the tree. Vertical bars indicate SE (n = 15).

maintaining normal embryo growth are inadequate in the endosperm of abnormal fruit. Indeed, it has been known that endosperm contains an abundance of metabolites and various plant growth regulators (Powell and Pratt, 1966; Rudall, 1992). Therefore, in dropped fruit, the transport of these substances from the endosperm to the embryo may have been limiting although the endosperm appear to grow continuously. When supply of assimilates to embryo is curtailed, cell growth in the embryo suffers.

Occurrence of collapsed cell nucleus in endosperm and embryo

The cell morphology of the endosperm and embryo in the on-tree fruit collected at Growth Stage 2 was investigated to seek the time, if and when collapse of the cell nuclei and shrinking of the cytoplasm occurred in endosperm and embryo in the normal intact fruit. Histological examination revealed that such phenomena did not occur in embryo throughout the investigation. When seasonal changes in the percentage of collapsed cell nuclei in endosperm in HFT and LFT in 2000 and HFT and SFT in 2001 were compared, collapsing of the cell nuclei occurred at 66 DAFB, the middle of Growth Stage 2 (Fig. 5). The percentages of the on-tree fruit with severely collapsed cell nuclei in the endosperm, that is rank 2 (almost the whole cell nuclei are collapsed) in 2000 and sum of 50–90% and >90% in 2001 were higher in HFT than in LFT or SFT. The onset of collapsing cell nucleus correlated well with the time that growth of endosperm in dropped fruit ceased. The peak of physiological fruit drop occurred almost 10 days after the collapse of the cell nuclei in endosperm. However the basis for 50 to 90% of the cell nuclei in endosperm of SFT fruit collapsed may be different from that in HFT because the length of endosperm of abnormal SFT fruit collected at 66 DAFB was 17.7 mm or near maximum size, whereas that of endosperm in HFT was about 10 mm. Therefore, the higher percentage of collapsed cell nuclei of endosperm in SFT fruit may be attributed to such factor(s) as apoptosis in usual endosperm degradation (Young and Gallie, 1999). Necrosis is induced by the lack of carbohydrates (Koblet et al., 1996; Walsh and Carrol, 1992) and inorganic nutrients (Lynch

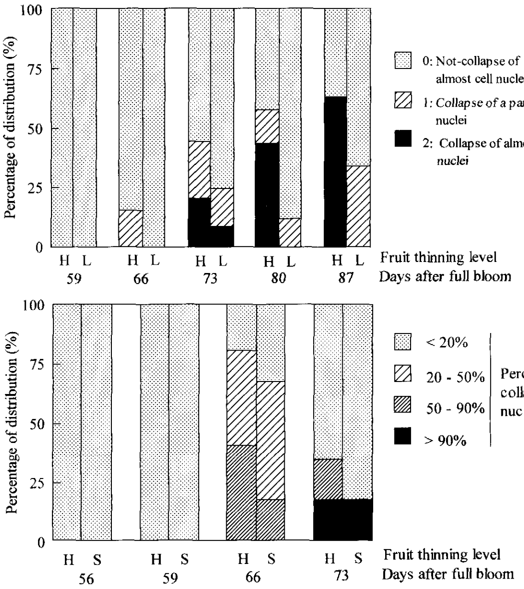

Fig. 5. Changes in the percentage of collapsed cell nuclei in endosperm in 'Shimizu Hakuto' peach trees under heavy fruit thinning (H), light fruit thinning (L) and standard fruit thinning (S) in 2000 (upper) and 2001 (lower).

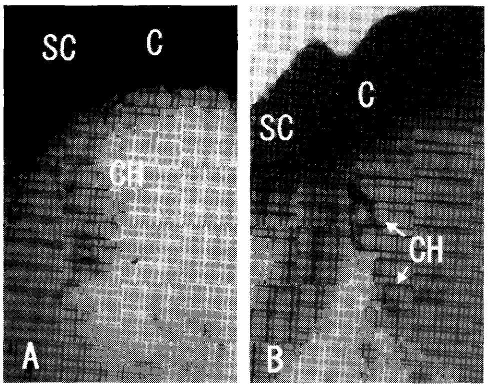

Fig. 6. Normal (A) and abnormal (B) haustoria in the 'Shimizu Hakuto' peach tree under heavy fruit thinning (2003). Fruit were collected at 57 days after full bloom, corresponding to early Growth Stage 2. CH, chalazal haustorium; C, chalaza; SC, seed coat. Note that chalazal haustorium has shrunk and has been unfastened from chalaza in B.

Table 2. Effect of fruit thinning level on the rate of fruit with shrunken haustorium in 'Shimizu Hakuto' peach (2003).

Collected date (DAFB[z])	Rate of fruit with shrunken haustorium (%)		Significance
	HFT[y]	SFT[y]	
54	28.6±10.4[x]	14.3±13.2	NS[w]
57	15.4±28.9	0 ± 0	NS
61	61.5±30.4	20.0± 0	NS
64	54.5±17.6	15.4±13.2	*
68	90.9±19.2	50.0± 0	*

[z] Days after full bloom.
[y] HFT and SFT indicate heavy fruit thinning and standard fruit thinning, respectively.
[x] Average±SD (n=3).
[w] NS and * indicate not significant and significant by *t*-test at $P<0.05$ between fruit thinning levels, respectively.

and Brown, 1997; Morard et al., 1996). According to these previous findings, we infer that assimilates or inorganic nutrients stored in the endosperm cell were exhausted by 66 DAFB. For developing embryo, collapse of the cell nuclei did not occur regardless of the degree of thinning. These results indicate three things. First, not all the carbohydrates and inorganic nutrients in the embryo are consumed with the stopping of embryo growth. Second, cell death or necrosis in embryo occurs just before fruit drop. Third, once the embryo dies, the fruit cannot survive and, therefore, drops.

Shrunken chalazal haustorium of endosperm in the first half of Growth Stage 2

Most of the chalazal haustoria reached the chalaza pole by 50 DAFB, but the morphology of the chalazal haustorium varied especially on fruits under the HFT treatment (Fig. 6). Normal chalazal haustorium became globular at the chalaza pole in the embryo sac and contained free cells, whereas the abnormal one appeared shrunken and unattached to the chalaza. The percentage of fruit with shrunken haustorium in the on-tree fruit collected from HFT and SFT trees in the first half of Growth Stage 2 (Table 2) reveals that seeds with abnormal haustorium began to immerge in the on-tree fruit at 54 DAFB. This date of abnormal haustorium in the on-tree fruit coincided with the time when embryo growth in dropped fruit was supposed to have stopped. Although there were no significant differences ($P=0.05$) in the percentage of fruit with abnormal haustorium between HFT and SFT from 54 to 61 DAFB, the percentage was consistently higher in the former than in the latter. In the last half of Growth Stage 2, most of the seeds in both treatments were filled with endosperm so that the morphology of chalazal haustorium could not be assessed. Rapid increase in the percentage of shrunken haustoria beyond 68 DAFB in HFT and SFT indicates that the chalazal haustorium is not needed for endosperm growth because most of endosperm has already reached the chalaza.

In recent years, the relationship between abnormal chalazal haustorium and premature fruit drop in *Prunus* species has been investigated (Dittmann and Stösser, 1999; Nakano et al., 1999). In plum and cherry, abnormality of chalazal haustorium was confirmed in the investigation on fruit drop which occurred in the last half of Growth Stage 1 (Dittmann and Stösser, 1999). Nakano et al. (1999) suggested that some abnormal symptoms in chalazal haustorium, referred to as "unreaching to chalaza", correlated with physiological fruit drop at the end of Growth Stage 1 in 'Hakuto' peach. In this study, all haustoria under both levels of fruit thinning seemed to have reached the chalaza because we started the investigation. However, some ovules exhibited shrunken haustoria in all thinning levels. Although the direct causes leading to the occurrence of abnormal haustorium at the beginning of Growth Stage 2 were uncovered in this study, certain stress in the fruit may have occurred at about 54 DAFB. Bagging of fruit at about 50 DAFB may have induced some stresses because bagging affects temperature, humidity, and air permeability around peach fruit (Kim et al., 2003).

Dittmann and Stösser (1999) observed that abnormality of haustorium leads to a decreased sink activity of the seed for nutrients. Thus, it is plausible that assimilates and mineral nutrients cannot be directly translocated into the endosperm with shrunken haustorium. However, the endosperm continued to enlarge until the middle of Growth Stage 2. The existence of another haustorium at the micropylar pole of endosperm has been reported in *Laviatae* and *Verbenaceae* species (Rudall, 1992). This micropylar haustorium has the ability to take up substances, which are transported simplastically through seed coat and stored in the nucellus for endosperm development. A conclusive evidence of micropylar haustorium in peach has not yet been found. In this study we observed a cluster of cells in nucellus cells at the micropylar pole (Fig. 7). Based on these results, necrosis may have started in the endosperm when the endosperm stopped supply of the nutrients stored in the nucellus and was utilized for growth.

In conclusion, embryo length in the fruit destined to drop was shorter than that of on-tree fruit. This difference coincided with the time when the endosperm stopped growing, the cell nuclei began to collapse, and haustorium became abnormal. We, therefore, conclude that starvation related to the dysfunction of chalazal haustorium leads to eventual necrosis of endosperm and cessation of embryo growth, which in turn, initiate the process of physiological fruit drop.

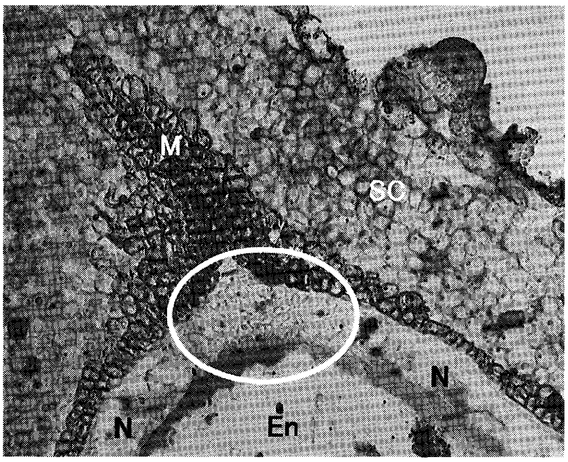

Fig. 7. Longitudinal cross section at micropyle pole of 'Shimizu Hakuto' peach seed. Section was stained by 0.1% toluidin blue O. Seed was collected at 50 days after full bloom in 2003. En, endosperm; M, micropyle; N, nucellus; SC, seed coat. Ellipse indicate a claster of cells which differed with nucellus cells in appearance.

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生理的落果との関連からみたモモ‘清水白桃’の胚乳細胞と吸器の形態的変化

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モモにおいて果実発育第2期末から第3期初めに起こる生理的落果の発生過程を解剖学的に明らかにするために，摘果程度の異なる‘清水白桃’を用いて，種子，特に胚乳の形態を4年間調査した．弱摘果区あるいは標準摘果区に比べて強摘果区では生理的落果率が有意に高かった．落果盛期に強摘果樹から落下した果実の胚乳長は，満開65日後に採取した樹上果の胚乳長に相当し，また胚長はその時期の樹上果の胚長よりも小さかった．落下した果実の胚乳と胚の細胞はともに細胞質の収縮や細胞核の消失といったネクロシスの典型的な症状を呈した．強摘果区では，樹上果における胚乳の細胞核の崩壊が，落下した果実における胚乳の成長停止時期に当たる満開66日後に認められ始めた．果実発育第2期の前半に採取した樹上果について，合点側吸器の形態を観察したところ，強摘果区，標準摘果区ともに，第2期初めにはほとんどの吸器が合点に到達していたが，満開54日後以降，強摘果区の多くの果実に合点側吸器の収縮異常が認められた．これらの結果は，落下する果実では以下のような一連の種子の退化過程の現象が起こっていることを示唆した．すなわち，合点側吸器の収縮や胚成長の抑制を引き起こす要因が発生した後，合点側吸器の収縮によって胚乳における貯蔵養分の蓄積量が低下するために胚への養分供給が劣り，最終的に胚の壊死が生じると考えられた．