



Growth-survival trade-offs and the restoration of non-forested open ecosystems

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ABSTRACT

The growth-survival trade-off has been extensively documented for phanerophyte species, whereas there is little evidence for non-phanerophyte species. However, information on the growth-survival trade-offs in non-phanerophyte species could be of great use in non-forested open ecosystem restoration by providing insights for plant production and transplantation, thus impacting the planning of cost-effective restoration actions. In this study, we explored the relationship between growth and survival of individual plants of non-phanerophyte species used in a coastal dune restoration project, and we investigated whether plant functional traits explained patterns of trade-off between growth and survival. We monitored 355 individual plants of 13 perennial non-phanerophyte species belonging to foredune and transition dune communities every 30 days after planting and calculated relative growth and survival rates. In addition, we regressed the relationship between growth and survival on values of leaf and floral traits. We found that, besides being a widely recognised axis of life history variation in phanerophyte species, the growth-survival trade-off can also be observed in perennial non-phanerophyte species. Species of different coastal dune communities (i.e., foredune vs. transition dune communities) differed with respect to the growth-survival trade-off, with plant species of foredune communities exhibiting higher growth but lower survival rates than plant species of transition dune communities. Leaf dry matter content and mean number of floral displays explained species position on the growth-survival trade-off axis; species with relatively high growth and low survival rates exhibited an acquisitive strategy, with low values of leaf dry matter content, but also a low sexual reproductive effort, as revealed by low number of floral displays. In contrast, plant species with relatively low growth and high survival rates exhibited a conservative strategy but also high sexual reproductive effort, suggesting that trade-offs occur in resource allocation among vegetative and reproductive plant structures. The trade-off we found between growth and survival in perennial non-phanerophyte species provides useful insights for planning cost-effective ecosystem restoration actions of non-forested open ecosystems, especially when the actions are nature-based and involve planting individual plants. The results of this study suggest that individual plant production for coastal dune restoration should disproportionately target plant species of foredune communities because they have low survival rates associated with low sexual reproductive effort. Planning plant production based on ecological knowledge of plant species' growth and survival after planting in the field could help achieve restoration goals while meeting project cost-effectiveness requirements.

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1. Introduction

The European Union (EU) has committed to an ambitious biodiversity recovery plan through its Biodiversity Strategy for 2030 and the Green Deal, which aims to achieve a sustainable and carbon-neutral economy by 2050. These policies aim to halt biodiversity loss and move toward sustainable development, with a focus on restoring degraded ecosystems, expanding the network of protected areas, and improving the effectiveness of management, governance, and funding. According to EU policy (EC, 2022), restoring ecosystems to good condition means promoting nature-based solutions that help halt biodiversity loss and mitigate climate change, ultimately linking healthy, functioning ecosystems to human well-being (Gittman et al., 2014; Guerry et al., 2015).

Over the past decade, major ecosystem restoration efforts have focused on forests, and forest restoration efforts have become increasingly common worldwide (Löf et al., 2019). However, this tree planting-focused strategy to address the climate crisis has led to forest restoration and/or recovery being viewed as a panacea (Tölgyesi et al., 2022) and has resulted in what Silveira et al. (2022) have termed “biome awareness disparity”, i.e., an insufficient appreciation of the importance of all biomes in conservation and restoration plans. In particular, non-forested open ecosystems such as grasslands have been shown to be extremely valuable due to their unique biodiversity (Dengler et al., 2014; Dixon et al., 2014) and their significant role in providing important ecosystem services such as carbon sequestration, water regulation, pollination, and erosion control (e.g., Bengtsson et al., 2019; Favarin et al., 2022).

Among non-forested open ecosystems (Biurrun et al., 2021), coastal dune ecosystems dominated by non-forested plant communities provide an invaluable natural first line of defence that can buffer erosion and protect areas further inland from the effects of sea-level rise and exceptional storms, making them an important landscape element for climate change adaptation (Guerry et al., 2022). In addition to buffering the impacts of sea-level rise and exceptional storms, coastal dune ecosystems support climate change mitigation through carbon sequestration (Drius et al., 2016; Del Vecchio et al., 2022), provide recreational opportunities (Della Bella et al., 2021), habitat for key plant and animal species (Fantinato, 2019), and other services (Everard et al., 2010; Drius et al., 2019). Nevertheless, they are currently among the most threatened ecosystems worldwide (Defeo et al., 2009), and most Mediterranean non-forested coastal dune habitats are classified as “threatened” at the European level (Janssen et al., 2016). The causes of the decline of coastal dune ecosystems are recurrent worldwide and include intense urbanisation that results in coastal dunes being replaced by settlements, infrastructure, and tourism-oriented facilities (Sperandii et al., 2018). In addition to the loss and fragmentation of coastal dunes (Malavasi et al., 2016), tourism has significantly impacted remaining coastal dune ecosystems through trampling and the spread of invasive alien plant species (Sperandii et al., 2019; Buffa et al., 2021). Sea-level rise and exceptional storms would therefore exacerbate local anthropogenic impacts to coastal dune ecosystems while also threatening urbanised coastal areas. This creates an urgent need for coastal dune restoration through viable and cost-effective nature-based solutions (Pontee et al., 2016) that can promote both biodiversity conservation of coastal dunes and ecosystem service delivery (Gómez-Pina et al., 2002).

A common element of nature-based solutions for coastal dune restoration in the Mediterranean is the planting of individuals of perennial species (Winters et al., 2020). Planting individuals of perennial species is a prerequisite for restoring dune function and increasing coastal resilience, even in areas with scarce sand supply (Muñoz-Vallés and Cambrollé, 2014). Plants stabilise sediment with their root systems and retain additional windblown sediment, which promotes dune growth (Bessette et al., 2018). However, despite the central role of plants in coastal dune restoration, our knowledge on the restoration of biodiverse, non-forested coastal dune systems remains limited. In most cases, the effectiveness of restoration actions has been quantified based on the physical characteristics of dunes (e.g., D’Alessandro et al., 2020; Walker et al., 2013), while the success of plant establishment has been neglected (e.g., Long et al., 2013; Calafat et al., 2021).

At the level of individual plant, most restoration studies have focused on phanerophyte species and selected plant growth and survival (also referred to by the complementary concept of mortality) as attributes to quantify establishment effectiveness (Bruel et al., 2010; Zamith and Scarano, 2006; Anton et al., 2015; Bayen et al., 2016; Macera et al., 2017). Current knowledge of growth and survival has been shown to be essential for understanding phanerophyte species dynamics and forest functioning (Fan et al., 2022). In addition, demographic trade-offs between growth and survival have been hypothesised to play a critical role in ensuring species coexistence in forests (Poorter et al., 2008). A demographic trade-off between growth and survival can be viewed as an axis of life-history variation in plant species, with fast-growing, short-lived plant species at one end of the axis and slow-growing, long-lived species at the other (Wright et al., 2010). Fast-growing species are able to accumulate biomass without tolerating stressful conditions, resulting in high growth rates but also low survival rates. In contrast, slow-growing species exhibit a more conservative strategy and tolerate stressful conditions, resulting in slower growth rates but also higher survival rates (Rozenaal and Chazdon, 2015). Although the growth-survival trade-off has been extensively documented in phanerophyte species, little attention has yet been paid to non-phanerophyte species. Evidence of the growth-survival trade-off in non-phanerophyte species has been experimentally documented (Balachowski et al., 2016; Balachowski and Volaire, 2018; Bristiel et al., 2018), however information on the growth-survival trade-offs in real-world systems could be of great use in ecosystem restoration by providing insights for individual plant production and transplantation, thus impacting the planning of cost-effective restoration actions.

In this study, we investigated the relationship between growth and survival of individuals of non-phanerophyte species used in a coastal dune restoration project on the northern Adriatic coast (Mediterranean Basin; Italy). Coastal dune ecosystems are characterised by pronounced environmental gradients that lead to the formation of a zonation of plant communities arranged parallel to the coastline (Torca et al., 2019; Del Vecchio et al., 2020). According to Ciccarelli (2015), the resource allocation strategy changes significantly among plant species belonging to different coastal dune communities, with the acquisitive strategy dominating in the foredune community, while the conservative strategy prevails in the plant communities of transition dunes. Therefore, we hypothesise that plant species of foredunes have higher growth rates, but also lower survival rates, than species growing in plant communities of transition

dunes. We also investigated whether plant functional traits (i.e., leaf and floral traits) explain patterns of trade-off between growth and survival. In addition to leaf traits, which are generally used to explain the growth-survival trade-off in phanerophyte species (Philipson et al., 2014; Fan et al., 2022), we examined the relationship between the growth-survival trade-off and floral abundance, which is a prerequisite for offspring production (Fantinato et al., 2021) and thus for the sustainability of individual plant establishment over time.

2. Methods

2.1. Study area

The restoration project took place on the North Adriatic coast, the northernmost part of the Mediterranean basin, and specifically along the coast of the Veneto region (northeastern Italy). The dune systems consist of narrow recent dunes (Holocene) of sandy carbonate deposits derived from rivers flowing into the Adriatic Sea. The North Adriatic coast has a temperate oceanic bioclimate (Del Vecchio et al., 2018). The average annual temperature is 13 °C and the average annual precipitation is 831.5 mm (Fantinato et al., 2018). Precipitation is mainly concentrated from September to November (seasonal distribution of precipitation, mean \pm SD: March-May, 66.0 \pm 8.3 mm; June-August, 63.4 \pm 8.2 mm; September-November: 92.4 \pm 18.5 mm; December-February, 54.9 \pm 6.4 mm; Del Vecchio et al., 2021). Until the 1950s, the northern Adriatic coast was almost entirely covered by sand dunes up to 10 m high (Bezzi and Fontolan, 2003). Today, few of these dunes remain, and the coast suffers from increasing erosion, a decrease in sand supply, a change in geomorphological processes, and intensive human use (Nordstrom et al., 2009), with summer beach tourism being one of the main sources of income for the region (Fantinato, 2019).

2.2. Restoration activities

The area was interested by restoration activities carried out as part of a large-scale European LIFE project (LIFE16 IT/NAT/000589 REDUNE; <http://www.liferedune.it/>; accessed October 3, 2022). The project aimed to restore and conserve plant communities of coastal dunes, promote environmentally friendly behaviors among stakeholders (e.g., citizens, visitors, managers), and raise awareness of the benefits of coastal dune ecosystems.

Plant communities targeted by the project and selected in this study included the non-forested open communities of the foredunes and transition dunes (Table 1). The pool of planted species was selected based on a reference state defined by a multi-site regional study and literature sources (e.g., Acosta and Ercole, 2015). Specifically, the species pool included all functional groups required for dune development and consolidation, in proportions similar to those observed during primary succession in other coastal dunes on the North Adriatic coast. The species pool used for plant community restoration included dominant native ecosystem engineer species and other subordinate focal species (i.e., plant species typical of dune habitats) that enhance dune biodiversity and esthetic value and play key roles in other ecosystem functions (e.g., maintaining robust pollination networks; Fantinato et al., 2018). Plant species nomenclature follows Bartolucci et al. (2018). Seeds used for plant production were collected from wild populations of the target species identified at sites along the Veneto coast. Seeds were collected from the greatest possible number of individuals, within the limits of numerical consistency of populations (ENSCONET, 2009). Dune species, except in a few cases (e.g., *Convolvulus soldanella*), do not require special nursery treatments to break seed dormancy, but special attention must be paid to the choice of sowing period (which for most species is the autumn equinox (September); de Francesco et al., 2021). Individual plants were grown from seed, raised in pots and planted out in the field once they have reached the mature stage, i.e., at the age of one or two years. Restoration of coastal dune plant communities then involved several actions specific to each community.

2.2.1. Foredunes

Restoration of foredune communities was accomplished using a soft-engineering approach. The foredunes were first built up with a light scraper and the resulting surfaces were then manually modeled. Woody debris found on the beach was used to stabilize the base of the dunes and decomposing wrack and stranded algae and plants were incorporated into the sand. Consolidation of the dunes was achieved by planting individuals of focal species. To restore foredune plant communities, two ecosystem engineer species (i.e.,

Table 1

Description of the habitats targeted in this study. A brief description with EUNIS and Nature 2000 classification codes is provided for each habitat.

Habitat	Description	EUNIS Habitat classification	Natura 2000 classification
Foredunes	Vegetation occupying the first stages of dune development, dominated by perennial species (especially tussocks and erect leafy species). Dominant species: <i>Calamagrostis arenaria</i> , <i>Euphorbia paralias</i> , <i>Medicago marina</i> , <i>Thinopyrum junceum</i> .	B1.3 "Shifting coastal dunes" (including B1.31 Embryonic shifting dunes and B1.32 White dunes)	2110 2120
Transition dunes	Well-drained or dry lands dominated by grasses or dwarf shrubs, with low productivity, occurring between the foredune and the scrub of the fixed dune. Dominant species: <i>Fumana procumbens</i> , <i>Lomelosia argentea</i> , <i>Poterium sanguisorba</i> , <i>Teucrium capitatum</i> , <i>Thymus pulegioides</i> . Annual species as <i>Silene conica</i> and <i>Festuca fasciculata</i> can be found in grassland clearings.	B1.4 "Coastal stable dune grassland (grey dunes)"	2130 *

Thinopyrum junceum and *Calamagrostis arenaria*) were planted in a checkerboard pattern. For *C. arenaria*, the distance between plants was approximately one meter, while for *T. junceum* and other subordinate focal species such as *C. soldanella*, *Echinophora spinosa*, *Eryngium maritimum*, *Euphorbia paralias*, and *Medicago marina*, the distance between plants was smaller, ranging from 30 cm to 70 cm. A total of 35,265 individuals were planted.

2.2.2. Transition dunes

Plant communities of transition dunes were restored by planting individuals of focal species in areas of bare sand created by natural erosion or human trampling. The planting scheme consisted of groups of three to six individuals of the same species spaced approximately 30 cm apart. The spacing between groups of individuals varied depending on the spatial arrangement of the bare sand areas. Planted individuals belonged to different species, including *Carex liparocarpos*, *Centaurea tommasinii*, *Chrysopogon gryllus*, *Fumana procumbens*, *Globularia bisnagarica*, *Helianthemum nummularium* ssp. *obscurum*, *Hypochoeris radicata*, *Koeleria splendens*, *Lomelosia argentea*, *Poterium sanguisorba*, *Scabiosa triandra*, *Silene otites*, *Teucrium capitatum*, *Teucrium chamaedrys*, and *Thymus pulegioides*. A total of 63,490 individuals were planted.

2.3. Data collection

We monitored newly planted individuals every 30 days for 18 months after planting, from May 2020 to October 2021. Due to the Covid 19 pandemic and national restrictions on on-site movement, we were unable to conduct monitoring between January and April 2021. On the first day of monitoring, plants were randomly selected, individually marked with labels, and their location recorded on topographic maps. In total, we marked 355 individuals of 13 perennial non-phanerophyte species. The number of individuals marked per species varied depending on the relative abundance of each species in restored dunes. Overall, four species belonged to the foredune communities, while the other nine belonged to the transition dune communities (Table 2).

At each survey, we assessed survival of marked individuals. Since in non-phanerophyte plants space occupancy patterns are associated with the architecture of their above-ground part (Lavorel and Garnier, 2002; Liira et al., 2002; Fantinato et al., 2019), we evaluated individual growth by measuring the maximum diameter (cm) of the above-ground part with a rigid ruler. Following the classification of plant growth forms by Cornelissen et al. (2003), the diameter was measured as maximum length between opposite stolons (creeping species), maximum length between opposite branches (dwarf shrubs and erect leafy species), maximum rosette diameter (short basal species), and maximum tuft basal diameter at 1 cm from the sand surface (tussock species). We recorded

Table 2

List of species monitored. For each species, the number of individuals monitored, their growth form and the mean values (mean \pm SD) of relative growth rate ($\text{cm}\cdot\text{cm}^{-1}\cdot\text{month}^{-1}$), survival rate (%), leaf area (LA; mm^2), leaf dry matter content (LDMC; %), specific leaf area (SLA; $\text{mm}^2\cdot\text{mg}^{-1}$), and mean number of floral displays are provided. Leaf traits of *Euphorbia paralias* were retrieved from Ciccarelli (2015).

Species	Number of individuals	Growth form	Relative growth rate ($\text{cm}\cdot\text{cm}^{-1}\cdot\text{month}^{-1}$)	Survival rate (%)	LA (mm^2)	LDMC (%)	SLA ($\text{mm}^2\cdot\text{mg}^{-1}$)	Mean number of floral displays
Foredunes								
<i>Calamagrostis arenaria</i>	30	tussock	0.06 \pm 0.04	75.64 \pm 5.67	640.43 \pm 226.88	32.60 \pm 4.04	8.13 \pm 0.93	0.93 \pm 2.00
<i>Convolvulus soldanella</i>	10	creeping	0.21 \pm 0.11	61.81 \pm 17.78	593.56 \pm 146.17	13.70 \pm 1.73	14.61 \pm 1.76	0.00 \pm 0.00
<i>Euphorbia paralias</i>	10	erect leafy	0.14 \pm 0.15	65.00 \pm 5.34	81.50 \pm 5.50	29.10 \pm 0.50	13.30 \pm 0.50	2.85 \pm 3.76
<i>Medicago marina</i>	10	dwarf shrub	0.12 \pm 0.10	58.18 \pm 11.67	106.47 \pm 15.82	30.84 \pm 0.79	14.22 \pm 1.10	2.40 \pm 3.36
Transition dunes								
<i>Carex liparocarpos</i>	20	tussock	0.05 \pm 0.04	100.00 \pm 0.00	251.83 \pm 32.93	42.48 \pm 2.52	13.15 \pm 0.66	1.00 \pm 1.12
<i>Fumana procumbens</i>	24	dwarf shrub	0.00 \pm 0.01	87.96 \pm 10.50	11.48 \pm 2.93	33.95 \pm 3.64	9.06 \pm 0.99	1.34 \pm 1.46
<i>Helianthemum nummularium</i> ssp. <i>obscurum</i>	20	dwarf shrub	0.05 \pm 0.04	90.71 \pm 8.28	116.31 \pm 22.76	25.66 \pm 2.58	10.5 \pm 2.58	11.30 \pm 18.99
<i>Koeleria splendens</i>	36	tussock	0.04 \pm 0.02	100.00 \pm 0.00	171.82 \pm 53.82	39.08 \pm 9.30	9.37 \pm 1.10	5.27 \pm 3.57
<i>Lomelosia argentea</i>	43	short basal	-0.05 \pm 0.11	95.73 \pm 3.86	56.37 \pm 13.79	34.31 \pm 8.56	12.14 \pm 2.56	4.57 \pm 4.60
<i>Teucrium capitatum</i>	44	dwarf shrub	0.07 \pm 0.15	100.00 \pm 0.00	40.70 \pm 10.74	36.28 \pm 11.73	13.60 \pm 1.96	2.25 \pm 2.88
<i>Teucrium chamaedrys</i>	20	dwarf shrub	0.08 \pm 0.05	97.50 \pm 5.09	80.51 \pm 17.05	42.72 \pm 3.55	9.05 \pm 1.06	2.00 \pm 0.00
<i>Thymus pulegioides</i>	44	dwarf shrub	0.07 \pm 0.15	99.09 \pm 1.43	40.29 \pm 10.27	30.51 \pm 4.92	14.14 \pm 3.37	11.59 \pm 14.47
<i>Silene otites</i>	44	short basal	0.05 \pm 0.05	94.81 \pm 3.29	239.6 \pm 187.13	31.9 \pm 2.37	9.3 \pm 2.17	0.95 \pm 1.07

maximum tussock basal diameter instead of maximum absolute diameter because the latter is a highly variable measure that is easily influenced by environmental factors such as wind, which can affect tussock shape. In addition, to evaluate sexual reproductive effort of planted individuals, we counted the number of floral displays on each individual (Zi et al., 2022). Depending on the plant species, a floral display consisted of a single flower (e.g., *F. procumbens*), a flower head (e.g., *L. argentea*), or a group of flowers that together formed a recognisable visual unit such as spikes and panicles (e.g., *C. arenaria*; Hegland and Totland, 2005).

As recent studies on the growth-survival trade-offs have started using functional traits to explain a species' position on the growth-survival trade-off axis (Philipson et al., 2014; Fan et al., 2022), at the peak of vegetative growth of the plants (late spring/early summer), for each species, we collected 5–12 randomly selected individuals (depending on availability and avoiding marked individuals; Cornelissen et al., 2003). For each individual, leaf functional traits were measured on four undamaged and well-developed leaves (Pérez-Harguindeguy et al., 2013). Specifically, we quantified leaf functional traits (i.e., leaf area, leaf dry matter content, and specific leaf area), which have been shown to provide meaningful information about vascular plant adaptations to different environmental conditions (Pierce et al., 2013, 2017). Leaf area (LA) is the size of the photosynthetic organ (mm^2). It measures how much a plant invests in photosynthesis. Leaf area is directly related to the plant's ability to absorb light and thus to the plant's productivity. High values of LA are associated with an acquisitive strategy (Ciccarelli, 2015). Leaf dry matter content (LDMC) quantifies leaf tissue density and ability to retain nutrients and it is quantified as the ratio of leaf dry mass to fresh mass expressed in percentage. High LDMC values are typical of plant species with a conservative strategy, while low LDMC values indicate a more acquisitive strategy (Baltieri et al., 2020). Species with high LDMC values have tough leaves and are poorly resilient to disturbance (Bernhardt-Römermann et al., 2011). Specific leaf area (SLA) is defined as the ratio of total leaf area to total leaf dry mass (expressed in $\text{mm}^2\cdot\text{mg}^{-1}$). It describes the amount of leaf area available for light capture per unit of biomass invested. High values of SLA are generally associated with disturbed environmental conditions (Freschet et al., 2010). We collected individuals by cutting the stem at 1 cm from the ground and we rehydrated them for 24 h to reach full turgidity. Laboratory measurements followed the standardised methods described by Pérez-Harguindeguy et al. (2013). We determined leaf fresh weight (LFW) and leaf area (LA). LA was determined using Leaf Area Measurement software (Askew, 2003). Leaf dry weight (LDW) was then determined after leaves were dried at 80 °C for 24 h, and specific leaf area (SLA) and leaf dry matter content (LDMC) were calculated. Due to difficulties in finding individuals with undamaged and well-developed leaves for *E. paralias*, data on leaf traits was retrieved from Ciccarelli (2015), who described leaf traits of plant species in the Mediterranean coastal dunes, i.e., under similar environmental conditions as in our study area.

2.4. Data analysis

Relative growth rates were quantified for each individual in each month according to Wright et al. (2010). The relative growth rate ($\text{cm}\cdot\text{cm}^{-1}\cdot\text{month}^{-1}$) was equal to $[\ln(\text{PD}_f/\text{PD}_i)]/(m_f - m_i)$, where PD_f and PD_i represent the plant diameter in a given month m_f and the initial month m_i , respectively. The relative growth rate of each species was therefore calculated by averaging the relative growth rates of individuals of the same species in each month. Survival rate was calculated as the percentage of living individuals in each month relative to the initial number of individuals marked (Fan et al., 2022).

To evaluate the correlation between the relative growth rate and survival rate of species, we performed a Spearman's rank correlation using the mean values per species quantified from the monthly replicates (Bland and Altman, 1995; Hamlett et al., 2003). We also performed a principal component analysis (PCA) based on the correlation matrix using the values of the relative growth rate and survival rate of each species in each month. Factor scores of the first principal component of the growth-survival trade-off were used to represent species positions on an axis of life-history variation among species.

To assess the relationship between the growth-survival trade-off and functional traits, we ran a linear mixed model (R-based package *lme4*). We regressed factor scores on the first principal component of the growth-survival trade-off (PC1) with respect to values of leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), and mean number of floral displays per species quantified as averages of floral display number recorded in each month. Moreover, we added to the model two random variables, i.e., species growth form, to account for species space occupation strategy, and species identity (nested within species growth form). Models were simplified by backward elimination of non-significant independent variables. The likelihood ratio test (LRT; *drop1* function; R-based package *stats*) was used to determine the significance of the model. All analyses were performed using R version 4.1.3 (R Core Team, 2022).

3. Results

The mean relative growth rate of individuals of non-forested open communities of coastal dunes was $0.061 \pm 0.099 \text{ cm}\cdot\text{cm}^{-1}\cdot\text{month}^{-1}$; however, the mean relative growth rate of individuals of foredune communities was three times that of individuals of transition dune communities ($0.13 \pm 0.11 \text{ cm}\cdot\text{cm}^{-1}\cdot\text{month}^{-1}$ and $0.04 \pm 0.08 \text{ cm}\cdot\text{cm}^{-1}\cdot\text{month}^{-1}$, respectively). The highest mean relative growth rate was recorded for *Convolvulus soldanella* with a mean relative growth rate of $0.214 \pm 0.107 \text{ cm}\cdot\text{cm}^{-1}\cdot\text{month}^{-1}$.

At 18 months after planting, the mean survival rate of planted individuals was $80.23 \pm 18.74\%$. The mean survival rate was higher for individuals of the transition dune communities ($90.33 \pm 10.93\%$) than in those of the foredune communities ($57.50 \pm 9.57\%$). The lowest survival rate was observed for *C. soldanella* and *Medicago marina*, with a survival rate of 40.00% in the last month of monitoring.

Spearman's rank correlation revealed a significant negative correlation between relative growth rate and survival rate ($R_s = -0.058$; $P = 0.037$), indicating that species with high relative growth rate have low survival rate. Individuals of the foredune communities had high relative growth rates, associated with low survival rates whereas individuals of the transition dune communities generally had lower relative growth rates but high survival rates (Table 2).

Factor scores of the first principal component of the growth-survival trade-off (PC1) ranged from -4.02 – 2.82 . Values near the negative extreme indicate high relative growth rates associated with low survival rates, while values near the positive extreme indicate low relative growth rates associated with high survival rates. Examining possible relationships between functional traits and the growth-survival trade-off (expressed as factor scores on the first principal component of the growth-survival trade-off; PC1), we found a significant positive relationship between leaf dry matter content (LDMC) and growth-survival trade-off ($t = 3.554$; $P = 0.001$; Fig. 1) as well as between mean number of floral displays and the growth-survival trade-off ($t = 1.946$; $P = 0.049$; Fig. 1). The results indicate that plant species with low relative growth rates associated with high survival rates exhibit a more conservative strategy (high LDMC values; Fig. 1) and produce a higher mean number of floral displays (Fig. 1) than plant species with high growth and low survival rates. No significant relationship was found between the growth-survival trade-off and the leaf area (LA) or the specific leaf area (SLA).

4. Discussion

The demographic trade-off between growth and survival is a recognised axis of life-history variation in phanerophyte species and has been widely used to address basic and applied issues related to forest ecology (e.g., to explain species coexistence in forests (Seiwa, 2007) or the impact of climate change on phanerophyte species (Benavides et al., 2015)). In the present study, we have broadened the evidence that the growth-survival trade-off can also be observed in perennial non-phanerophyte species, and that this kind of knowledge can highly contribute to the planning of cost-effective restoration actions. Fast-growing species pursue an acquisitive strategy, but this has been shown to be associated with poorer tolerance to stressful environmental conditions than slow-growing species (e.g., Sterck et al., 2011; Fan et al., 2022), resulting in high growth rates coupled with low survival rates. In contrast, slow-growing species adopt a more conservative strategy and are better adapted to tolerate stressful environmental conditions, resulting in slower growth rates coupled with high survival rates (Rozendaal and Chazdon, 2015). Plant species strategy (acquisitive vs. conservative) represents a major field of research in plant science (e.g., Pierce et al., 2022), and the available information on the strategy in different plant species is increasing (Pierce et al., 2017). Nature-based restoration actions that foresee planting can benefit from this growing knowledge to improve their success and cost-effectiveness. Among the costs associated with ecosystem restoration, expenditures for native species production could be an important budget item (Della Bella et al., 2021) that increases with the number of individual plants to be produced. Planning plant production based on ecological knowledge of species growth and survival after planting in the field, which is significantly related to plant species strategies, could help achieve restoration goals while meeting project cost-effectiveness requirements.

When dealing with coastal dune non-forested open ecosystems, we showed that perennial plant species of different coastal dune communities (i.e., foredune vs. transition dune communities) differed in terms of the trade-off between growth and survival, with plant species of foredune communities having relatively higher growth and lower survival rates than plant species of transition dune communities. Coastal dune ecosystems do represent an ideal model to test basic and applied ecological issues. In coastal dune ecosystems, environmental stresses such as nutrient and water availability, as well as disturbance factors in the form of wave action, sand burial, and substrate erosion vary greatly inland from the shoreline (Acosta and Ercole, 2015). This, in turn, leads to the selection of plant species based on their resource economic traits and strategies (i.e., acquisitive vs. conservative species), as well as their ability to withstand environmental disturbance (Torca et al., 2019). Decomposing wrack and stranded algae and plants along the shoreline can be an important source of nutrients in coastal dune ecosystems (Del Vecchio et al., 2020), which are inherently nutrient-poor systems, so plant species of foredunes may be less constrained by nutrient availability and adopt a more acquisitive strategy than species of transition dunes (Ciccarelli, 2015). In addition, natural disturbance decreases from the shoreline to the inland, resulting in

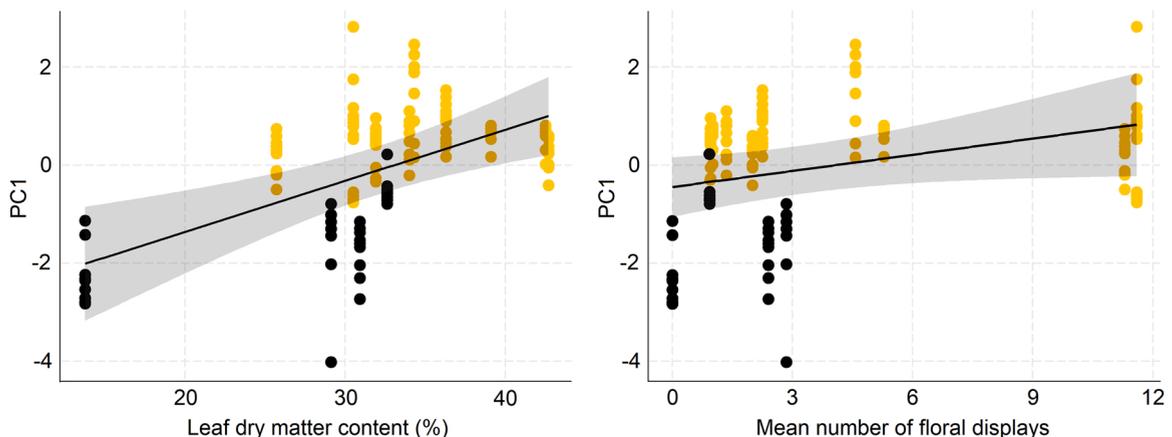


Fig. 1. Relationship between leaf dry matter content (LDMC; %) and mean number of floral displays and the growth-survival trade-off (expressed as factor scores on the first principal component of the growth-survival trade-off; PC1). Black circles indicate species of the foredune communities, while yellow circles indicate species of the transition dune communities. Lines represent the estimates of the linear mixed models (LMM). Gray band represents 95% confidence interval around the regression line.

disturbance-adapted plant species occurring in plant communities closer to the seashore, while less disturbance-adapted conservative species occur in plant communities further inland (Silan et al., 2017). As for e.g., burial, not only many foredune species possess a higher tolerance to sand burial compared to inland species, but they also show growth stimulation and allocate more biomass into leaves and above-ground stems (Maun, 1998). Many foredune perennial grasses, including *Calamagrostis arenaria*, are so well adapted to this disturbance factor that they actually require burial to maintain high vigor (Maun, 2009).

Consistent with recent studies on the growth-survival trade-off, in which leaf traits have been used to explain a phanerophyte species' position on the growth-survival trade-off axis (Philipson et al., 2014; Fan et al., 2022), we showed that the growth-survival trade-off was also significantly associated with leaf traits in perennial non-phanerophyte species. Namely, we found that the growth-survival trade-off was positively associated with leaf dry matter content (LDMC). Plants with higher tissue density (i.e., higher LDMC values) have been shown to retain nutrients, namely, to adopt a conservative strategy, and to be less resilient to disturbance compared to plants with fleshier leaves (Bernhardt-Römermann et al., 2011). It is therefore not surprising that the highest LDMC values were found in species of transition dune communities, and these were associated with low growth and high survival rates, while the lowest values were found in plant species of foredune communities that actually had high growth and low survival rates.

Interestingly, we found that the trade-off between growth and survival was also positively related to the mean number of floral displays, suggesting that conservative species produced more floral displays on average than acquisitive species. Trade-offs in resource allocation determine the ability of plants to survive and grow under constraints imposed by the environment and other organisms (Cheplick, 1995). Since the availability of resources to plants is limited, the simultaneous allocation of resources to different plant structures and physiological processes is likely to be constrained. Therefore, plant species allocate resources to those structures and physiological processes that most enhance their fitness relative to the ecological and biotic features of the ecosystem in which they live (Liu et al., 2009). As stated above, sand burial has been found to stimulate the growth of plant species of foredune communities and *C. arenaria* in particular (Nolet et al., 2018), which may invest their resources in biomass production and in vegetative propagation rather than in floral structure production. In contrast, plant species of transition dunes are characterised by low investment of resources in biomass production, reflected in low growth rates, and may invest more resources in floral structures. Moreover, since transition dunes are nutrient-poor, plant species may engage in high levels of sexual reproductive effort to escape stressful environmental conditions (Macek and Lepš, 2008), which may not be the case for plant species of foredunes that can benefit from decomposing wrack and stranded algae and plants.

The results of this study suggest that restoration of coastal dune ecosystems that includes plant production should disproportionately target plant species of the foredune communities because they have relatively low survival rates associated with low sexual reproductive effort. In addition, it is noteworthy that *C. arenaria* had the highest survival rate among foredune plant species. *C. arenaria* is considered an ecosystem engineer that plays a central role in dune formation (Della Bella et al., 2021); therefore, targeting *C. arenaria* in the early stages of restoration and introducing subordinate species once the system has become more stable could help promote foredune development and achieve restoration goals. In contrast, plant species of transition dunes exhibited relatively high survival rates and high sexual reproductive effort, potentially ensuring temporal sustainability of transition dune restoration without the need to produce large numbers of individuals to replace dead plants. Although we did not address below-ground traits, including roots and clonal traits (Yannelli et al., 2022), in the present study, we cannot exclude the hypothesis that resource allocation in below-ground structures promotes on-spot persistence, recovery after disturbance and space occupancy in plant species of foredune communities (Balachowski et al., 2016), ensuring temporal sustainability of restored foredune communities despite low sexual reproductive effort of their focal species.

Knowledge of successful implementation of nature-based solutions for coastal dune restoration is still insufficient, and successful large-scale restoration faces many challenges. Measures cited by the EU to achieve restoration goals include understanding past successes and failures in order to properly plan nature-based restoration actions considering the current state of degraded ecosystems and their restoration potential (Miller et al., 2017; Lindenmayer, 2020). Given the range of restoration approaches and the urgency to implement restoration actions on an increasing number of coasts, it is also important to provide information on restoration techniques to managers so that they can plan restoration actions based on a cost-effectiveness analysis. Our study demonstrates the utility of applying ecological knowledge based on theoretical and empirical studies to make restoration increasingly sustainable and cost-effective, and ultimately to address today's urgency to restore and maintain non-forested open ecosystems in the face of ongoing global environmental change.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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