# CHAPTER 1
# LITERATURE REVIEW

## 1.1 INTRODUCTION

In most vascular plants there are restricted areas of relatively loosely arranged cells, suberized or non-suberized, in the periderm which are called lenticels (Fahn, 1974).

Lenticels are lens-shaped (Kuo-Huang and Hung, 1995) macroscopic openings that occur on the surfaces of roots, shoots, some fruits like apples, pears, avocados and mangos (Dietz *et al*., 1988; Esau, 1965; Fahn, 1974; Silvester and Harris, 1989) and even on vegetative leaves (Neish, 1995). Singh and Pant (1997) described the occurrence of lenticels on ovules of five *Cycas* species. The fruit of tomatoes, blueberries and persimmon were reported to be devoid of lenticels (Brown and Considine, 1982).

As seen from the surface, lenticels appear as masses of loose cells, usually protruding above the surface through a fissure in the periderm (Esau, 1965). Depending on the orientation of the fissure, transverse and longitudinal lenticels are recognized (Wetmore, 1926). In stems and roots, the fissures of the lenticels are usually closely related to the phloem rays (Kuo-Huang and Hung, 1995).

In perennial plants lenticels can survive for several years in which cases the phellogen is dormant during winter and regains activity every spring (Klebahn, 1884). The gross anatomy of mature lenticels in many plants has been described, but only a few published reports are referring to the development of lenticels (Jacob *et al*., 1989).

As mentioned previously, lenticels also occur on mango fruit (Oosthuyse, 1998). Producers of mangos have a serious problem with postharvest discolouration of mango lenticels (Oosthuyse, 2002), because the dark coloured spots on the fruit give an undesirable appearance (Tamjinda *et al.,* 1992). Although superficial, it can substantially reduce consumer acceptance and the retail value of the fruit (Loveys *et al.*, 1992).

## 1.2 ORIGIN, FORMATION AND STRUCTURE OF LENTICELS

### 1.2.1 Lenticels on stems

The stage of plant organ development at which lenticel formation commences may differ from species to species and is dependent on the persistence of the epidermis on the organ (Esau, 1965). In the case of aboveground plant organs with secondary growth, the cuticle, stomata and epidermis are sloughed off as a result of periderm formation (Groh *et al.*, 2002). Lenticels may appear prior to periderm initiation or lenticels and periderm may arise simultaneously (Fahn, 1974). They usually arise below stomata (Adams, 1975) or under groups of stomata where the function of the stomata is gradually transferred to the lenticel (Fahn, 1974). In some species, with a low stomatal index, lenticels can form between stomata or, where there is a high stomatal index, lenticels may develop below some of them (Fahn, 1974).

During the ontogeny, parenchyma cells under the stomatal cavity divide in different planes, chlorophyll disappears and a mass of rounded thin-walled cells, with prominent intercellular spaces, is formed (Esau, 1965; Kuo-Huang and Hung, 1995). The division of the cells progresses inwards into the cortex and the orientation of the divisions become more and more periclinal until the phellogen of the lenticel is formed (Adams, 1975; Kuo-Huang and Hung, 1995). In

some species the phellogen is continuous with the outer cell layer of cortex just below the epidermis (Kuo-Huang and Hung, 1995).

The phellogen gives rise to the phelloderm in the interior and complementary cells towards the exterior (Langenfield-Heyser, 1997) (Fig. 3.12 A and B). Complementary cells may be suberized or non-suberized (Fahn, 1974). As the filling tissue and complementary cells increase in quantity, the epidermis is ruptured and filling tissue protrudes above the surface (Kuo-Huang and Hung, 1995). The exposed cells die and wither away but are replaced by others developing from the phellogen (Esau, 1965).

Intercellular spaces are present in the tissue of the lenticels and therefore they, like stomata, are prominent structures in the process of gaseous exchange (Esau, 1965; Fahn, 1974; Mauseth, 1988). Lenticels can therefore be regarded as passages for watervapour and gas exchange (Groh *et al.*, 2002).

The lenticellular phellogen of some species like *Phytolacca dioica* L. (Fig. 3.12B) also forms a seasonal closing layer apart from the phelloderm and complementary cells. These are seasonal layers of compact cells alternating with the complementary tissue (Fig. 3.12B) (Langenfield-Heyser, 1997). Despite their compact nature, the closing layers as well as the phellogen contain intercellular spaces for gaseous exchange (Fahn, 1974). The closing layer also ruptures as a result of the renewed production of new complementary cells (Fig. 3.12B) (Kuo-Huang and Hung, 1995).

Several structural features contribute to physiological functions of lenticels: (a) extent, structure and porosity of complementary cells; (b) diameter and extent of intercellular spaces in the lenticel phellogen; (c) extent of lenticel phelloderm and of chlorenchyma

radially adjacent, further their structure, porosity and metabolic activity; (d) continuity of intercellular spaces connecting metabolic active sites in the organ interior of lenticels to the outer environment (Langenfield-Heyser, 1997).

LENTICELS ON POTATO TUBERS

The apical tissues of a growing potato tuber bear stomata and as the tissue ages and lateral buds develop, these stomata become lenticels (Hayward, 1974).

Lenticels often proliferate in wet soils, while in dry soils deposits of suberin and sometimes a cork barrier may form. These changes may affect the permeability of lenticels to gasses and their susceptibility to pathogens (Adams, 1975). They may have domed centres of loosely packed cells or a raised flat plateau in the centre. The centre of the lenticels is porous through which gaseous exchange takes place (Hayward, 1974).

Hayward (1974) also stated that wax structures in and around the pores of lenticels can be a contributing factor in the regulation of water loss from the tuber.

### 1.2.2 Lenticels on roots

FLOODED CONDITIONS

Exposure of roots to water-logged conditions results in the formation of hypertrophied lenticels on the submerged portions (Angeles *et al.*, 1986). Upon flooding, hypertrophic lenticels or pneumatodes can be observed on submerged stems, root collars or at the basis of adventitious roots of many tree species (Larson *et al.*, 1991). Langenfield-Heyser (1997) state that only flood-tolerant species are

able to form hypertrophied lenticels, but according to Aronen and Häggman (1994), Scot's pine (*Pinus sylvestris*), a flood-intolerant tree, also produces lenticels in water-saturated conditions. Roots of mangos grown in hydroponic systems also formed lenticels (Pers. comm; Robbertse, 2003[*])

Hypertrophy of lenticels starts with swelling of filling tissue, an increased activity of lenticel phellogen, enlargement and loosening of complementary cells and an increment of lenticel phelloderm. With extended flooding, enhanced activity of the phellogen goes beyond the lenticel, so that an excess of phellem is formed (Larson *et al.*, 1991), cells in the cortex enlarge and intercellular spaces grow and form a continuous network of wide intercellular spaces from stem to root (Aronen and Häggman, 1994).

Roots of certain trees occurring in estuaries, like those of mangrove trees, have pneumatophores. The roots of these trees are periodically exposed to flooded conditions due to the fluctuation of the tides, and therefore these pneumatophores or hypertrophic roots are essential. There are two physiological roles of hypertrophic lenticels. Hypoxia or anoxia leads to production of toxic metabolites through fermentation in flooded roots, like ethanol, acetaldehyde and ethylene. These compounds escape from the roots through the lenticels (Kawase, 1981). The second physiological role is to facilitate entry of atmospheric $O_2$ into flooded roots (Angeles *et al.*, 1986; Topa and McLoed, 1986).

[*] Prof. P.J. Robbertse, Department Plant Production and Soil Science, University of Pretoria, Pretoria, 0002, South Africa

### 1.2.3 Lenticels on fruit

*Pyrus malus*

The structures on the pome of an apple can scarcely be regarded as lenticels, because it is seldom that periderm is associated with these structures.

Pome lenticels are derived in various ways: breaking of stomata caused by the stretching of the epidermis; breaks in the epidermis caused by complete removal of trichomes associated with young fruit; other breaks in the epidermis where the epidermis can't keep track with the development and expansion of the inner tissue (Clements, 1935).

Some lenticels can be regarded as open lenticels and others as closed lenticels (Clements, 1935). Closing of lenticels may be brought about in one of the following ways: 1) A cuticle may seal over the lenticel opening and thus seal the lenticel. 2) A cuticle develops over sublenticellular cells. 3) No cuticle develops in the lenticel, but sublenticellular cells become suberized. 4) A phellogen develop that results in a suberized layer. Open lenticels can likewise develop in different ways: 1) Stoma remains open with substomatal cells incompletely modified or completely modified, but with large intercellular spaces. 2) Lenticel has been firmly closed, but has been broken by the tension of the developing fruit, often the tear may extend into parenchymatous cells of storage tissue. 3) Those that are in various stages of repair. Breaks in young fruit may be repaired quite rapidly, but the older the fruit such tears are less easily covered.

These structures are therefore not similar to the lenticels of woody stems. It is only an occasional pome lenticel, that shows the development of a distinct phellogen (Clements, 1935)

*Prunus avium* L.

The epidermis of the 'Royal Ann' cherry is covered with a continuous cuticle which is interrupted by stomata (Wilson *et al.*, 1972). In the sour cherry, stomata are fully differentiated 18 days before full bloom and no stomata differentiate thereafter (Tukey and Young, 1939). According to Wilson *et al.* (1972) stretching and rupturing of the stomata due to fruit growth and enlargement can be the beginning of lenticel development, though, the lenticels observed was not "true" lenticels.

*Cucumis melo* L.

The surface network of tissue commonly referred to as the "net" in the fruit, is an elaborate system of interconnected lenticels (Webster and Craig, 1976). Phelloderm and complementary tissue, derived from a subepidermal periderm, are visible 14 days after anthesis and are well-developed 30 days after anthesis (Combrink *et al.,* 2001). Cork cells protrude through the surface fissures as the fruit enlarges.

Lenticels develop from stomata that have been covered with an extensive cuticle, thus rendering the stomata nonfunctional (Webster and Craig, 1976) or from cracks in the epidermis caused by rapid fruit growth. This may explain why fruit, developed under slow growth rates, tends to be poorly netted (Combrink *et al.,* 2001).

*Mangifera indica* L.

Dietz *et al.* (1988) maintain that mango fruit lenticels might originate in one of two ways: from preformed stomata or by shearing of the fruit epidermis as a result of rapid fruit growth. Tamjinda *et al.* (1992)

found that cells directly below the lenticel were smaller than surrounding cells and had larger intercellular spaces.

## 1.3 DISORDERS

Physiological discolouration occurring directly around apple lenticels is called lenticel spots. These spots often appear at harvest-time and seem to be favoured by high nitrogen applications, early harvest, high humidity and temperatures of 21–27°C after harvesting (Richmond and Dewey, 1969). Susceptibility of the fruit to lenticel spot also seems to vary widely from year to year and from orchard to orchard. Pathogens such as *Alternaria* sp. can penetrate through such a lenticel (Richmond and Dewey, 1969).

It is well known in the mango fruit industry worldwide that, by one way or another, mango lenticels may turn black and consequently depreciate the economic value of the fruit. Much research on the causal aspects has already been done, but no clear answer has been found to elucidate the problem (O'Hare and Prasad, 1992; Shorter and Joyce, 1998; Tamjinda *et. al.*, 1992).

## 1.4 PHYSIOLOGY

### 1.4.1 Entrance of water

Intercellular spaces of lenticels can be infiltrated with water (Schönherr and Ziegler, 1980). However, under normal circumstances, they are not filled with water (Kleban, 1884) and are not wettable (Schönherr and Ziegler, 1980). Reasons for non-wettability of intercellular spaces could be suberization (Ish-Shalom-Gordon and Dubinsky, 1992) and/or a lining with wax crystals (Hayward, 1974).

For gas exchange, it is hugely advantageous that lenticellular intercellular spaces cannot be filled with water (rain, floodwater); the entrance of $O_2$ through lenticels to the interior of plant tissue would

otherwise be reduced, since migration of $O_2$ in water is about 300 000 times slower than in air (Langenfield-Heyser, 1997).

### 1.4.2 Gas exchange

Gaseous transport through lenticels depends on the number and area of lenticels on a given organ surface, on their degree of opening, developmental stage of the lenticel, species (type of lenticel and non-lenticellular periderm), season and environment (Langenfield-Heyser, 1997). Klebahn (1884) postulated that diffusive resistance of lenticels to gasses depends on the width of the intercellular spaces, on the path length through complementary cell layers and on their structure.

Carbon dioxide produced during respiration can be transported by the transpiration stream (Martin *et al.,* 1994), however, a considerable amount can leave the stems *via* lenticels. Diffusion of $CO_2$ through stem periderm with lenticels, open or sealed, was measured after chemical absorption (KOH) (Klebahn, 1884) or by means of an infrared gas analyzer (Langenfield-Heyser, 1997).

By its metabolic activity, lenticel chlorenchyma could reduce the loss of $CO_2$ from the stem and thus improve $CO_2$ refixation (Langenfield-Heyser *et al.,* 1996). This is especially important at times of high respiration rates such as spring, when lenticels must be open to facilitate transport of $O_2$ to the metabolic active tissues of the stem interior (Langenfield-Heyser, 1997).

### 1.4.3 Lenticellular transpiration

Usually lenticels are more permeable to water than the rest of the periderm (Groh *et al.,* 2002). Transpiration rate through older lenticels is lower than through younger ones. In water-saturated atmospheres, lenticellular transpiration is reduced to 16.5%, rising to

50% when the periderm dries (Langenfield-Heyser, 1997). Klebahn (1884) also observed that lenticel transpiration differed seasonally, with higher transpiration rates in summer than in winter.

It is suggested that the rate of lenticellular transpiration is not only dependant on the structure of the lenticel, but also on the type of non-lenticellular periderm, its permeability, its longevity and its influence on the structure of long lasting lenticels (Langenfield-Heyser, 1997).

## 1.5 SUMMARY

Lenticels are usually formed below stomata, usually on the surface of organs where the epidermis is replaced by a periderm. Cells below the substomatal cavity divide into different planes until the phellogen is formed. The phellogen gives rise to the phelloderm and complementary tissue, with intercellular spaces to allow gas exchange. Lenticels do not have any regulating mechanism like guard cells in the stomata regulating gas exchange and transpiration, but the complementary tissue protects the interior from excess transpiration and also from pathogens (Kuo-Huang and Hung, 1995). Because of suberization and/or lining of wax crystals of the complementary cells, lenticels cannot be filled with water under normal conditions.

Resultant upon the absence of phellogen, subsequent phelloderm and complementary cells in mango fruit lenticels, they are different from the lenticels described above or from typical lenticels. They have a rather ineffective physical barrier to protect the interior of the fruit from unwanted factors like pathogens, chemicals and water.

The reason for lenticel discolouration is still unknown and the purpose of this study is to determine the mechanism of mango lenticel discolouration in an effort to find a solution, which may enable us to prevent or reduce its

occurrence. The lack of literature on mango lenticel development and structure (Tamjinda *et al.,* 1992) inspired us to study the ontogeny of mango lenticels in detail, in order to understand and relate structure to discolouration.

**REFERENCE LIST**

ADAMS, M.J. 1975. Potato tuber lenticels: development and structure. *Ann. Appl. Biol.* 79(3), 267-273.

ANGELES, G., EVERT, R.F. AND KOZLOWSKI, T.T. 1986. Development of lenticels and adventitious roots in flooded *Ulmus Americana* seedlings. *Can. J. For. Res.* 16, 585-590

ARONEN, T.S. AND HÄGGMAN, H.M. 1994. Occurrence of lenticels on roots of Scots Pine seedlings in different growth conditions. *Plant Physiol.* 143, 325-329.

BROWN, K. AND CONSIDINE, J. 1982. Physical aspects of fruit growth. Stress distribution around lenticels. *Plant Physiol.* 69, 585-590.

CLEMENTS, H.F. 1935. Morphology and physiology of the pome lenticels of *Pyrus malus*. *Bot. Gaz.* 97, 101-117.

COMBRINK, N.J.J., AGENBAG, G.A., LANGENHOVEN, P., JACOBS, G., MARAIS, E.M. 2001. Anatomical and compositional changes during fruit development of 'Galia' melons. *S. Afr. J. Plant Soil.* 18(1), 7-14.

DIETZ, T.H., THIMMA RAJU, K.R. AND JOSHI, S.S. 1988. Structure and development of cuticle and lenticels in fruits of certain cultivars of mango. *Acta Hort.* 231, 457-460.

ESAU, K. 1965. *Plant Anatomy* (2nd Ed). John Wiley and Sons, Inc., New York, USA.

FAHN, A. 1974. *Plant Anatomy* (3rd Ed). Pergamon Press, Oxford, UK.

GROH, B., HÜBNER, C. AND LENDZIAN, K.J. 2002. Water and oxygen permeance of phellems isolated from trees: the role of waxes and lenticels. *Planta.* 215, 794-801.

HAYWARD, P. 1974. Waxy structures in the lenticels of potato tubers and their possible effects on gas exchange. *Planta* 120, 273-277.

ISH-SHALOM-GORDON, N. AND DUBINSKY, Z. 1992. Ultrastructure of the pneumatophores of the mangrove *Avicennia marina*. *S. Afr. J. Bot.* 58, 358-362.

JACOB, A., LEHMANN, H. AND STELZER, R. 1989. Entwicklung und structur von lentizellen der Buche (*Fagus sylvatica* f. *purpurea* Ait.). *Flora* 183, 417-427.

KAWASE, M. 1981. Anatomical and morphological adaptations of plants to waterlogging. *Hort. Sci.* 16, 30-34.

KLEBAHN, H. 1884. Die rindenporin. Ein beitrag zur kenntnis des baues und der function der lenticellen und der analogen rindenbildungen. *Jen. Ztsch. Nat.* 27, 537-591. (Quoted by Langenfield-Heyser, 1997).

KUO-HUANG, L.L. AND HUNG, L.F. 1995. The formation of lenticels on the branches of *Ficus microcarpa* L. f. *Taiwania* 40(2), 139-150.

LARSON, K.D., DAVIES, F.S. AND SCHAFFER, B. 1991. Floodwater temperature and stem lenticel hypertrophy in *Mangifera indica* (Anacardiaceae). *Am. J. Bot.* 78, 1397-1403.

LANGENFELD-HEYSER, R. 1997. Physiological functions of lenticels. In: *Trees – Contributions to modern tree physiology* (Rennenberg, H., Eschrich, W. and Ziegler, H., ed.) Backhuys Publishers, Leiden, Netherlands.

LANGENFELD-HEYSER, R., SCHELLA, B., BUSCHMANN, K. AND SPECK, F. 1996. Microautoradiographic detection of $CO_2$-fixation in lenticel chlorenchyma of young *Fraxinus exelsior* L. stems in early spring. *Trees* 10, 255-260.

LOVEYS, B.R., ROBINSON, S.P., BROPHY, J.J. AND CHACKO, E.K. 1992. Mango sapburn: components of fruit sap and their role in causing skin damage. *Aust. J. Plant Physiol.* 19, 449-457.

MARTIN, T.A., TESKEY, R.O. AND DOUGHERTY, P.M. 1994. Movement of respiratory $CO_2$ in stems of loblolly pine (*Pinus taeda* L.) seedlings. *Tree Physiol.* 14, 481-495.

MAUSETH, J.D. 1988. *Plant Anatomy.* The Benjamin Cummings Publishing Company, Inc., California, USA.

NEISH, P.G. 1995. Anatomy of leave-margin lenticels in *Eucalyptus denticulata* and three other eucalypts. *Aust. J. Bot.* 45, 211–221.

O'HARE, T. J. and PRASAD, A. 1992. The alleviation of sap-induced skin injury by calcium hydroxide. *Acta Hort.* 321, 372-381.

OOSTHUYSE, S.A. 2002. Lenticel damage in mango: Influence of harvest date and cold storage conditions. *S. A. Mango Growers Assoc. Yearbook,* 22,20-27.

OOSTHUYSE, S.A. 1998. Effect of environmental conditions at harvest on the of lenticel damage in mango. *S. A. Mango Growers Assoc. Yearbook,* 18, 15-17.

RICHMOND, A.E. AND DEWEY, D.H. 1969. Distinguishing characteristics of the 'jonathan spot' and lenticel spot disorders in the 'Jonothan' Apple fruit. *J. Amer. Soc. Hort. Science.* 94, 245-248.

SCHÖNHERR, J. AND ZIEGLER, H. 1980. Water permeability of *Betula* periderm. *Planta* 147, 345-354.

SHORTER, A. J. AND JOYCE, D. C. 1998. Effect of partial pressure infiltration of calcium into 'Kensington' mango fruit. *Australian Journal of Experimental Agriculture*, 38, 287-294.

SILVESTER, W.B. AND HARRIS, S.L. 1989. Nodule structure and nitrogenase activity of *Coriaria arborea* in response to varying $PO_2$. *Plant Soil* 118, 97-109.

SINGH, R. AND PANT, D.D. 1997. On occurrence of lenticels in seeds of *Cycas* L. *Phytomorph.* 43(3), 325-331.

TAMJINDA, B., SIRIPHANICH, J. AND NOBUCHI, T. 1992. Anatomy of lenticels and the occurrence of their discolouration in mangoes (*Mangifera indica* cv. Namdokmai). *Kasetsart J.* 26, 57-64.

TOPA, M.A. AND MCLOED, K.W. 1986. Aerenchyma and lenticel formation in pine seedlings: A possible avoidance mechanism to anaerobic growth conditions. *Physiol. Plant.* 68, 540-550.

TUKEY, H.B. AND YOUNG, J.O. 1939. Histoulogical study of the developing fruit of sour cherry. *Bot. Gaz.* 100, 723-749.

WEBSTER, B.D. AND CRAIG, M.E. 1976. Net morphogenesis and characteristics of the surface of muskmelon fruit. *J. Amer. Soc. Hort. Sci.* 101(4), 412-415.

WETMORE, R.H. 1926. Organization and significance of lenticels in dicotyledons. I. Lenticels in relation to aggregate and compound storage rays in woody stems. Lenticels and roots. *Bot. Gaz.* 82, 71-88.

WILSON, L.A., BEAVERS, D.V. AND CAIN, R.F. 1972. Structure of the 'Royal Ann' cherry cuticle and its significance to cuticular penetration. *Amer. J. Bot.* 57(7), 722-728.