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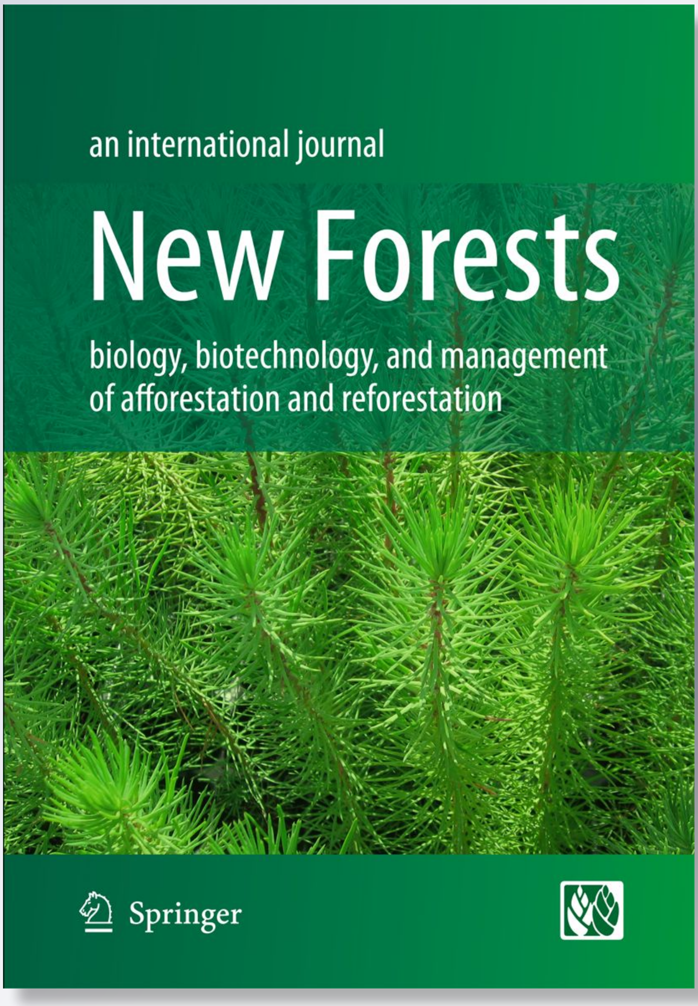

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Long term losses caused by foliar diseases on growth and survival of *Eucalyptus globulus* in Uruguay

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Abstract *Eucalyptus globulus* is the most important forest species in Uruguay, with more than 250,000 ha of commercial plantations. Despite its high susceptibility to diseases, production losses caused by foliar diseases have not been properly quantified in this country. This study analyzes the effects of foliar damage on growth and survival using data from a progeny test of *E. globulus* naturally infected by Teratosphaeria leaf disease and eucalypt rust (*Puccinia psidii*). The severity of leaf spots and defoliation were quantified 8 months after planting and tree growth and mortality were evaluated 2, 4 and 6 years later. The trial had a high incidence of foliar damage, with a mean leaf spot severity of 28.7% and a mean defoliation of 37%. The greatest impact of foliar damage, both on growth rate and mortality, occurred in the first 2 years after damage was assessed. During this period, leaf spot severity less than 40% and defoliation below 50% did not affect growth, while survival was affected when leaf damage was 70% or greater. By the sixth year both stem growth and survival were affected by severe foliar damage (spotting or defoliation of 80% or more), with a loss of up to 25% in diameter and an accumulated mortality over 70%. It has been established for the first time that under the intensive Uruguayan productive conditions, *E. globulus* trees can tolerate a relatively high degree of leaf spotting or defoliation but severe foliar damage in the first months can cause considerable production losses, putting at risk the economical viability of this species.

Keywords Disease severity · Foliar diseases · Growth response · *Puccinia psidii* · *Teratosphaeria* spp.

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Introduction

Several pathogens affect the foliage of eucalypts. Some of them, like *Teratosphaeria cryptica* (=*Mycosphaerella cryptica*), *Teratosphaeria nubilosa* (=*Mycosphaerella nubilosa*) and *Puccinia psidii*, are considered serious threats in various countries due to the extent of damage caused in young plantations of different *Eucalyptus* species (Coutinho et al. 1998; Park et al. 2000; Mohammed et al. 2003; Smith 2006; Barber et al. 2008; Hunter et al. 2009). Various species of *Mycosphaerella* and *Teratosphaeria* cause the diseases known as Mycosphaerella leaf disease (MLD) and Teratosphaeria leaf disease (TLD) (Crous 1998; Crous et al. 2007; Hunter et al. 2011). These diseases produce necrotic spots of different size, shape and colour, premature defoliation and, in the case of severe infection, death of apical buds, twigs and branches (Park et al. 2000). The eucalypt rust, *P. psidii*, produces yellow pustules on new leaves, petioles and buds, and on highly susceptible hosts it causes necrosis and deformation of the affected tissues (Ferreira 1983).

A reduction of photosynthetic area produced by foliar diseases can cause a loss of growth and it also predisposes the plant to other pathogens or adverse abiotic factors (Carnegie et al. 1994). The effects of leaf diseases on growth of *Eucalyptus* species have been quantified in naturally infected plantations or in controlled experiments (Lundquist and Purnell 1987; Stone et al. 1998; Carnegie et al. 1994; Carnegie and Ades 2001). However, in most cases the impact of defoliation on tree growth of *Eucalyptus* has been studied after insect damage (Jordan et al. 2002; Pinkard et al. 2006a; Rapley et al. 2009) or by artificial defoliation tests (Abbott et al. 1993; Collett and Neumann 2002; Pinkard et al. 2006b, 2007). Some of these studies have shown that 10% leaf damage is enough to cause loss of growth on *Eucalyptus globulus* (Carnegie and Ades 2003; Pinkard et al. 2006a). However, Rapley et al. (2009), found no effects on growth of *Eucalyptus nitens* when leaf damage was less than 60%. Growth reductions between 4 and 17% in *E. globulus* have been reported with leaf damage levels of 20% (Carnegie and Ades 2003; Milgate et al. 2005; Smith 2006).

The degree of leaf damage on young eucalypts required to cause growth losses and the magnitude of the losses are influenced by severity, pattern, timing and frequency of leaf damage (Wills et al. 2004; Pinkard et al. 2006b). Studies on *Eucalyptus marginata*, *Eucalyptus regnans* and *E. globulus* showed that repeated or chronic defoliations have greater effects on tree growth than an isolated defoliation event (Candy et al. 1992; Abbott et al. 1993; Collett and Neumann 2002; Wills et al. 2004). Growth losses caused by leaf damage are also related to tree age, site quality and nutritional status (Pinkard and Beadle 1998; Smith 2006). The long term growth response to defoliation has been classified as type 1, when there is an initial decline in tree growth and a subsequent recovery of the growth rate of a healthy tree, and type 2, when the reduction of growth rate is permanent (Snowdon 2002). According to Smith (2006), growth rate of *E. globulus* damaged by *Mycosphaerella* spp. follows a type 1 response with less than 80% foliar damage and a type 2 response when damage is above that degree of damage.

There are currently more than 500,000 ha of commercial plantations of *Eucalyptus* in Uruguay, with *E. globulus* the most planted species, covering approximately 250,000 ha (Petraglia and Dell'Acqua 2006). Susceptibility to diseases is the major productive limitation of this species and this has restricted its planting to more suitable areas in the southeast region (Balmelli et al. 2004). The presence of various species of *Mycosphaerella* and *Teratosphaeria* affecting eucalypts, including *Mycosphaerella marksii*, *Mycosphaerella walkeri*, *Mycosphaerella vespa*, *Mycosphaerella aurantia*, *Mycosphaerella heimii*, *Mycosphaerella lateralis*, *Mycosphaerella scytalidii*, *Teratosphaeria suberosa*, *Teratosphaeria ohnowa* and *Teratosphaeria pluritubularis* has been reported in Uruguay (Wingfield 1999; Balmelli et al. 2004; Pérez et al. 2009a). Similarly, eucalypt rust (*P. psidii*) also affects these trees in the country (Telechea et al. 2003). However, it was only since 2007, when *T. nubilosa* was first recorded (Pérez et al. 2009b), that significant damage began to appear in first and second year *E. globulus* plantations. Systematic surveys conducted since 2008 in *E. globulus* plantations in Uruguay have shown that foliar diseases, mainly due to *T. nubilosa*, are widely distributed in the country and are causing high degree of defoliation (Balmelli et al. 2009a; Pérez et al. 2009b; Simeto et al. 2010). Despite the economic importance of *E. globulus* in Uruguay, its susceptibility to various diseases and the severity of damage recorded in commercial plantations, the production losses caused by foliar diseases have not been adequately quantified. On the other hand, as most studies that analyze the impact of the loss of foliage are based on defoliation by insects or by artificial defoliation, there is a relatively small body of literature quantifying impacts of leaf diseases on eucalypt growth. The present work was performed on a field trial of *E. globulus* in southeastern Uruguay naturally infected by TLD and eucalypt rust (*P. psidii*). To better understand the long term effects of foliar diseases and the need to implement control strategies, the objectives of the study were: a) to establish a threshold of damage for both leaf spotting and defoliation and b) to quantify tree growth and survival losses over a period of 6 years.

Materials and methods

Study site and population assessed

Data were obtained from a progeny test of *E. globulus* established in September 2002 in Rocha (Lat. 34°10′19.65″S; Long. 54°2′4.27″W; Alt. 170 m) by the National Institute of Agricultural Research in Uruguay (INIA). The trial was established on a loamy sandy soil, which had been previously used for animal production on natural pastures. Soil preparation consisted of: herbicide application (glyphosate, 3 L/ha), tillage made in bands and pre-planting herbicide application (glyphosate, 2.25 L/ha). Fertilizer (140 g/plant 16:27:2 N:P:K + microelements) and herbicide (Goal + Arnes: 1.5 + 1.5 L/ha on 1.4 m wide planted band) were applied immediately after planting. Trees were planted at a spacing of 3.65 m × 2.0 m (1,370 stems/ha). In the following autumn, glyphosate was applied (3 L/ha) beneath the trees, with a low volume applicator (Micromax). Grass control was subsequently performed by cattle grazing. The genetic material consisted of 230 open pollination families of different seed sources (INIA's breeding population, local selections and introductions from Australia and Chile). The experimental design for the trial was a randomized complete block with single-tree plots and 24 replications. In this way, each block had 230 plants and the full test originally had 5,520 plants occupying an area of 4.0 ha.

Disease assessment and growth measurements

In May 2003 (8 months after planting) the severity of symptoms caused by TLD and by eucalypt rust was assessed. The degree of damage was quantified on each tree, using two parameters: (1) severity of leaf spots (percentage of leaf area affected) and (2) defoliation (percentage of leaves prematurely abscised). The evaluations were carried out for the whole crown, using visual scales adapted from Lundquist and Purnell (1987) and from Carnegie et al. (1994). For both, severity of leaf spots and defoliation, trees were categorized according to disease classes of 0, 10, 20, 30, 40, 50, 60, 70 and 80% or more. Although rust symptoms are different to those of TLD, the severity of spotting was jointly assessed because it was not possible to separate both symptoms accurately. On the other hand, as eucalypt rust does not produce leaf fall, defoliation relates only to the damage caused by TLD (Coutinho et al. 1998). A second inspection undertaken during foliar change, at 20 months after planting, revealed that in the meantime there were no new outbreaks of disease. The total height of all trees was measured in May 2003 (together with damage evaluation) and again in May 2005 (2 years after damage assessment). Thereafter, growth was assessed by measuring diameter at breast height in May 2005, June 2007 and June 2009 (2, 4 and 6 years after damage assessment, respectively). After each measurement of tree growth, percentage of survival (number of living trees divided by number of trees originally planted) was calculated.

Data analyses

The effects of foliar damage on growth and mortality were analyzed at the phenotypic level, considering the population as a genetically heterogeneous unit. Tree heights and diameters at each measurement date were used to calculate the growth rate from the time when disease assessment was performed. Height increment was calculated for the first 2 years and diameter increments were calculated for two different periods: from 2 to 4 years and from 4 to 6 years after damage assessment. The number of plants surviving at each measurement date was used to calculate the mortality between measurements and the cumulative mortality.

Normality of the data set was tested using Normal Probability Plots, which showed no important departures from normality, and homogeneity of variance was tested by predicted versus residual plots, which showed constant error variance. Analysis of variance (ANOVA) were carried out to test the effect of foliar damage (spot severity and defoliation scores) on growth traits (mean tree height and diameter and mean height and diameter increments) and on mean mortality between consecutive measurements. Undamaged trees, i.e. trees in disease class 0, were considered as disease free controls. Multiple mean comparisons were made with the Tukey–Kramer test. A threshold model was used to describe the relationship between foliar damage (spot severity and defoliation) at 8 months and tree diameter 6 years after damage. Statistical analyses were performed using the GLM and REG procedures in SAS (SAS Institute 1997).

Results

Effects of foliar damage on growth

The trial had a very high incidence of leaf disease at the time of damage assessment, 8 months after planting. Of the total trees, 88.2% showed some leaf spots and 94.4% had some defoliation. The mean spot severity for all trees in the trial was 28.7% and the mean defoliation was 37%. However, the damage was highly variable and ranged from trees with no damage to trees with the foliage almost completely spotted or shed (Table 1).

Table 1 Number of trees of *E. globulus* with each level of damage (spot severity and defoliation), caused by foliar diseases at 8 months of age, in a trial installed in 2002 in Rocha, Uruguay

Disease class spot severity (%)	No. of trees	Disease class defoliation (%)	No. of trees
0	536	0	254
10	614	10	230
20	1,320	20	708
30	511	30	393
40	748	40	1,919
50	201	50	320
60	341	60	489
70	75	70	58
80+	204	80+	179
Total	4,550		4,550

Spot severity

Significant differences between spot severity classes were found for tree heights and diameters in all evaluations. For the growth increments, significant differences were found in all periods except for diameter increments at the last evaluation period (4–6 years after damage assessment) (Table 2). At the time of foliar damage assessment, the mean tree height of undamaged trees (0% spot severity) did not differ significantly from that of trees with leaf spotting class equal or less than 70%, but heavily spotted trees (at least 80% spot severity) had a mean height significantly lower than undamaged trees. Tree measurements taken 2 and 4 years after damage assessment showed that trees within spot severity classes of 40–80% were significantly shorter and had a significantly smaller diameter than trees of lower leaf spotting classes. At the final growth evaluation (6 years after damage) the mean diameter of trees in spotting classes of 50% and above was significantly smaller than that of undamaged or lightly damaged trees.

Tree height increment during the first 2 years after damage assessment was affected by leaf disease. Undamaged and lightly damaged trees (up to 30% leaf spots class) had similar height increments, being significantly greater than those on trees with more severe damage. Between 2 and 4 years after damage was assessed, diameter increments of undamaged or lightly damaged trees only differed significantly from those recorded in the more severely damaged trees (leaf spot class of 80% or higher). At the last evaluation period (4–6 years after damage), growth rate was not significantly affected by foliar damage.

Growth curves of average diameter of trees with different severities of leaf spotting were divergent until the third year (2 years after damage) and thereafter were approximately parallel (Fig. 1). Therefore, following an initial detrimental effect of leaf spots, the growth rate of trees with different severities of leaf spotting was similar. Although the impact of leaf spots on growth decreased over time, the cumulative loss of diameter of severely spotted trees (leaf spot class of 80% or higher), expressed as percentage of diameter of undamaged trees, was 25.2% after 6 years.

Defoliation

The premature fall of affected leaves also had a detrimental effect on growth, with significant differences between defoliation classes for all growth traits (mean tree height at damage assessment and 2 years later, mean diameter at 2, 4 and 6 years after damage) and

Table 2 Comparisons between spot severity classes (0–80%) of *E. globulus* trees for mean ± SE tree height at damage assessment and 2 years after damage assessment (a.d.a.), mean ± SE tree diameter (2, 4 and 6 years a.d.a.), mean ± SE height increment (first 2 years a.d.a.) and mean ± SE diameter increment (2–4 and 4–6 years a.d.a.)

Spot severity class (%)	Height (m) At damage assessment	Height (m) 2 years a.d.a.	Diameter (cm) 2 years a.d.a.	Diameter (cm) 4 years a.d.a.	Diameter (cm) 6 years a.d.a.	Height increment (m) first 2 years a.d.a.	Diameter increment (cm) 2–4 years a.d.a.	Diameter increment (cm) 4–6 years a.d.a.
0	2.53abc ± 0.06	9.88a ± 0.09	11.53a ± 0.18	16.02a ± 0.19	18.04a ± 0.22	7.31a ± 0.05	4.28ab ± 0.08	1.71a ± 0.07
10	2.55ab ± 0.06	9.79a ± 0.09	11.38a ± 0.19	16.00a ± 0.17	17.97a ± 0.19	7.20a ± 0.07	4.31ab ± 0.09	1.68a ± 0.06
20	2.51abc ± 0.05	9.80a ± 0.06	11.28a ± 0.13	15.92a ± 0.11	17.97a ± 0.12	7.24a ± 0.03	4.49a ± 0.08	1.74a ± 0.04
30	2.59a ± 0.04	9.86a ± 0.06	11.38a ± 0.12	16.00a ± 0.11	18.11a ± 0.15	7.23a ± 0.05	4.46ab ± 0.12	1.76a ± 0.06
40	2.47bc ± 0.05	9.51b ± 0.07	10.67b ± 0.15	15.35b ± 0.17	17.55ab ± 0.18	6.98b ± 0.04	4.39ab ± 0.09	1.75a ± 0.06
50	2.49abc ± 0.06	9.37bc ± 0.14	10.36b ± 0.25	14.73bc ± 0.30	16.59bc ± 0.36	6.78bc ± 0.10	4.11abc ± 0.17	1.49a ± 0.09
60	2.40c ± 0.05	9.01cd ± 0.11	9.60c ± 0.20	14.16cd ± 0.35	16.30cd ± 0.44	6.54cd ± 0.10	4.11bc ± 0.15	1.70a ± 0.10
70	2.33bc ± 0.06	8.55d ± 0.13	8.69c ± 0.22	13.10de ± 0.38	14.71de ± 0.49	6.10d ± 0.13	4.14abc ± 0.22	1.45a ± 0.15
80+	2.01d ± 0.05	7.67e ± 0.20	7.27d ± 0.28	11.57e ± 0.39	13.50e ± 0.43	5.37e ± 0.17	3.45c ± 0.21	1.34a ± 0.10

The means within each column designated by different letters are significantly different ($P < 0.05$)

SE Standard error (n = 24)

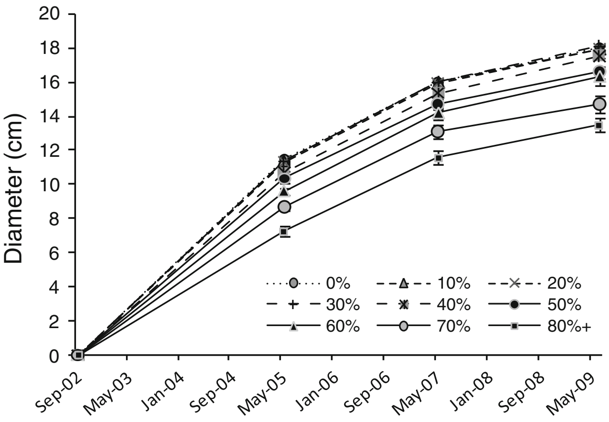


Fig. 1 Mean diameter (±SE) of *E. globulus* trees with different severity of leaf spotting (classes 0–80%) caused by foliar diseases, at 2, 4 and 6 years after damage assessment

for all growth rate traits (height increment on the first 2 years after damage and diameter increment from 2 to 4 and from 4 to 6 years after damage) (Table 3). Initial growth was affected in those trees which suffered heavy defoliation. At the time of damage assessment, mean tree height of heavily defoliated trees (defoliation of 80% or more) differed significantly to the height of trees with lower levels of defoliation or without defoliation. At 2, 4 and 6 years after damage assessment, trees that suffered a defoliation of 50% or more were significantly shorter and had smaller diameters than undefoliated or lightly defoliated trees.

During the first 2 years after damage assessment, the height increment was significantly affected when the defoliation class was equal to or greater than 50%. From 2 to 4 years after damage, diameter increments only were significantly reduced in trees that were 60% defoliated. On the last evaluation period (from 4 to 6 years after damage assessment) diameter increments of undamaged trees significantly differed from trees that presented 60 and 70% defoliation.

The impact of early defoliation on subsequent tree growth declined with time. Growth curves of average diameter of trees in high defoliation classes diverged from the curves of those with low or no defoliation for the first 2 years but thereafter remained approximately parallel (Fig. 2). Even so, the accumulated reduction in diameter of trees severely defoliated (70 or 80% defoliation), expressed as percentage of diameter of undamaged trees, reached 20.0% after 6 years.

Spot severity and defoliation

A negative correlation was observed between severity of leaf spots at 8 months and tree diameter 6 years after damage ($r = -0.175$; $P < 0.001$) and between defoliation at 8 months and tree diameter 6 years after damage ($r = -0.190$; $P < 0.001$). The threshold model revealed that at the last growth evaluation (6 years after damage assessment) an average diameter of 17.7 cm was maintained up until 40% of foliar damage (spot severity and defoliation) (Fig. 3). When foliar damage exceeded 40% a negative relationship was observed, with a reduction of diameter of 0.88 cm with each 10% increase in spot severity and a reduction of 0.90 cm with each 10% increase in defoliation (Fig. 3).

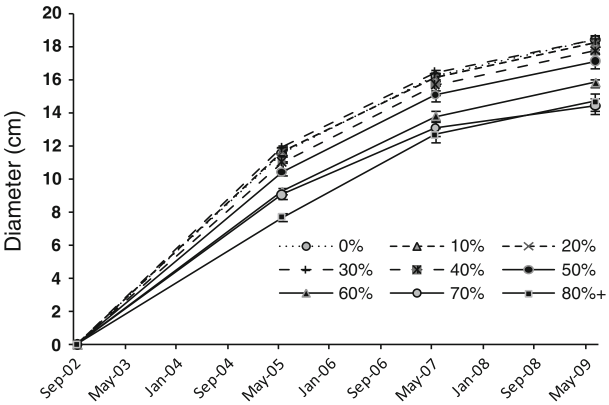
Table 3 Comparisons between defoliation classes (0–80%) of *E. globulus* trees for mean ± SE height at damage assessment and 2 years after damage assessment (a.d.a.), mean ± SE tree diameter (2, 4 and 6 years a.d.a.), mean ± SE height increment (first 2 years a.d.a.) and mean ± SE diameter increment (2–4 and 4–6 years a.d.a.)

Defoliation class (%)	Height (m) at damage assessment	Height (m) 2 years a.d.a.	Diameter (cm) 2 years a.d.a.	Diameter (cm) 4 years a.d.a.	Diameter (cm) 6 years a.d.a.	Height increment (m) first 2 years a.d.a.	Diameter increment (cm) 2–4 years a.d.a.	Diameter increment (cm) 4–6 years a.d.a
0	2.53bcd ± 0.07	9.90ab ± 0.13	11.56ab ± 0.24	16.19ab ± 0.20	18.42a ± 0.24	7.34ab ± 0.09	4.38a ± 0.13	1.81a ± 0.10
10	2.70ab ± 0.05	9.89ab ± 0.13	11.64a ± 0.26	16.07ab ± 0.32	18.15ab ± 0.43	7.19ab ± 0.10	4.10a ± 0.15	1.67ab ± 0.11
20	2.60abc ± 0.05	9.91a ± 0.09	11.62a ± 0.19	16.14ab ± 0.19	18.22a ± 0.22	7.27ab ± 0.05	4.28a ± 0.09	1.71ab ± 0.08
30	2.63bcd ± 0.04	10.07a ± 0.07	11.89a ± 0.15	16.36a ± 0.18	18.42a ± 0.23	7.38a ± 0.05	4.39a ± 0.13	1.82a ± 0.08
40	2.47d ± 0.04	9.69b ± 0.04	11.02b ± 0.09	15.68bc ± 0.09	17.74ab ± 0.09	7.15b ± 0.03	4.45a ± 0.06	1.74ab ± 0.04
50	2.52bcd ± 0.05	9.39c ± 0.11	10.37c ± 0.20	15.05c ± 0.33	17.10b ± 0.40	6.82c ± 0.09	4.48a ± 0.19	1.67ab ± 0.11
60	2.32e ± 0.05	8.80d ± 0.12	9.23d ± 0.19	13.77d ± 0.32	15.79c ± 0.26	6.41d ± 0.12	4.10b ± 0.18	1.51bc ± 0.09
70	2.36cde ± 0.09	8.79cd ± 0.14	9.04de ± 0.25	13.06d ± 0.49	14.39c ± 0.47	6.28cde ± 0.17	3.89ab ± 0.31	1.18c ± 0.11
80+	1.96f ± 0.05	7.90e ± 0.22	7.69e ± 0.28	12.65d ± 0.42	14.65c ± 0.54	5.66e ± 0.20	4.18a ± 0.27	1.51abc ± 0.14

The means within each column designated by different letters are significantly different ($P < 0.05$)

SE Standard error (n = 24)

Fig. 2 Mean diameter (±SE) of *E. globulus* trees with different severity of defoliation (classes 0–80%) caused by foliar diseases, at 2, 4 and 6 years after damage assessment



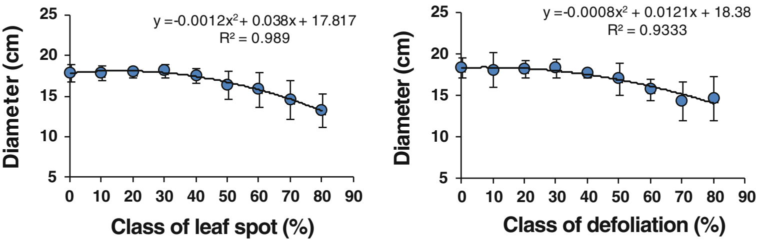


Fig. 3 Threshold model fitted between severity of leaf spots (*left*) and defoliation (*right*) and tree diameter of *E. globulus* 6 years after damage assessment

Effects of foliar damage on mortality

Spot severity

Leaf disease at 8 months after planting significantly affected average mortality in all subsequent assessed periods (Table 4). In the first 2 years after damage, the trees in 0% severity class had on average a mortality rate of 4.2%. Mortality values were similar up to 60% of spot severity class and increased, significantly differing, in trees in higher spotting classes (70 and 80%). From 2 to 4 years and from 4 to 6 years after damage, mortality was significantly higher only on the more severely damaged trees (leaf spot class of 80% or more). Trees with that class of damage had, at the final evaluation (6 years after damage assessment), an accumulated mortality of 71.7%, being significantly higher than the mortality of undamaged or lightly damaged trees (Fig. 4).

Defoliation

Significant differences in average mortality between defoliation classes were found in the first 2 years, and from 2 to 4 years after damage assessment, but not in the last period of evaluation (from 4 to 6 years after damage) (Table 5). In the first 2 years, mortality of trees without defoliation did not significantly differ from mortality of trees in defoliation classes up to 60%. Between 2 and 4 years after damage, trees in the highest defoliation class (80% or more) had a mortality rate significantly higher than trees in any other class of

Table 4 Comparisons between classes of spot severity (0–80%) of *E. globulus* trees for mortality ± SE on the first 2 years, from 2 to 4 years and from 4 to 6 years after damage assessment and for accumulated mortality ± SE at 6 years after damage

Spot severity class (%)	Mortality (%) first 2 years after damage	Mortality (%) 2–4 years after damage	Mortality (%) 4–6 years after damage	Mortality (%) 6 years after damage
0	4.2a ± 1.37	6.5a ± 1.29	4.2a ± 0.87	14.2a ± 1.91
10	5.4a ± 1.35	6.9a ± 1.14	4.1a ± 1.04	15.4a ± 2.18
20	6.0a ± 0.84	4.8a ± 0.58	5.3a ± 0.58	15.2a ± 1.03
30	3.5a ± 1.07	5.1a ± 1.02	7.4a ± 1.10	15.2a ± 1.58
40	7.7ab ± 1.31	6.4a ± 1.06	6.9a ± 0.98	19.6ab ± 1.65
50	12.3ab ± 2.72	8.8a ± 2.79	6.6a ± 1.78	25.8ab ± 3.22
60	11.5ab ± 2.25	9.8a ± 2.11	10.3a ± 1.94	28.4b ± 2.84
70	19.8b ± 5.60	4.6a ± 2.05	3.3a ± 2.37	25.6ab ± 5.61
80+	49.8c ± 4.97	31.2b ± 5.63	22.6b ± 5.23	71.7c ± 13.99

The means within each column designated by different letters are significantly different ($P < 0.05$)

SE Standard error (n = 24)

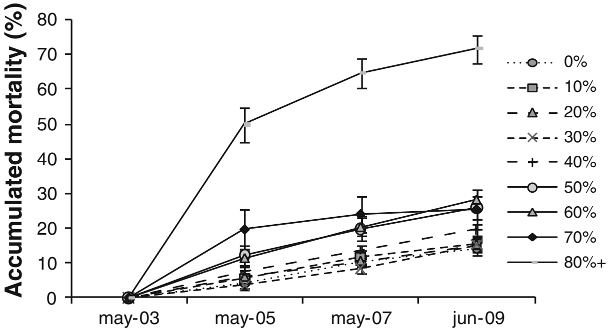


Fig. 4 Average mortality (±SE) of *E. globulus* trees with different severity of leaf spotting (classes 0–80%) caused by foliar diseases, accumulated at 2, 4 and 6 years after damage assessment

defoliation. At the final evaluation (6 years after damage) accumulated mortality values for trees in defoliation classes up to 50% were similar and increased, significantly differing, for trees in higher defoliation classes (60–80%). The accumulated mortality of the more severely defoliated trees (80% defoliation class) reached 74.3%, being also significantly higher than that of trees with 60 and 70% defoliation (Fig. 5).

Discussion

Eucalypt rust (*P. psidii*) and TLD were both present in the trial during the first months; therefore, the severity of leaf spotting measured at 8 months included the symptoms of both diseases. In contrast, as *P. psidii* does not cause defoliation in eucalypts (Ferreira 1983; Coutinho et al. 1998), and because the canopies had not yet closed (which can result in shading of lower leaves and subsequent leaf fall), the defoliation recorded was only the result of TLD. The severity of the leaf spotting and defoliation caused by these diseases were assessed when plants had been in the field for 8 months, although symptoms had probably begun to appear some months earlier. The fact that severely damaged trees had

Table 5 Comparisons between classes of defoliation (0–80%) of *E. globulus* trees for mortality ± SE on the first 2 years, from 2 to 4 years and from 4 to 6 years after damage assessment and for accumulated mortality ± SE at 6 years after damage

Defoliation class (%)	Mortality (%) first 2 years after damage	Mortality (%) 2–4 years after damage	Mortality (%) 4–6 years after damage	Mortality (%) 6 years after damage
0	3.0a ± 0.96	9.9a ± 4.42	5.5a ± 1.65	17.5a ± 4.46
10	1.6a ± 0.88	8.0a ± 2.24	5.9a ± 1.51	14.9a ± 2.36
20	6.2a ± 2.18	5.8a ± 1.22	6.1a ± 0.75	16.7a ± 2.48
30	6.3a ± 1.47	2.2a ± 0.76	4.0a ± 1.47	12.0a ± 1.90
40	7.1a ± 0.66	5.7a ± 0.56	5.8a ± 0.60	17.5a ± 0.92
50	8.0a ± 2.44	5.0a ± 1.32	8.0a ± 1.63	19.6a ± 2.62
60	15.1ab ± 2.97	15.8a ± 2.87	13.6a ± 4.08	37.3b ± 3.69
70	24.9b ± 6.96	4.6a ± 3.40	16.1a ± 7.15	39.5b ± 8.31
80+	54.5c ± 5.42	41.6b ± 7.33	11.2a ± 4.13	74.3c ± 5.50

The means within each column designated by different letters are significantly different ($P < 0.05$)

SE Standard error (n = 24)

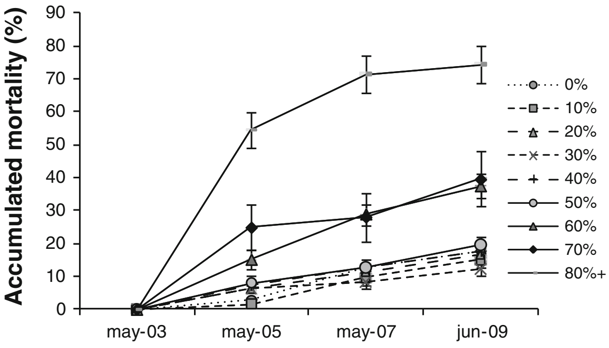


Fig. 5 Average mortality (±SE) of *E. globulus* trees with different severity of defoliation (classes 0–80%) caused by foliar diseases, accumulated at 2, 4 and 6 years after damage assessment

less growth at the time of evaluation indicates that by that time they had already begun to express the negative effect of disease on growth.

The greatest impact of early foliar damage (both leaf spotting and defoliation) on the growth rate of trees occurred during the first 2 years after damage. This could be explained by the fact that both eucalypt rust and TLD mainly affect juvenile foliage, which in *E. globulus* is replaced by adult foliage between the second and third year. While the growth rate declined in trees with a leaf spot severity of 40% or more, or when the defoliation was 50% or more, trees that had low damage were not affected. In this way, 30% of leaf spots or 40% of defoliation seem to be the limits of tolerance for growth. Since defoliation implies a total loss of photosynthetic area, a greater effect on growth, compared with the effect of leaf spots, would be expected. However, the effects of leaf spots and defoliation on tree growth were very similar. This could be explained by the shed of severely spotted leaves occurred after disease assessment, which could potentially confound the results, or by a higher light entry in defoliated crowns, which increases the rate of photosynthesis of surviving leaves and promotes bud sprouting, thus allowing to some degree the compensation of the loss of leaf area (Pinkard et al. 2007). There are several studies that report effects on growth at degrees of damage well below those found here. Carnegie and Ades (2003) and Pinkard et al. (2006a) found that growth of *E. globulus* was affected with a foliar damage as low as 10%. Similar results were reported by Smith (2006), also for *E. globulus,* and by Lundquist and Purnell (1987) for *E. nitens,* who found negative effects on growth when defoliation produced by *Mycosphaerella* spp. exceeded 20 and 25%, respectively. However, on sites of high productivity, Pinkard (2003) found no growth losses in *E. globulus* with up to 40% defoliation, while Rapley et al. (2009) found no effect on growth with less than 60% defoliation in *E. nitens*.

The impact to early foliar damage, even for spotting and defoliation of 80%, was no permanent (type 1 response according with Snowdon 2002) since the reduction in growth was significant only for 2 years in the case of defoliation and for 4 years in the case of leaf spotting. This result contrasts with those reported by Smith (2006) who found on *E. globulus* a permanent reduction of growth (type 2 response) when foliar damage by *Mycosphaerella* was 80% or higher. However, after 6 years, trees with more than 40% of foliar damage had a reduction of approximately 0.90 cm in diameter for each 10% increase of damage. Thus by year seven, very close to the average harvest age of 9 years for cellulose production in Uruguay, trees that suffered severe foliar damage (80% or greater) during the first months of growth, had an accumulated diameter reduction of 20–25% compared with undamaged trees. Several authors have reported growth losses in *E. globulus* of between 4 and 17% for leaf damage of only 20% (Carnegie and Ades 2003; Milgate et al. 2005; Smith 2006). The differences among results of different studies may be related to the influence of site factors, such as the availability of water and nutrients (Smith 2006). Pinkard (2003) suggested that the effects of damage caused by Mycosphaerella leaf disease might be reduced on sites of high productivity because trees have a greater opportunity to recover. Carnegie and Ades (2001) reported lower *Mycosphaerella* effects on trees fertilized with phosphorus and Pinkard et al. (2006a, 2007) observed lower effects of defoliation on trees fertilized with nitrogen than on unfertilized trees. The trial used for this study was located on a fertile well drained soil and received a very intensive silvicultural management, evidenced by the high growth rates achieved. All of these factors could have contributed to minimize the negative effects of the diseases.

In addition to the effect on growth, severe foliar damage during the first 8 months had a detrimental impact on survival, mainly in the immediate 2 years, indicating that the first months of growth are a critical period for trees. However, Collett and Neumann (2002) found no effect of defoliation, even up to 100%, on *E. globulus* survival up to 11 months post damage. In this study, mortality up to 2 years after damage was not affected in those trees that had low severity of spots or low defoliation. However, when either leaf spotting or defoliation exceeded 70%, mortality increased sharply, reaching values of 50% in severely damaged trees. Thus, 60% of foliar spotting or defoliation seems to be the threshold after which the survival of trees begins to be compromised. Carnegie et al. (1994) suggest that the loss of leaf area leads to a reduction in growth rate and this in turn puts the tree on disadvantage to compete with their neighbors and it increases their susceptibility to other pathogens and/or adverse abiotic factors. Considering the whole period of evaluation, leaf spotting affected the subsequent survival only when the severity was 80% or more, while a defoliation of 60% was enough to affect survival. Although the death of the trees cannot be attributed directly to the leaf diseases, the accumulated mortality 6 years after damage of trees with more severe foliar damage, both leaf spots and defoliation, exceeded 70%, being four times higher than mortality of undamaged trees. This aspect is of great importance in Uruguay, where the productivity of *E. globulus* depends mainly on the number of trees per hectare which survive until harvest (Balmelli and Resquin 2005).

In recent years in Uruguay there has been severe damage in young plantations of *Eucalyptus,* caused by *T. nubilosa.* Although this pathogen was not present when the assessment of damage took place in this study (its presence in Uruguay was reported in 2007 (Pérez et al. 2009b), disease surveys conducted since 2008 have shown that *T. nubilosa* is widely distributed in the country, causing an average foliage loss of 40% in spring 2008 and 46% in spring 2009 in the southeast region, the area of greatest importance for *E. globulus* (Balmelli et al. 2009a; Simeto et al. 2010). According to the results obtained in the present study, *E. globulus* trees could withstand this degree of leaf damage without a significant long term loss of growth. However, *T. nubilosa* is currently causing a progressive increase of foliar damage throughout the year (in autumn 2009 the average damage in the above-mentioned survey was 12%, reaching 46% in spring (Balmelli et al. 2009b and Simeto et al. 2010) and in the second year, with 80% defoliation being common (Balmelli et al. 2011). Several authors have shown that repeated defoliation has a greater detrimental effect on *Eucalyptus* growth than an isolated defoliation event (Candy et al. 1992; Abbott et al. 1993; Collett and Neumann 2002; Wills et al. 2004). According to Landsberg and Ohmart (1989), the worst scenario is a chronic, severe loss of functional foliage, causing the cessation of growth, followed by crown dieback and finally tree mortality. In this study there was a single event of damage, so our results do not allow predicting the effects caused by the occurrence of repeated or chronic infections. However, it is very likely that the severity and high frequency of damage events currently recording by *T. nubilosa* in the first and second year in *E. globulus* commercial plantations causes considerable production losses, putting at risk the economical viability of this species.

Eucalyptus globulus used to be planted in all forestry zones of Uruguay, but during the last years, due to the increase of the incidence and severity of diseases, the species has been replaced by *Eucalyptus grandis* and *Eucalyptus dunnii* in all but the southeast region. The extent of damage now being suffered in that region, mainly due to *T. nubilosa*, suggests that if effective disease management methods are not found, in a few years the species could no longer be planted in Uruguay. This already happened in South Africa in the 1930s and more recently in high risk areas in Tasmania where *E. globulus* was replaced by *E. nitens* (Lundquist 1987; Mohammed et al. 2003). Due to economic, environmental and operational constraints, silvicultural options for minimizing the effects of disease damage in eucalypt plantations are very limited. Various strategies have been proposed, including site selection (i.e. avoid planting on high-risk sites) (Carnegie 2007), the application of fungicides (Carnegie and Ades 2003), the increase of tree vigour and tolerance through intensive forestry or by plant defense activators (Stone 2001; Mohammed et al. 2003) or accelerating recovery of trees by remedial fertilizer applications (Pinkard et al. 2006a, b, 2007; Carnegie 2007). However, the most economical and feasible approach to reducing diseases to an acceptable level in eucalypt plantations is the use of resistant planting stock (Carnegie et al. 1994; Dungey et al. 1997; Tibbits et al. 1997; Alfenas et al. 2004; Milgate et al. 2005). With the objective of developing genotypes of *E. globulus* resistant to foliar diseases, INIA and a group of forestry companies initiated a collaborative program of selection and evaluation of clones. Thus, it is expected that deployment of disease resistant clones will reduce the incidence and severity of foliar diseases, allowing the continuity of *E. globulus* cultivation in Uruguay.

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