Anatomical basis of LMA variations drive to different photosynthetic and water storage strategies in two *Sesleria* species from mountain dry grasslands

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Introduction

Plant and leaf traits directly affect ecosystem processes ensuring carbon dioxide, nutrient and water exchanges between soil and atmosphere through the photosynthetic activity. Nevertheless, a great within sites variation in plant and leaf traits can be found resulting in different adaptive strategies in coexisting species. Leaf mass per unit of leaf area (LMA) is an important trait to understand plant functional ecology being the outcome of leaf anatomy and related to photosynthesis. We hypothesized that LMA was the main predictor of the adaptive strategies of *Sesleria nitida* (S1) and *S. juncifolia* (S2) growing on Mount Terminillo (Central Apennines, Loc. Sella di Leonessa, 1895 m a.s.l., Italy) and cultivated *ex situ* (Botanical garden of the Sapienza University of Rome (41°54'08''N, 12°31'03''E), breaking LMA down into leaf anatomical components (i.e. leaf tissue density and thickness) and relating them to photosynthesis.

Sesleria nitida develops on steep screes characterized by discontinuous swards with a steep inclination and exposed to a limited cryoturbation due to the prolonged and snow cover in winter.

Sesleria juncifolia grows along crests on the summit areas exposed to cold winds blowing mainly from the northeast and where the soil remains without snow cover for long periods.

Materials and methods

Gas exchange measurements were carried out monthly on 5 fully expanded leaves per plant and species from January to July 2013. Net photosynthesis per unit leaf area (A_a, µmol m^{-2} s^{-1}), stomatal conductance (g_s, mol m^{-2} s^{-1}), leaf temperature (T_l, °C), and intercellular CO_2 concentration (C_i, µmol mol air^{-1}) were measured by an ADC LCA4 (UK), equipped with a leaf chamber (PLC, ADC, UK). Measurements were carried out at PPFD > 1 300 µmol photon m^{-2} s^{-1} from 9:30 a.m. to 12:30 p.m. Net photosynthesis per unit leaf mass (A_m, nmol CO_2 g^{-1} s^{-1}) was also determined.

Leaf morphological traits were determined on 20 fully expanded sun leaves per species. LMA (g m^{-2}) and leaf tissue density (LTD, g cm^{-3}) were calculated according to **[1]**. Total leaf thickness (LT, cm) was determined by light microscopy, using an image analysis system (Axiovision AC software). The volume of leaf tissues (t) per unit of leaf area (VAt) was calculated according to **[2]**. The volume for the mesophyll (VA_m), epidermis (VA_e), vascular plus sclerenchymatous tissues (VA_{v+s}) and air spaces (VA_a) were calculated.

Results and Discussion

LTD explains 69% of LMA variations in *S1* while the relationship with LT is not significant (Figure 1). Moreover, LTD is negatively correlated with LT in *S1* driving to a 17% higher VA_a, which increases the CO_2 partial pressure at the carboxylation sites **[3]**. This result is also attested by the significant relationship between LTD and both net photosynthesis per unit leaf area (A_a) and mass (A_m) (R= 0.56 and -0.49, respectively) (Table 1), highlighting the role of LTD in determining the photosynthetic process in *S1*. LMA scaled with both LTD and LT explaining 82% and 70% of LMA variations in *S2* (Figure 1). Moreover, the positive relationship between LTD and LT (R^2 = 0.52) highlights the leaf variables control of the photosynthetic process. In particular, LTD and LT control the transactions of carbon and water through the leaf surface, being positively related to A_a (R= 0.93 and 0.79 for LTD and LT, respectively) (Table 1), according to **[3]**. Nevertheless, an increase of both LT and LTD decreases A_m (R = -0.9 and -0.8, respectively). This may be justified by the control of water losses in *S2* through a reduction of CO_2 diffusion due to the increase in LT and LTD, attested by 6% and 30% lower C_i and g_s compared to *S1*.

Conclusions

By analyzing variations in LMA components we demonstrate that *S. nitida* maximizes carbon uptake (by 10% in respect to *S. juncifolia*) mainly by LTD reduction and VA_a increase. On the other hand *S. juncifolia* reduces photosynthetic capacity by increasing both LTD and LT in order to maximize water storage. The highlighted differences in leaf traits are the result of the adaptation of the two species to the different ecological contexts where they grow.

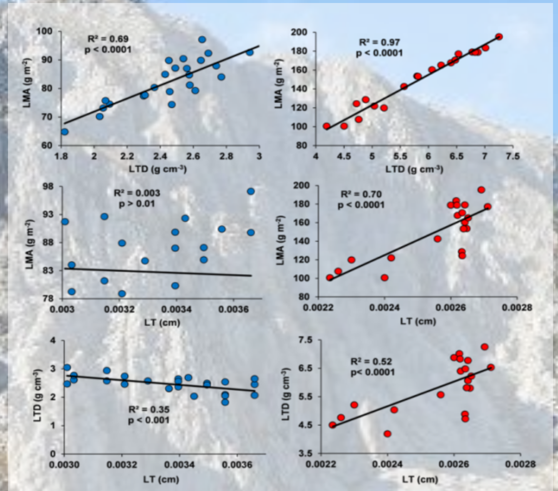

Figure 1. Regression analysis between LMA and its components (LTD and LT) for *S1* (blue points) and *S2* (red points). (n = 20, $p \leq 0.01$).

	S1	
A_a **vs**	**Regression**	**R^2**
LMA	0.091x + 2.67	**0.61**
LTD	1.82x + 5.70	**0.32**
LT	528.30x + 8.40	0.01
A_m **vs**		
LMA	-0.44x + 159.6	**0.19**
LTD	-13.61x + 157.1	**0.24**
LT	10.12x + 89.47	0.07
	S2	
A_a **vs**	**Regression**	**R^2**
LMA	0.34x + 4.33	**0.91**
LTD	1.06x + 3.17	**0.86**
LT	5710.8x - 5.19	**0.63**
A_m **vs**		
LMA	-0.23x + 98.44	**0.83**
LTD	-7.45x + 107.25	**0.82**
LT	-37842x + 160.35	**0.64**

Table 1. Regression analysis between net photosynthesis per unit leaf area and mass against LMA, LTD and LT for *Sesleria nitida* (*S1*) and for *S. juncifolia* (*S2*). Individual measurements were used as experimental units. Bold values of R^2 indicate significant regressions (n = 20, p ≤ 0.01).

References

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