Adaptability and interspecific variability in growth and leaf traits of eucalypt

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Effective adaptability of plants to new environments can be analysed in terms of survival rate. Analysing the traits that favour adaptation to environmental changes provides a more in-depth understanding of the mechanisms involved. Local adaptation occurs because different environmental factors exert selective pressure across habitats. Understanding the leaf mechanisms underlying plant survival and growth is crucial to determine why local adaptation involves trade-offs. A comparative provenance test on 29 eucalyptus species was conducted to improve our understanding of species adaptation strategies on coastal plains of Pointe-Noire, Republic of the Congo. We studied the different functional traits to determine how plants function and to highlight the different species' adaptive strategies. For each species, survival, growth traits and leaf traits were measured, and the climatic factors of the origin area for each species was taken into account. Cluster analysis was performed on groups of species with a similar growth strategy. The results revealed general trends that explain the physiological mechanisms involved in the species' local adaptation. Indeed, species have survived to current environmental changes by adjusting their specific leaf area plasticity. The 32 provenances of eucalyptus were subdivided into four groups by cluster analysis. The first cluster included two species (*E. pilularis* and *E. peltata*) that are totally unsuited to the local conditions in Pointe-Noire, with the slowest growth rate and smallest specific leaf area. The second cluster contained species that showed a wide variety of growing strategies, allowing them to adapt to local conditions. The third cluster included a species that is specialised in obtaining large quantities of resources, while investing very little in growth. The fourth cluster included species that acquired and used resources at a slow rate. Leaf anatomy was quite responsive to climatic conditions. We evaluated the different strategies and found that eucalyptus species had very diverse functional traits, which may explain their broad ecological range.

Keywords: Adaptability, *Eucalyptus*, Foliar Traits, Growth Strategies, Clustering Analysis

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Introduction

The predictions suggest that Africa will be severely impacted by climate change. There is a significant risk that many forest ecosystems will not have the adaptive capacity to supply vital goods and services (FAO 2015). To face global climate changes, species must adapt to new environments (Jump & Peñuelas 2005, Franks & Hoffmann 2012). Thus, although this is a daunting task, understanding the capacity of species to adapt is increasingly important for conservation and biodiversity management (Loo et al. 2011, Dillon et al. 2014). Such task entails the study of morphological, physiological and phenological characteristics involved in the ecological strategies adopted in response to environmental factors (Pérez-Harguindeguy et al. 2013).

The study of functional traits, especially in plants, has a long tradition in ecological research (Vandewalle et al. 2010). Leaf traits may reflect adaptation mechanisms of plants to the environment; in particular, leaf morphological traits like specific leaf area, leaf thickness and leaf density may

better reflect the changes in environmental factors (Ahrens et al. 2020) such as temperature, light intensity and water status. Conversely, environmental changes can led to unprecedented changes in ecosystems including plant growth strategies.

The trade-offs between functional traits depends on how plants acquire, use and conserve the resources (Reich et al. 2003). The plasticity in functional traits is responsible for much of the phenotypic variation observed in non-native populations, and allows introduced species to grow successfully in new conditions, despite the limited genetic variation (Drenovsky et al. 2012). Genetic diversity within and among stands is the linchpin for current and future forest development, and is crucial for the survival and adaptation of species (Kremer 2000).

The current production context which involves unsustainable land use changes, as well as future climate change scenarios, call for more detailed studies on local varietal adaptation in order to reduce the use of land and optimize future timber production. In this context, the eucalyptus im-

provement programme in the Congo should move towards the selection of plastic genotypes with a more efficient use of resources.

Adapting to different environmental conditions entails costly fitness trade-offs (VanWallendael et al. 2019). Assisted migration involving individuals or populations of a species is potentially an important strategy to respond to climate change, though this approach is not widely used (FAO 2014). In general, several Eucalyptus species show remarkable plasticity, which allows adaptation to hostile environments, especially nutrient-poor soils (Cossalter et al. 1999) and hot arid areas (Saadaoui et al. 2018). Although certain species are known to better perform on poor soils (Laclau et al. 2016), few studies focused on the physiological basis of this ecological feature.

In the Congo, the first attempts to introduce eucalyptus date back to 1953. Subsequently, several species and provenance trials have been conducted. Several studies on their productivity revealed that only some species were adapted to local conditions (Groulez 1964). However, leaf relationships explaining the species' responses have not been studied in the Congo, especially in Pointe Noire, where eucalyptus plantations have been established.

This study aims to understand the local adaptation mechanisms of 29 eucalyptus species using leaf traits in the Republic of Congo. We asked three research questions: (i) Do functional traits vary among eucalyptus species at different ages? (ii) What are the trade-offs among functional traits? (iii) Can the potential adaptation of eucalyptus species in the Pointe-Noire conditions be determined by examining the relationships between growth and functional traits?

Material and methods

Study site and sampling

This study is based on data from a provenance trial conducted at the Kissoko forestry station (04° 45′ 51″ S, 11° 59′ 21″ E) in the south of Republic of the Congo. Mean annual rainfall is approximately 1200 mm; daily temperature is 25-26 °C in the rainy season (October to May) and 22-23 °C in the dry season (June to September). The average monthly rainfall during the rainy season ranges from 83 to 92 mm, and during the dry season from 1 to 20 mm (Jamet & Rieffel 1976). Relative humidity is high (85%) with low seasonal variability (2%). The soil is ferralitic and highly desaturated in bases (Nzila 2001).

We conducted the present study in a Eucalyptus provenance trial which included 32 provenances belonging to 29 species (Tab. 1). The seeds used for seedling production were collected from different parts of Australia (North, North East, East and South East coasts) and Indonesia (Fig. 1).

Tree measurements

The experimental design consisted of 4 blocks of 128 plots (32 per block); each plot contains 9 trees representing a single provenance. The plots were randomly distributed into the blocks. Originally, each plot was planted with spacing of 4.70 × 2.65 m (about 800 trees ha⁻¹). Trees were measured at two dates: after 15 months (1.2 years) since their establishment (in February during the short dry season) and after 54 months (4.5 years, in April during the main rainy season).
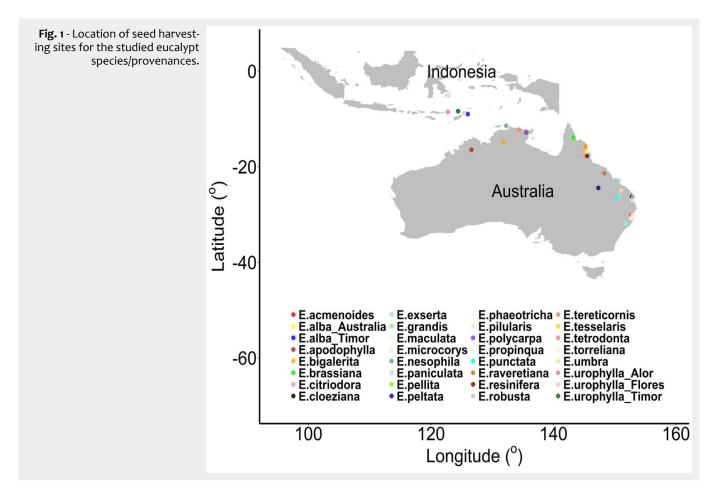
We first evaluated the survival rate (SR, %) of the trees at each age at the plot level, and the difference in survival between 54 and 15 months (eqn. 1):

$$SR = \frac{n_{live}}{n_{tot}} \cdot 100 \qquad (1)$$

where n_{live} is the number of live trees at the plot level and n_{tot} is the total number of tree established in the plot. On each tree, we performed non-destructive quantitative measurements including collar circumference, total height and leaf measurements. Collar circumference (CC, cm) was measured with a tape around the trunk base. Total tree height (HT, m) was measured with a Vertex® IV (Haglöf, Långsele, Sweden) hypsometer at a distance approximately equivalent to tree height. Leaf variables, including specific leaf area (SLA), leaf thickness (LT, mm) and leaf density (LD, kg m⁻³) were measured for 10 leaves per tree harvested from the upper and lower crown. The 10 adult leaves were chosen with a fully expanded blade (juvenile and senescent leaves were excluded) and free of damage. Leaf thickness was measured immediately after leaf removal with a digital micrometer (Mitutoyo, Kawasaki, Japan) at a point mid-way along the length of the leaf and mid-way between the median and leaf edge. Leaf area was measured in the laboratory using scans and the software MatLab® (MathWorks Corp., Natick, MA, USA) for image processing.

Leaves were then dried at 65 °C to constant weight. The dry weight was used in conjunction with the area measurements to calculate specific leaf area (SLA, m² kg⁻¹)

Tab. 1 - List of studied species and their subgenera.

Species code	Subgenus	Species	Provenance
1	Alveolata	E. microcorys	Beerburrum (Australia)
2	Blakella	E. tesselaris	Mareeba (Australia)
3	Corymbia	E. citriodora	Ord Irvinbanck (Australia)
4		E. maculata	Rockhampton (Australia)
5		E. nesophila	Jimmy's Creek, Coboutg Peninsula (Australia)
6		E. peltata	Mantuan (Australia)
7		E. polycarpa	Est Gue Goyder river (Australia)
8		E. torelliana	Flaggy Creek, QLD (Australia)
9	Eucalyptus	E. acmenoides	Wild Cattle (Australia)
10		E. phaeotricha	Noosa Heads (Australia)
11		E. pilularis	Moleton (Australia)
12		E. umbra	Elliot river (Australia)
13	Eudesmia	E. tetrodonta	SE Maningrida (Australia)
14	Idiogenes	E. cloeziana	Gympie (Australia)
15	Minutifructus	E. raveretiana	Exe Creek, Ouest Mckay (Australia)
16	Symphyo-myrtus	E. alba	Sud Cooktown (Australia)
17		E. alba	Natar Bora (Timor)
18		E. apodophylla	Ouest Pentecost river, Gibb River (Australia)
19		E. bigalerita	S-O Katherine Kununurra river (Australia)
20		E. brassiana	Cape York peninsula, Coen (Australia)
21		E. exserta	Mckay Rockhampton (Australia)
22		E. grandis	Est Atherton, QLD (Australia)
23		E. paniculata	Nord Raymond Terrasse (Australia)
24		E. pellita	Pinnacle (Australia)
25		E. propinqua	Clouds Creek SF Grafton (Australia)
26		E. punctata	Barakula SFNW Chinchilla (Australia)
27		E. resinifera	10km Ravenshoe (Australia)
28		E. robusta	Noosa (Australia)
29		E. tereticornis	Helenvale (Australia)
30		E. urophylla	Mte Lewotobi (Indonesia)
31		E. urophylla	Flores Arbau Ulu (Indonesia)
32		E. urophylla	Arafalaca, Ouest Alor (Timor)

Fig. 1 - Location of seed harvesting sites for the studied eucalypt species/provenances.

using the following formula (eqn. 2):

$$SLA = \frac{LA}{LM} \qquad (2)$$

where *LA* and *LM* are respectively the area and the dry mass of 10 sampled leaves. The leaf density (*LD*, kg m⁻³) was calculated using *SLA* and *LT* (Sefton et al. 2002) as follows (eqn. 3):

$$LD = \frac{1}{SLA \cdot LT} \qquad (3)$$

Climate data

We used data from the meteorological stations (http://www.bom.gov.au/) at each site where we collected the seeds of eucalyptus species in Australia and Indonesia. The following 18 climatic variables were considered (Tab. S1 in Supplementary material): 1- average annual rainfall (AAR); 2- maximum annual rainfall (MAR); 3- minimum annual rainfall (mAR); 4- maximum monthly average rainfall (MMAR); 5- minimum monthly average rainfall (mMAR); 6- number of months of rainfall less than 50 mm (NR50); 7- average annual temperature (AAT); 8- maximum monthly temperature (MMT); 9- minimum average temperature (mMT); 10- maximum monthly average temperature (MMAT); 11- minimum monthly average temperature (mMAT); 12- number of days below 40 °C (ND40); 13- number of freezing days (NFD); 14- annual potential evapotranspiration (PE); 15- annual solar radiation (SR); 16- altitude (A); 17- longitude

(Long); 18- latitude (Lat). Data on the same 18 climatic variables were also collected at the planting site (Pointe-Noire).

Statistical analysis

The following linear mixed model was used to perform ANOVA for survival rate (at the plot level), functional traits and growth (at tree level – eqn. 4):

$$y = \mu + X_b b + Z_{sb} sb + Z_{sp} sp + \varepsilon \qquad (4)$$

where *y* is the vector of the response variable; μ is the overall mean; *X* and *Z* are the design matrix connecting the fixed and random effects to the data, respectively; *b* is a vector of fixed effects due to the blocks; $sb \sim N(0, \sigma^2_{sbld})$ is a vector of the random subgenus effect; σ^2_{sb} is the variance related to the subgenus effect; Id is the identity matrix; $sp \sim N(0, \sigma^2_{spld})$ is a vector of the random species effect; σ^2_{sp} is the variance related to the species effect; ε $\sim N(0, \sigma^2_{\varepsilon ld})$ is a vector of the residual effect. Before performing ANOVA on survival rate, we calculated an angular arc sinus transformation (eqn. 5)

$$p' = \arcsin \sqrt{p} \qquad (5)$$

where *p'* is the transformed value of survival rate and *p* is the original value of survival rate for each plot.

To detect covariations among functional traits, we used pairwise Pearson's multiple correlation tests to analyse bivariate and

multivariate relationships. To analyse the multivariate relationships, a principal component analysis (PCA) was performed in order to identify the similarities between the climatic characteristics of the area of origin of the species and the area where the species were introduced. At provenances level, functional traits were estimated from the tree measurements at 15 and 54 months (Tab. S2 in Supplementary material). The *k*-means partitioning method was performed to assign observations to clusters relating to growth and functional traits at the age of 54 months.

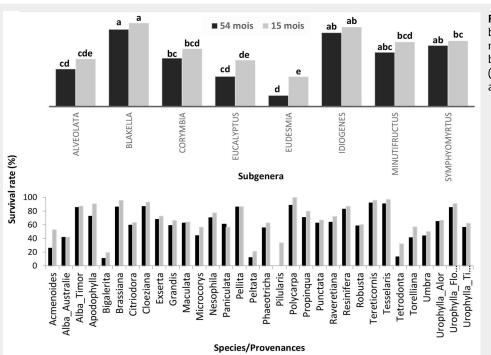All statistical analyses were performed using the open-source software R v. 4.0.3.

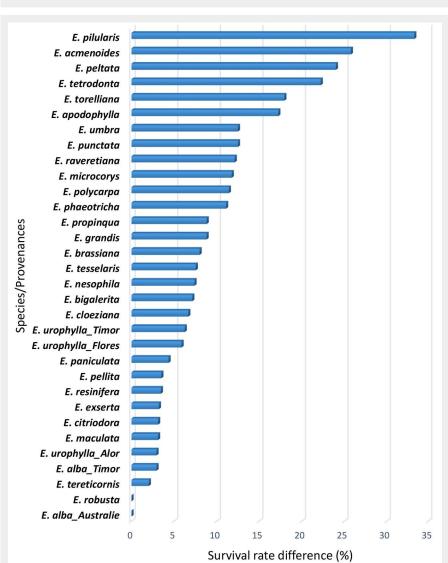**Results**

Variation of functional traits between species

Survival rate

The survival rate was significantly different between subgenera at 15 (P = 0.0003) and 54 months (P<0.001). Likewise, a similar effect was observed among species at 15 months (P<0.001) and at 54 months (P<0.001). At both ages, the subgenera Blakella and Idiogenes had the highest survival rates of 91% and 87%, respectively, whereas the subgenera Eucalyptus and Eudesmia had the lowest survival rates of 35% and 13%, respectively (Fig. 2). The species *E. tetrodonta* (17%), *E. peltata* (12%) and *E. pilularis* (0%) had the lowest survival rates at 54

Fig. 2 - Mean values of survival rate by subgenera and species/provenances. Different letters above the bars indicate significant differences (p<0.05) between group means after Tukey's test.

Fig. 3 - Difference in survival rate (%) of eucalyptus species/provenances between 54 and 15 months after tree establishment.

months, while *E. tereticornis* (96%) and *E. tesselaris* (97%) had the highest survival rates at the same age (Fig. 2). The survival rate of *E. robusta* and *E. alba_*Australia remained the same between 15 and 54 months. That of species like *E. tereticornis, E. alba_*Timor, *E. urophylla, E. maculata, E. citriodora, E. exserta, E. resinifera* and *E. pellita* did not change considerably, while for *E. pilularis, E. acmenoides, E. peltata, E. tetrodonta, E. torelliana* and *E. apodophylla*, the change of survival rate over time is very marked (Fig. 3).

Growth and leaf traits

Growth traits increased according to ages from 15 months to 54 months. The ANOVA results showed significant differences between species of the same subgenus and between subgenera for all traits (Tab. 2). Leaf thickness (*LT*) remained almost stable, while specific leaf area (*SLA*) increased and leaf density (*LD*) decreased from 15 to 54 months. The subgenera Symphyomyrtus, Idiogenes, Eucalyptus and Corymbia showed greater variations in *LT*, whereas their *SLA* values remained low. In contrast, the subgenera Minutifructus, Eudesmia, Blakella and Alveolata had high *SLA* and low *LT* values. The Flores provenance of *E. urophylla* showed one of the best growth rates and a high *SLA* value.

Correlations between traits

The juvenile-adult correlations (Fig. 4) indicated close ranking at different ages for *LT* and height. In contrast, the *LD* ranking changed completely from 15 to 54 months. There was a strong and positive correlation between height and collar circumference at 15 months (Pearson's $r = 0.79$) and 54 months (Pearson's $r = 0.84$), and a moderate and positive correlation between

growth and survival (Pearson's *r* = 0.41 to 0.57). Between 15 and 54 months, the correlation of individual *SLA* values was moderate (Pearson's *r* = 0.49). Further, there was a weak correlation between growth and *SLA* (Pearson's *r* = 0.10 to 0.28). We found a negative correlation between *SLA* and *LD* (Pearson's *r* = -0.59 to -0.50), as well as between *SLA* and *LT* (Pearson's *r* = -0.67 to -0.42), and also between *LD* and *LT* (Pearson's *r* = -0.50 to -0.17) from 15 to 54 months.

PCA and clustering analysis

The PCA results indicated that the main components (two first axes) account for 66% of the total variation (Fig. 5). The two main components were associated with temperature and solar radiation (41.16%) and rainfall (24.84%), respectively. The results showed that species like *E. tereticornis* (from Halenvale), *E. nesophilla* (Coboutg peninsula), *E. tetrodonta* (South Est Maningrida), *E. polycarpa* (Est Gue Goyder river), *E. brassiana* (Cape York peninsula) and *E. alba* (Timor) were found in areas where the climatic conditions are similar to the Congolese coastal savannas (Fig. 5). On the contrary, *E. punctata, E. maculata, E. acmenoides* and *E. resinifera* were originated from areas whose climatic conditions differed from the area of introduction.

The results of the cluster analysis suggest that the 32 provenances analyzed can be subdivided into four groups (Fig. 6). The first cluster included *E. pilularis* and *E. peltata*, with the lowest growth rate and the smallest *SLA*. At the end of the trial, no individuals representing *E. pilularis* were present. The second cluster contained species with a wide variety of responses in terms of their growth strategy. Some species had a very high growth rate and a large *SLA*, for example, *E. cloeziana, E. urophylla*_Flores and *E. alba*_Timor. This clus-

Tab. 2 - Descriptive statistics and Anova results of variables studied at 15 and 54 months. (SR): survival rate (%); (HT): tree height (m); (SLA): specific leaf area (m² kg⁻¹); (LT): leaf thickness (mm); (LD): leaf density (kg m⁻³); (SD): standard deviation; (Max): maximum; (Min): minimum. 15 and 54 indicate the age tree (in months).

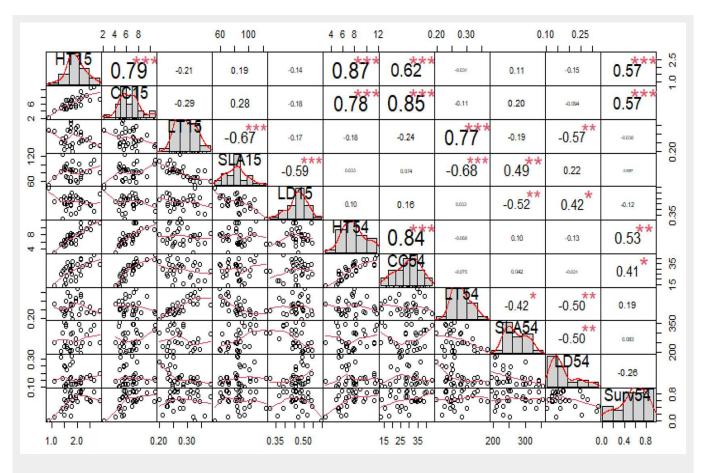| Traits	Unit	Mean	SD	Max	Min	(Pr > F)		
						Block	Sub-genus	Species/Provenance
SR15	%	68.93	21.07	100.00	17.85	0.273	0.0003	<0.0001
SR54	%	61.24	23.40	91.83	0.00	0.177	<0.0001	<0.0001
HT15	m	2.02	0.87	5.55	0.55	0.195	0.023	0.003
HT54	m	7.99	3.26	18.60	1.50	<0.0001	<0.0001	<0.0001
CC15	cm	7.27	3.87	26.12	0.94	0.188	0.068	0.003
CC54	cm	29.98	12.84	72.80	1.50	<0.0001	<0.0001	<0.0001
SLA15	m² kg⁻¹	80.43	16.79	148.84	45.76	0.392	<0.0001	<0.0001
SLA54	m² kg⁻¹	259.73	102.00	529.46	38.36	<0.0001	<0.0001	<0.0001
LT15	mm	0.28	0.05	0.46	0.14	0.0002	<0.0001	<0.0001
LT54	mm	0.27	0.05	0.42	0.16	<0.0001	<0.0001	<0.0001
LD15	kg m⁻³	0.46	0.06	0.60	0.32	<0.0001	<0.0001	<0.0001
LD54	kg m⁻³	0.18	0.11	1.15	0.08	<0.0001	<0.0001	<0.0001

Fig. 4 - Correlations between juvenile and adult traits. (HT): total tree height (m); (CC): collar circumference (cm); (LT): leaf thickness (mm); (SLA): specific leaf area (m² kg⁻¹); (LD): leaf density (kg m⁻³); 15 and 54 indicate the age of tree (in months).
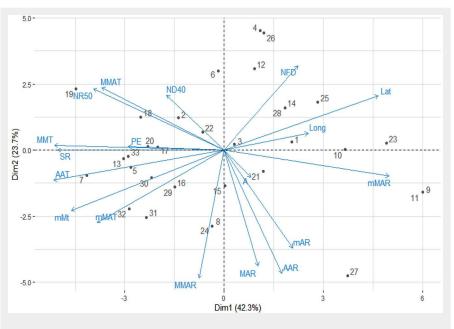
Fig. 5 - Principal component analysis biplot. Numbers refer to the different eucalypt species/provenances. (1): *E. microcorys*; (2): *E. tesselaris*; (3): *E. citriodora*; (4): *E. maculata*; (5): *E. nesophila*; (6): *E. peltata*; (7): *E. polycarpa*; (8): *E. torelliana*; (9): *E .acmenoides*; (10): *E. phaeotricha*; (11): *E. pilularis*; (12): *E. umbra*; (13): *E. tetrodonta*; (14): *E. cloeziana*; (15): *E. raveretiana*; (16): *E. alba_*Australia; (17): *E. alba_*Timor; (18): *E. apodophylla*; (19): *E .bigalerita*; (20): *E. brassiana*; (21): *E. exserta*; (22): *E. grandis*; (23): *E. paniculata*; (24): *E. pellita*; (25): *E. propinqua*; (26): *E. punctata*; (27): *E. resinifera*; (28): *E. robusta*; (29): *E. tereticornis*; (30): *E. urophylla_*Mte Lewotobi; (31): *E. urophylla_*Flores; (32): *E. urophylla_*Timor; (33): Pointe-noire (planting site).

ter also included species with medium growth rates and low *SLA*, like *E. robusta* and *E. brassiana*, and species with slower growth and higher *SLA*, like *E. toreliana*. Altogether, cluster 2 can be divided into two others clusters: (i) C2a including provenances 14, 31, 22, 24, 30, 4, 3 (Fig. 6) having a good growth and survival, as well as medium-high *SLA*; and (ii) C2b including provenances 21, 8, 20, 7, 27, 29, 23, 28, 10, 32, 5, 5, 17 (Fig. 6) with various characteristics. The species in cluster 3 had large *SLA*
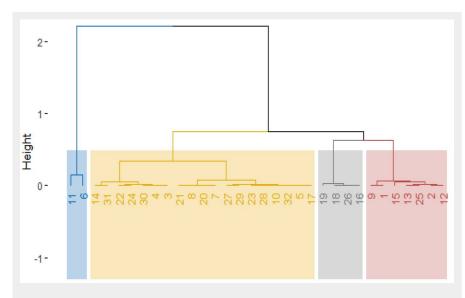
values but slow growth. The last cluster includes the species with slow growth and small *SLA*, like *E. tesselaris*.

Discussion

Variability of functional traits among species

Survival is the first fundamental criterion to assess adaptation (Gardner 2017). Plants compete for light, water, nutrients, air and space to survive. In our study, ranking species according to their survival rate changed significantly from 15 months to 54 months. The 100% mortality of *E. pilularis* trees after 54 months from establishment reflects their very poor adaptation to the local conditions in Pointe-Noire. This result corroborated those obtained by Brezard (1982) in the same region. It is worth noting that the climate of the original area for *E. pilularis* is very different from that at the plantation site. However, this result needs to be confirmed as only 9 plants of this species were initially included in the experiment (Tab. S2 in Supplementary material).

Species with a low survival rate but good growth, like *E. citriodora*, were not necessarily poorly adapted in the study area, as several factors may be involved, such as plantation density leading to competition between species. Indeed, intense competition between adjacent plots could have led to differences between fast- and slow-growing species, with the suppression of the latter species (Hunde et al. 2007).

Our study revealed a difference of survival rate and growth both among species of the same subgenus and among subgenera. One of the characteristics in which species of the same or different habitats vary is their growth potential. In a common environment, trade-offs between functional traits are the basis for the observation of different growth strategies and finally different strategies of adaptation (Reich et al. 2003). Adaptations can be divided into two general categories: functional adaptations, which help an organism to survive in its environment; and growth and reproductive adaptations, which help an organism to grow and reproduce successfully. Both are required to ensure the "full adaptation".

Correlation

All growth traits were positively correlated between 15 and 54 months since tree establishment. The stability of leaf thickness and the decrease in leaf density led to an increase in *SLA* between 15 and 54 months. This result can be explained by the fact that water was a limiting factor at 15 months, while at 54 months this was less limiting because of the root development over a larger area and greater depth (Thongo M'Bou 2008).

Our results showed negative and significant correlations between *SLA*, *LT* and *LD*. These results corroborated those of Vile et al. (2005) and Niinemets (1999). Low val-

Fig. 6 - Cluster dendrogram of species/provenances. Cluster 1: (11) *E. pilularis* and (6) *E. peltata*; Cluster 2: (14) *E. cloeziana*, (31) *E. urophylla_*Flores, (22) *E. grandis*, (24) *E. pellita*, (30) *E. urophylla_*Mte Lewotobi, (4) *E. maculata*, (3) *E. citriodora*, (21) *E. exserta*, (8) *E. torelliana*, (20) *E. brassiana*, (7) *E. polycarpa*, (27) *E. resinifera*, (29) *E. tereticornis*, (23) *E. paniculata*, (28) *E. robusta*, (10) *E. phaeotricha*, (32) *E. urophylla_*Timor and (5) *E. nesophila*, (17) *E. alba_*Timor; Cluster 3: (19) *E. bigalerita*, (18) *E. apodophylla*, (26) *E. punctata* and (16) *E. alba_*Australia; Cluster 4: (9) *E. acmenoides*, (1) *E. microcorys*, (15) *E. raveretiana*, (13) *E. tetrodonta*, (25) *E. propinqua*, (2) *E. tesselaris* and (12) *E. umbra*.

ues for SLA due to thicker and/or denser leaves contribute to leaf life span, nutrient retention and protection against desiccation (Ackerly et al. 2002). From the correlations between height and functional traits, we were able to identify the different species' strategies to acquire and use the available environmental resources.

Species' adaptive strategies

Functional traits play a critical role in the adaptation process (Bouvet et al. 2020). Understanding local adaptive species traits according to climatic factors is key when it comes to developing plantation strategies (Wright et al. 2018). It was firstly assumed that species from areas with climatic conditions similar to those occurring in Pointe-Noire would be better suited than those from areas with a different climate. This hypothesis was only verified for one species, *E. tereticornis*, which achieved a good balance between resource acquisition and use. However, some species from areas with very different climatic characteristics compared to those at Pointe-Noire appear to be more suitable, as in the case of most species in cluster 2. These species thrive in humid, subhumid, tropical or subtropical regions with rainfall of 1100 to 1500 mm and a dry season lasting 1 to 5 months. A similar rainfall pattern is found in the Congo. The eucalypts' adaptations allow many species to thrive under often difficult conditions, with poor soils and highly variable rainfall. Consequently, a small number of eucalypt species are grown very successfully in plantations (Saadaoui et al. 2018). Genetic diversity is valuable for species survival and adaptation. Some individuals carry genes that allow them to respond to environmental constraints and enhance their adaptive capacity more successfully than others (Savolainen et al. 2013). Genetic variations can, therefore, modulate the local effects of environmental change (Parmesan 2006). Local adaptation can be constrained by natural selection and gene flow (Kawecki & Ebert 2004, Leimu & Fischer 2008). Previous studies revealed that local adaptation among different populations (and provenances) of *E. camaldulensis* could be due to variation in adaptive phenotypes, which correspond to the local environment. These include morphological traits (growth form, leaf thickness, stomatal density and phenology – James & Bell 1995), growth rate (Otegbeye 1985), wood properties (El-Lakany et al. 1980), physiological responses (Morshet 1981), and drought tolerance (Lemcoff et al. 2002). The adaptive clines inferred from phenotypic variation were supported by evidence of genetic adaptation in coding genes (Thumma et al. 2012).

Leaf traits do not vary randomly, but depend on trade-offs from investing carbon in leaves (Wright et al. 2004). Specific leaf area is an important functional trait because it is an indicator of relative growth rate, stress tolerance and leaf life span. It is generally assumed that intraspecific *SLA* variation is largely due to environmentally induced phenotypic plasticity (Liu et al. 2017). However, genetic effects should also be considered such as local adaptation or genetic drift (Scheepens et al. 2010). At the interspecific level, functional traits can explain community composition and structure (Lavorel & Garnier 2002, Díaz et al. 2004). They can also be used to classify plant species' strategies according to Grime (1977) or to explain species occurrence and distribution (Díaz et al. 1998). Our results suggest that population of different eucalypt species could be able to survive under different climate conditions by adjusting their *SLA*. In the long term, phenotypic plasticity may allow populations to adapt genetically to environmental changes *via* genetic assimilation (Price et al. 2003).

The results of cluster analysis showed that the first group includes two species which are totally unsuited to the local conditions in Pointe-Noire. Conversely, species of the second cluster can adapt to the local conditions in Pointe-Noire because of their greater plasticity. Some species can rapidly exploit the environmental resources and allocate them to development, while others show a slow resource acquisition but a fairly efficient use. We found that species in the third cluster had strategies allowing them to acquire resources rapidly with a slow return in terms of investment on leaf economic spectrum (Wright et al. 2004). According to Lambers & Poorter (1992), these species are specialised in acquiring large quantities of resources (water, light, carbon), while investing very little in growth. Finally, the fourth cluster includes species whose strategy involves a slow acquisition and use of resources, thus resulting in their poor growth due to the reduced photosynthetic capacity.

Conclusion

Our study provides important advances for the understanding the adaptive strategies of *Eucalyptus* spp. in the experimental conditions at Pointe-Noire, Republic of Congo. Based on leaf traits and growth, four major groups of species were identified: (i) species with a large *SLA* and good growth; (ii) species with a small *SLA* and poor growth; (iii) efficient species with small *SLA* and very good growth; and (iv) species with large *SLA* and poor growth. The species included in the groups (ii) and (iv) are the least suitable to the environmental conditions at the trial site; those in the group (iv) maximise the capture of resources, but have poor growth.

Following this study, it would be relevant to determine the differential expression of genes involved in growth in different provenances and contrasting environments. Further study should focus on species' different strategies for acquiring and using resources in their area of origin and the area of introduction. A combined phenotypic and genomic approach (Steane et al. 2017) should be included in future studies of plant adaptation to local conditions in the Republic of the Congo.

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Supplementary Material

Tab. S1 - Climatic variables at the sites of seed origin and at the planting site.

Tab. S2 - Characteristics of the studied species indicating provenance and number of sampled trees at the beginning of the experiment.

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