VARIABILITY OF BARK STRUCTURE IN PLANTATION-GROWN EUCALYPTUS GLOBULUS

by

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SUMMARY

The bark structure of *Eucalyptus globulus* Labill. grown in plantations in Central Portugal is described, based on specimens extracted at six height levels from ten 15-year-old trees. No significant variation of qualitative features between trees was observed. The non-collapsed phloem is characterised by multiseriate tangential rows of phloem parenchyma alternating with rows of phloem fibres, interspersed with large sieve tubes and their respective companion cells, and uniseriate rays. With the onset of sieve tube collapse (collapsed phloem), some parenchyma cells expand and sclerify, the course of rays becomes irregular, and ray dilatation is initiated. The periderm is composed of a phellem of lignified cells with horseshoe thickening (phelloids), followed by a layer of cells with suberised tangential walls, and a phelloderm with a variable number of layers of thin-walled cells. Age-related secondary changes give rise to a specific within-tree pattern of axial variation. Both the intensity of sclerification of phloem parenchyma cells and the degree of ray dilatation increase with tree age.

Key words: Eucalyptus globulus Labill., bark structure, secondary structural changes.

INTRODUCTION

Eucalyptus globulus Labill. is a fast growing species with a high economic value for pulp wood production. In Europe, *E. globulus* plantations occupy approximately 1.2 million ha (700,000 ha in Portugal) and are exploited in a short rotation coppice system with an average 10–12 year rotation cycle. Growth rates may reach mean values of approximately 20 m^3 ha^{-1} year^{-1}. Bark comprises approximately 16% of the merchantable bole dry weight. The trees are either debarked immediately after harvest and bark is left on the site, or drum-debarked at the pulp mill and bark is used as fuel.

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The bark anatomy of plantation-grown *E. globulus* and other *Eucalyptus* species has received little attention (Chattaway 1953, 1955a–e; Alfonso 1987; Quilhó & Sardinha 1995; Quilhó & Pereira 1997). However, bark may play an important role in the tree's susceptibility to insect attacks, for instance by *Phoracanta semipunctata*, the only known pest of *E. globulus* in Europe.

Bark is a highly heterogeneous material that requires specific and tedious techniques for specimen preparation, probably one of the reasons for the relatively few studies. The lack of knowledge on bark structure and its age-related modifications has also limited its use in taxonomic work (Trockenbrodt 1991). Information on the variability of bark structure, especially within and between individuals of a single species, is essential for an estimation of the diagnostic value of bark anatomical features (Trockenbrodt 1992); only a few publications have dealt with the age-related trends of bark structure (Trockenbrodt 1991, 1994).

This paper describes the bark anatomy of *E. globulus*, considering the between-tree structural variability and the age-related axial variation within tree.

MATERIAL AND METHODS

The anatomical studies were conducted with ten 15-year-old *Eucalyptus globulus* trees harvested at the end of the 1st rotation period. Five trees were randomly selected from each of two 100 tree plots situated in the region of Castelo Branco, in Central Portugal (39° 30' N; 7° 46' W; altitude 300 m; rainfall 825 mm and a mean temperature of 16 °C).

Mean tree height was 19.7 m (15.1–23.8 m) and mean DBH 16.7 cm (11.9–22.9 cm). Bark represented, on average, 13.2% of stem dry weight. The bark specimens were taken along the stem at different percentage levels of total height (5%, 15%, 35%, 55%, 75%); an additional specimen was taken at breast height.

Transverse and longitudinal microscopic sections approximately 17 μm thick were prepared with a Reichert sliding microtome after impregnation with DP 1500 polyethylene glycol (Richter 1990). The sections were stained with malachite green and hematoxylin, as well as with a triple staining of chrysodine/acridine red and astra blue, and mounted in Euparal. Sudan 4 was used for selective staining of suberin. Light microscopic observations were also made with dissociated elements after staining with astra blue. Individual specimens were taken sequentially from the cambium towards the periphery and macerated in CH_3COOH and H_2O_2 1:1 at 60 °C for 48 hours.

The terminology follows mainly Trockenbrodt (1990) and Richter et al. (1996).

RESULTS

The bark of *E. globulus* is dark grey, deciduous, smooth to slightly fissured, detaching in long strips; fissures are usually longitudinal and narrow. Lenticels are scarce and difficult to observe. The bark consists of an inner region of non-collapsed phloem, followed by collapsed phloem and a single periderm (Fig. 1, 2). Annual growth increments were not detected. The non-collapsed phloem is uniform with alternating tan-
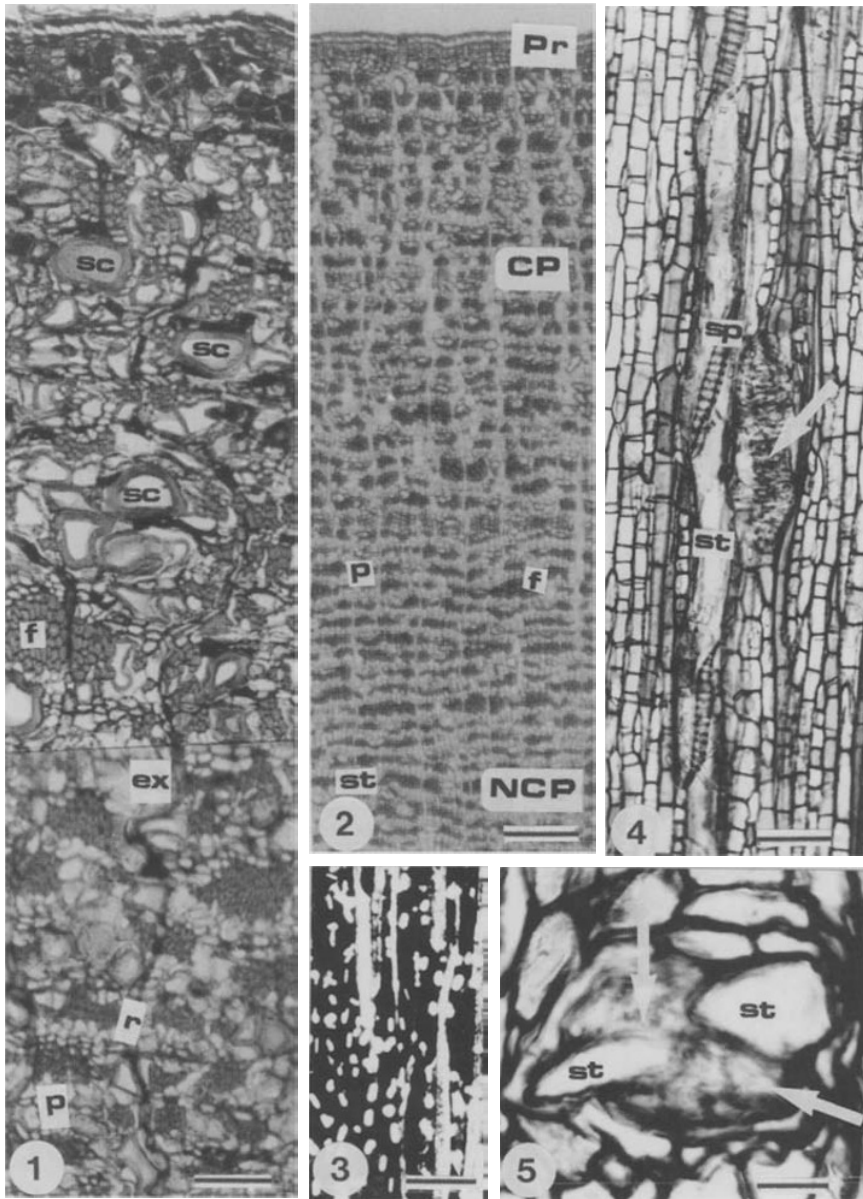
Fig. 1–5. *Eucalyptus globulus* bark. – 1: TS, general view of collapsed phloem and periderm of an older bark specimen (5% of tree height); fibres (f), parenchyma (p), ray (r), expanded parenchyma cells (ex), and sclereids(sc). – 2: TS, young bark specimen (75% of tree height). CP = collapsed phloem, NCP = non-collapsed phloem, Pr = periderm, fibres (f), parenchyma (p), siebe tube (st). – 3: TLS, calcium oxalate crystals in chambered bark parenchyma cells under polarised light. – 4: TLS, sieve tube (st) member with compound sieve plate (sp) and junction complex (arrow). – 5: TS, junction complex (arrow) and sieve tubes (st). — Scale bars = 100 μm in Fig. 1 & 3; 217 μm in Fig. 2; 56 μm in Fig. 4; 25 μm in Fig. 5.
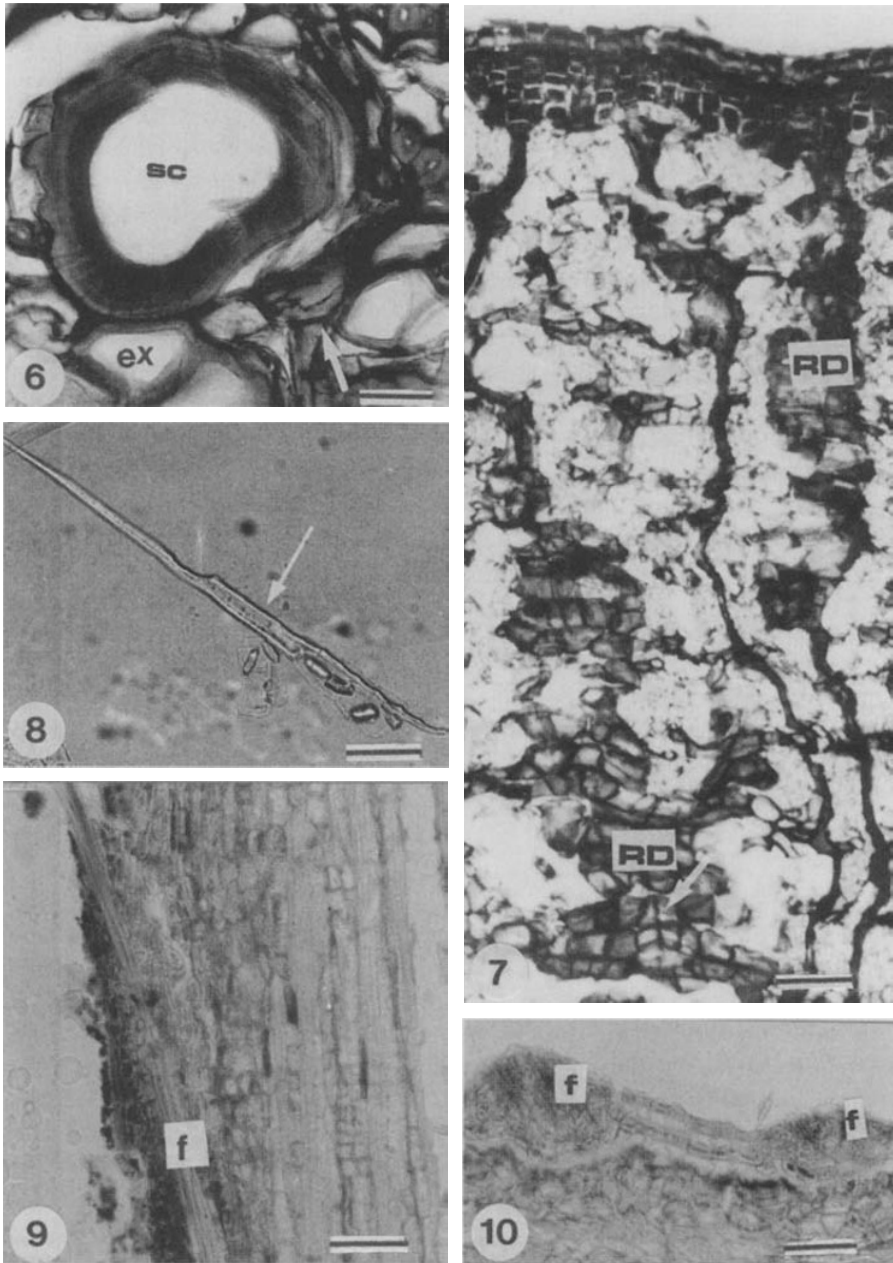
Fig. 6–10. *Eucalyptus globulus* bark. – 6: TS, expanded parenchyma cells (ex) and sclereid (sc); distortion of phloem ray (arrow). Specimen taken at DBH. – 7: TS, dilatation tissue in collapsed phloem at DBH. Dilated ray (RD), tangential ray cells division (arrow). – 8: Fibre sclereid, arrow (macerated material taken at the 15% height level). – 9: TLS, fibres (f) penetrate the periderm. – 10: TS, fibres (f) penetrate the periderm.— Scale bars = 28 μm in Fig. 6; 56 μm in Fig. 7; 100 μm in Fig. 8–10.

gential bands of parenchyma (p), fibres (f) and diffusely distributed, large sieve tubes (st) (Fig. 2). No differences between different height levels were evident. The transition from non-collapsed to collapsed phloem is gradual. The collapsed phloem is characterised by the collapse of sieve tubes, the distortion of rays and the expansion of parenchyma cells. In specimens taken from the top (75% and 55% height levels), changes were small, increasing gradually downwards within the tree (height levels 35% and 15%), while at lower levels (5% and DBH) a pronounced disarray of the tissues became evident (Fig. 1).

Axial parenchyma is in tangential bands of variable width: 2 or 3 cells at the top (75% and 55% of tree height, Fig. 2), increasing progressively at 35% and 15% levels, up to 5 cells at the base. The increase in width is accompanied by an increasing disorder in the collapsed-phloem. Prismatic calcium oxalate crystals are abundant in the axial parenchyma cells (Fig. 3). Individual phloem parenchyma cells are round to rectangular in transverse outline. The thin unlignified walls have minute, round, primary pit fields; cells sometimes contain brown organic contents.

Sieve tubes (st) are loosely dispersed between parenchyma strands and fibres (Fig. 2), mostly solitary or in small groups; transverse sections are rectangular to polygonal, cell walls are thin and unlignified. Sieve plates are scalariform compound, oblique, with 7–15 sieve areas per plate (Fig. 4), equally spaced and with many minute sieve pores (arrow). No variation was observed in the number of sieve areas between and within trees. Sieve areas were also occasionally present on the lateral walls. Companion cells are very small in diameter and difficult to recognise in transverse as well as in longitudinal sections.

So called 'junction complexes' between sieve tubes can be observed in all specimens. In transverse section these structures appear in form of a lattice (Fig. 5) and are especially evident in longitudinal sections (Fig. 4), provided that individual sieve tubes are closely spaced.

Phloem rays (r) are predominantly uniseriate and heterocellular composed of procumbent cells and a single marginal row of square cells (Fig. 4). Rays follow a more or less straight course in the non-collapsed phloem, but become rather irregular towards the periphery. At the beginning of the collapsed phloem, the rays start undulating. At younger age levels (75% and 55% of tree height), only slight distortion of rays was observed (Fig. 2). At 35% and 15% of tree height, rays started to dilate somewhat, simultaneously with the enlargement of axial parenchyma cells and the first formation of sclereids (Fig. 6). At still later stages of development (DBH and 5%), some phloem rays develop funnel-shaped dilatation growth (Fig. 7) through tangential cell division.

Fibres (f) form tangential bands or clusters alternating with bands of axial parenchyma cells (Fig. 2); diffuse phloem fibres are very rare. They are axially elongated with prominent pits.

Sclereids (sc) are mostly isodiametric, of variable shape and size, and occur single or in clusters. They are characterised by a thick, lignified polylamellate secondary wall (Fig. 6) traversed by minute pit canals (arrow). Sometimes polygonal crystals are present. Their number increases from the beginning of the collapsed phloem towards the periderm and from top to bottom of the tree.
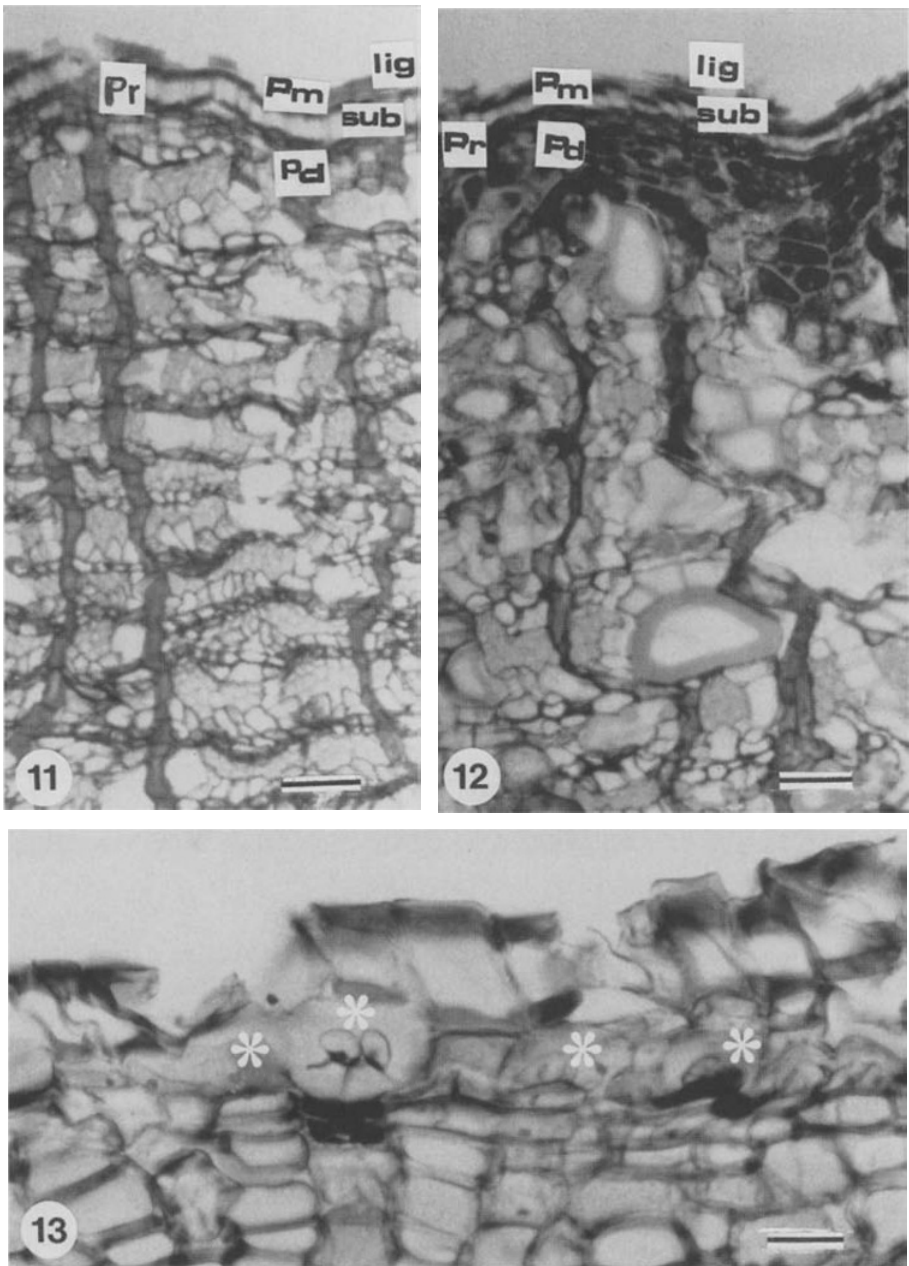
Fig. 11–13. *Eucalyptus globulus* bark. – 11: TS, periderm (Pr) and collapsed phloem (specimen from 75% of tree height). Phellem (Pm) with lignified cells (lig) and suberised cells (sub). Phelloderm (Pd). – 12: TS, periderm (Pr) and collapsed phloem (specimen from 5% of tree height). Phellem (Pm) with lignified cells (lig) and suberised cells (sub). Phelloderm (Pd). – 13: Ruptured periderm with suberin sealing (✳). — Scale bars = 56 µm in Fig. 11 & 12; 25 µm in Fig. 13.

Fibre sclereids (sclerotic fibres) are similar to the fibres, but shorter (Fig. 8), and become long, slender elements at maturity.

Periderm constitutes a single, continuous layer, more or less parallel to the tree circumference and sometimes penetrated by fibres (Fig. 9, 10). The phellem (Pm) is composed of uniseriate, concentric layers of thin-walled, partially suberised cells (only tangential walls) alternating with layers of lignified cells (phelloids). These phelloids are usually flattened radially, square or rectangular in transverse section, and develop 'horseshoe' thickenings on the inner tangential walls (Fig. 11, 12). The single layer phellogen is composed of radially flattened, rectangular and thin-walled cells (transverse section). The phelloderm (Pd) consists of a variable number of layers of thin-walled cells in neat radial alignment, 2 or 3 cells wide in younger (Fig. 11) and 4 or 5 cells wide in older material, sometimes with interspersed sclerified cells and filled with dark brown organic compounds (Fig. 12). Lenticels are very few and their within-tree distribution does not follow any particular pattern. The suberised tissue layers alternate regularly with loose, non-suberised tissue. In older material, a rupture of the periderm was observed, and masses of suberin (Fig. 13) are deposited as sealing material.

DISCUSSION

The bark structure was very similar in the ten trees studied. There were no differences between trees in the structural organisation or in the characteristics of the different tissues. Furthermore, the age-related development of bark structure (followed by its axial variation) was similar for all trees. The uniform and regular alternating tissues of the non-collapsed phloem was observed in all specimens and this agrees with observations for the genus *Eucalyptus* (Chattaway 1953; Alfonso 1987) and with the phloem 'stratification' mentioned by Roth (1981) for various taxa of Myrtaceae. The changes in tissue organisation and cell morphology observed in the collapsed phloem represent the adjustment of the secondary phloem to tree growth (Bamber 1962; Trockenbrodt 1991). In consequence, the extent of disorganisation of the collapsed phloem is clearly related to growth and represents the only significant axial variation in the secondary phloem of *E. globulus*.

Tangential bands of axial parenchyma are described for the genus *Eucalyptus* (Alfonso 1987). Their number/bands vary within the tree, increasing from the top to the base. The same was observed for other dicotyledons (Zahur 1959). Calcium oxalate crystals are abundant (Fig. 3). Alfonso (1987) recorded the same type of crystals in other species of *Eucalyptus*. The crystals are always located in chambered parenchyma strands, as in *Eugenia* spp. or other Myrtaceae (Chattaway 1959; Bamber 1962; Roth 1981; Van Wyk 1985). The type and location of crystals are similar for the different stages of bark development (see also Trockenbrodt 1995).

Sieve tubes are only discernible in the non-collapsed phloem. The functional period of these cells is short and they become obliterated and crushed after a short period of time. The same types of sieve tubes and sieve plates observed in *E. globulus* are also recorded for different *Eucalyptus* spp. (Alfonso 1987).

Junction complexes between sieve tubes, as observed in *E. globulus*, have also been reported for *E. calophylla, E. marginata* and other Myrtaceae (Tippett & Hill 1984).

The phloem rays are similar to xylem rays in *E. globulus* (Jorge et al. 1996), i.e., predominantly uniseriate and heterocellular. This agrees with observations by other authors (Alfonso 1987), and confirms Van Wyk (1985) who emphasises the uniformity and the few diagnostic characters of phloem rays in Myrtaceae.

The distortion of rays in the collapsed phloem is in part a result of the crushing of the sieve tubes. The extent of the ray tissue changes (distortion, cell division and dilatation) varies axially within the tree and becomes more evident in older samples, near the base (Fig. 7). These changes have also been described by Chattaway (1953) and Alfonso (1987) for the genus. However, in *E. globulus* the dilatation tissue is not as pronounced as reported for *E. propinqua, E. punctata, E. terecticornis,* and *E. dunnii* (Alfonso 1987). This radial (from the cambial region towards the periderm) and axial (from the top to the base) variation of phloem rays reveals the significant influence of age. Similar age trends were reported for various other species, e.g., *Quercus robur, Ulmus glabra* and *Populus tremula* (Trockenbrodt 1991).

The mechanical phloem tissue includes fibres, sclereids and fibre-sclereids. Phloem fibres resemble wood fibres (Jorge et al. 1996), but are longer, indicating considerable apical intrusive growth.

Sclereids originate from axial parenchyma cells and lack the typical intrusive growth of the phloem fibres. These parenchyma cells, 'expanded parenchyma cells' (ex) or 'cells of intermediate type' (Richter et al. 1996), gradually enlarge and cell walls thicken radially as well as tangentially (Fig. 6), finally developing into sclereids by the progressive sclerification of the walls. Their number increases continuously from the collapsed phloem towards the periderm, and from top to bottom of the tree.

Fibre sclereids are shorter than phloem fibres. They originate from axial parenchyma cells (see Fig. 8). The forms of sclerification are similar to those reported by Alfonso (1987) for the genus *Eucalyptus* .

In all the trees studied no sequential periderm formation was observed. The periderm was similar in all samples observed.

Eucalyptus globulus belongs to the group of smooth, deciduous-barked, 'gum'-type eucalypts. According to Chattaway (1953, 1955d) the smooth bark surface results from the occurrence of lignified, thickened cells of the phellem (Fig. 11, 12), which agrees with our observations.

The periderm varies axially, with the effect of tree age evident from the degree of sclerification, i.e., with an increasing number of sclerified cells per phelloderm layer in older samples (DBH and 5% of tree height). Similarly, the amount of organic compounds deposited in the parenchyma cells also increases with age (Fig. 12).

Sometimes the periderm is penetrated by fibres (Fig. 9, 10). These fibres, perhaps of primary origin, are pushed up during the secondary development and eliminated by the periderm. The rupture of the periderm observed in some trees, as a consequence of the increase in stem girth and sealed with amounts of suberin (Fig. 13), is a phenomenon previously described by Chattaway (1953).

CONCLUSIONS

The bark structure of plantation-grown (Central Portugal) *E. globulus* does not differ markedly from other *Eucalyptus* species in terms of composition and age related secondary changes, as described by various authors for other species from different origins.

No between-tree variation was observed. Secondary structural changes within trees are related to age and give rise to a typical within-tree pattern of axial variation characterised by an increase of the intensity of sclerefication and the degree of ray dilatation from top to bottom of the tree.

REFERENCES

Alfonso, V. 1987. Caracterização anatómica do lenho e da casca das principais espécies de Eucalyptus L'Hérit. cultivados no Brasil. Tese de Doutoramento. Instituto de Biociências da Universidade de São Paulo. 189 pp.

Bamber, R. K. 1962. The anatomy of the barks of Leptospermoideae. Austral. J. Bot. 10: 25–54.

Chattaway, M.M. 1953. The anatomy of bark. I. The genus Eucalyptus. Austral. J. Bot. 1: 402–403.

Chattaway, M.M. 1955a. The anatomy of bark. II. Oil gland in Eucalyptus species. Austral. J. Bot. 3: 23–27.

Chattaway, M.M. 1955b. The anatomy of bark. III. Enlarged fibres in bloodwoods (Eucalyptus spp.). Austral. J. Bot. 3: 28–38.

Chattaway, M.M. 1955c. The anatomy of bark. IV. Radially elongated cells in the phelloderm of species of Eucalyptus. Austral. J. Bot. 3: 39–47.

Chattaway, M.M. 1955d. The anatomy of bark. V. Eucalyptus species with stringy bark. Austral. J. Bot. 3: 165–169.

Chattaway, M.M. 1955e. The anatomy of bark. VI. Peppermints, boxes, ironbarks, and other eucalypts with cracked and furrowed barks. Austral. J. Bot. 3: 170–176.

Chattaway, M. M. 1959. The anatomy of bark. VII. Species of Eugenia (sens. lat.). Trop. Woods 111: 1–14.

Jorge, F., T. Quilhó & H. Pereira. 1996. Variabilidade das fibras da casca e do lenho da Eucalyptus globulus Labill. In: Congresso Florestal Hispano Luso, Livro de Actas: 247–252. Pamplona.

Quilhó, T. & H. Pereira. 1997. Variabilidade de tecidos da casca de Eucalyptus globulus Labill. de diferentes proveniências. In: Conferência IUFRO sobre Silvicultura e Melhoramento de Eucaliptos: 397–402. Salvador, Brazil.

Quilhó, T. & R. Sardinha. 1995. Bark anatomy of Eucalyptus globulus Labill. (Myrtaceae). Silva Lusitana 3: 173–190.

Richter, H.G. 1990. Wood and bark anatomy of Lauraceae III. Apidostemon Rohwer & Richter. IAWA Bull. n.s. 11: 47–56.

Richter, H.G., S. Viveiros, E. Alves, A. Luchi & I.C. Costa. 1996. Padronização de critérios para a descrição anatómica da casca: lista de características e glossário de termos. IF Série Registros (16): 1–25. São Paulo.

Roth, I. 1981. Structural patterns of tropical barks. In: Encyclopedia of plant anatomy. Vol. IX, Part 3. Gebr. Borntraeger, Berlin.

Tippett, J.T. & T.C. Hill. 1984. Junction complexes between sieve tubes in the secondary phloem of Myrtaceae. Annals of Botany 53: 421–429.

Trockenbrodt, M. 1990. Survey and discussion of the terminology used in bark anatomy. IAWA Bull. n.s. 11: 141–166.

Trockenbrodt, M. 1991. Qualitative structural changes during bark development in Quercus robur, Ulmus glabra, Populus tremula and Betula pendula. IAWA Bull. n.s. 12: 5–22.

Trockenbrodt, M. 1992. Bark structure: variation and systematic utility. IAWA Bull. n.s. 13: 233 (Abstract).

Trockenbrodt, M. 1994. Quantitative changes of some anatomical characters during bark development in Quercus robur, Ulmus glabra, Populus tremula and Betula pendula. IAWA J. 15: 387–398.

Trockenbrodt, M. 1995. Calcium oxalate crystals in the bark of Quercus robur, Ulmus glabra, Populus tremula and Betula pendula. Annals of Botany 75: 281–284.

Van Wyk, A.E. 1985. The genus Eugenia (Myrtaceae) in southern Africa: structure and taxonomic value of bark. S. Afr. J. Bot. 51: 157–180.

Zahur, M.S. 1959. Comparative study of secondary phloem of 432 species of woody dicotyledons belonging to 85 families. Cornell Univ. Agr. Expt. Stat. Mem.