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Competition, traits and resource depletion in plant communities

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Abstract Although of primary importance to explain plant community structure, general relationships between plant traits, resource depletion and competitive outcomes remain to be quantified across species. Here, we used a comparative approach to test whether instantaneous measurements of plant traits can capture both the amount of resources depleted under plant cover over time (competitive effect) and the way competitors perceived this resource depletion (competitive response). We performed a large competition experiment in which phytometers from a single grass species were transplanted within 18 different monocultures grown in a common-garden experiment, with a time-integrative quantification of light and water depletion over the phytometers' growing season. Resource-capturing traits were measured on both phytometers (competitive response traits) and monocultures (competitive effect traits). The total amounts of depleted light and water availabilities over the season strongly differed among monocultures; they were best estimated by instantaneous measurements of height and rooting depth, respectively, performed when either light or water became limiting. Specific leaf area and leaf water potential, two competitive response traits measured at the leaf level, were good predictors of changes in phytometer performance under competition, and reflected the amount of light and water, respectively, perceived by plants throughout their lifespan. Our results demonstrated the relevance of instantaneous measures of plant traits as indicators of resource depletion over time, validating the trait-based approach for competition ecology.

Keywords Competitive response · Competitive effect · Phytometer · Plant functional trait · Resource competition

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Introduction

Competition for resources is one of the major processes explaining the local abundance of plant species (e.g. Grime 1979; Tilman 1982). According to resource-based competition theories (e.g. MacArthur 1972; Tilman 1980, 1982), changes in plant biomass or density are likely to affect the availability of resources, which in turn influences the performance of other plants. As demonstrated by the study conducted by Gaudet and Keddy (1988), who showed that the performance of phytometer plants grown under different neighbouring communities was negatively related to neighbour height, a trait-based approach has the potential to predict the outcome of resource competition among species (Keddy 1992; McGill et al. 2006). In this pioneer study, the resources at the bases of the interactions between phytometers and neighbours were not, however, quantified. This was subsequently done in a number of studies aiming at identifying how plant traits could affect competitive outcome via their direct effects on resource depletion.

(a)

COMPETITIVE EFFECT TRAITS	Resource availability under plant cover	COMPETITIVE RESPONSE TRAITS → Plant Performance → Plant fitness

Competitive effect   *Competitive response*

(b)

Plant height / Rooting depth	Light depletion (L_c) / Water depletion (W_c)	Specific leaf area (SLA) / Predawn leaf water potential (Ψ_{base}) → Total above-ground biomass → Plant fitness

NEIGHBOUR   PHYTOMETER
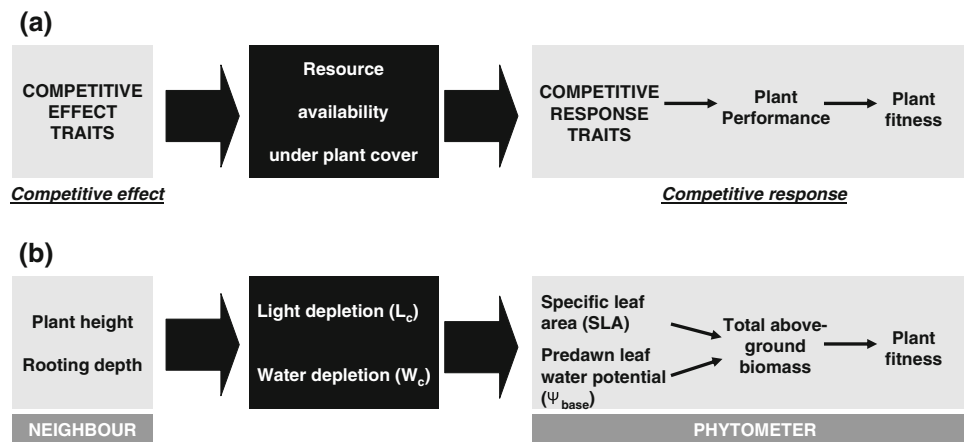
Fig. 1 A framework linking plant traits, resource depletion and competitive outcome. **a** General aspects of the trait-based framework. Competitive effect traits quantify the change in local resources due to plant activity. Competitive response traits modulate plant performance and, in fine individual fitness, when local resources change due to competition. **b** Application to competition for light and water as designed in the present experiment. Competitive effect traits (two size-related traits: plant height and rooting depth) measured on neighbours capture the change in local light and soil water availability (L_c and W_c, respectively) due to plant activity. Competitive response traits linked to changes in light and water availability (specific leaf area SLA, and predawn leaf water potential Ψ_{base}, respectively) measured on phytometers, modulate total above-ground biomass as a determinant of phytometer performance. See text for more detail

A literature survey of such studies for terrestrial vegetation shows that general relationships between plant traits and resource depletion have been difficult to establish (see Electronic Supplementary Material, ESM, Table S1), a point previously stressed by Craine (2005). A first reason is that an adequate quantification of resource depletion is often lacking in many of the studies using a trait-based approach. A second issue is that the temporal variability of the availability of the resources investigated (nutrients, light and water) is seldom taken into account, although this can modify substantially the outcome of inter-specific interactions (Dybzinski and Tilman 2007). In non-equilibrium communities, the amount of resources varies with time in relation to the phenology of organisms, making the interpretation of instantaneous measurements of resource levels problematic (Violle et al. 2007a). Hence, the present study was primarily designed to establish quantitative relationships between selected plant traits and resource depletion, taking into account temporal fluctuations in resource availability. This was done using a time-integrative indicator of resource depletion, R_c, representing the cumulative amount of resource depleted by the vegetation over the growing season (Violle et al. 2007a).

Resource depletion is the main mechanism through which a plant suppresses the growth of other plants, a process defined as a 'competitive effect' by Goldberg (1990). The other component of competitive ability is the 'competitive response' of plants (Goldberg 1990), i.e. the ability of plants to grow and survive in response to resource depletion due to competition. These two components are difficult to separate in natura since they are both linked to resource capture-related mechanisms (Goldberg 1996) and mostly occur at the same time. Conceptually, these can be disentangled using a

trait-based framework (Fig. 1a), in which resource depletion ('resource availability under plant cover' in Fig. 1a) plays a central role. Two types of traits are identified: (1) competitive effect traits, which affect resource availability through plant activity (see above and ESM Table S1); and (2) competitive response traits, which capture the response of a plant to the change in resource availability due to the activity of other plants. Here, we quantified the relationships between competitive effect traits and resource depletion in monocultures of 18 species from a Mediterranean secondary succession grown in a common-garden experiment, and chosen to simulate a large range of competitive effects. Two resources were investigated: light, for its paramount importance in aboveground competition (Grime 1973; Newman 1973; Wilson and Tilman 1991); and water, the main resource limiting plant growth in Mediterranean environments (Rosenzweig 1968; Miller 1981; Joffre et al. 1987). These are also the two less investigated resources as identified from our literature survey (ESM Table S1). Building on Gaudet and Keddy (1988), we assessed how well plant height could account for time-integrated light depletion (L_c) under the canopies of the 18 species (neighbours, hereafter). Similarly, we assessed whether rooting depth, a key trait in the competition for water in water-limited environments (Casper and Jackson 1997), could be related to the time-integrative indicator of water depletion (W_c).

The impacts of resource depletion by neighbours were quantified by transplanting individuals from a single species used as a 'phytometer' within the monocultures (see, e.g., Goldberg and Fleetwood 1987; Gaudet and Keddy 1988). Three competitive response traits were measured on these phytometers (cf. Fig. 1b).

1. Total above-ground biomass was used as an estimate of overall phytometer performance, as traditionally done in competition experiments (Aarssen and Keogh 2002).
2. Specific leaf area (SLA, the ratio of leaf area to leaf dry mass) was used to quantify how phytometers perceived light depletion by neighbours (above-ground competition). SLA is indeed an important trait controlling light interception by the leaf and related to a leaf capacity to acquire carbon (Gutschick and Wiegel 1988). Within species, SLA increases with decreasing light availability (cf. Björkman 1981; Valladares et al. 2000); this is considered as an adaptive response, since a higher SLA under light-limiting conditions allows a unit leaf biomass to intercept more light.
3. Predawn leaf water potential (Ψ_{base}) was used to assess how phytometers perceived the soil water environment as modified by the evapotranspiration of neighbours (competition for water, below-ground). Ψ_{base} is measured at a time when soil and plant water potentials tend to equilibrate, before the onset of transpiration (Scholander et al. 1965; Boyer 1995).

Based on instantaneous measurements of these different plant traits, our study therefore addresses three questions: (1) do above-ground and below-ground traits of neighbours correlate with the cumulative amount of light and water depletion (L_c and W_c, respectively); (2) how is phytometer performance affected by resource depletion; and (3) are the response traits measured at the leaf level good predictors of changes in phytometer performance?

Materials and methods

The competition experiment

The experiment was conducted in the "Centre d'Ecologie Fonctionnelle et Evolutive" located in Montpellier, France (43°59′N, 43°51′E). The mean annual temperature was 14.9°C and the total annual precipitation was 607 mm. The soil was a clay loam soil, with low organic matter (2.5%). At the beginning of the experiment, in October 2003, total C and N concentrations were 1.5 and 0.14%, respectively, and the pH was 7.8, which was close to the pH values of the old-field succession from which the species originated (cf. Garnier et al. 2004). The 18 species grown as neighbours (Table 1) were selected among dominant species of a Mediterranean successional sere (Garnier et al. 2004), to represent a gradient of resource use (Violle et al. 2007a). These species belong to contrasting growth forms corresponding to different leaf area distributions along the stem; the morphology of their root system is also different, which potentially corresponds to different ways of extracting soil water

(Table 1). In autumn 2003, four replicated monocultures of each neighbour (1.2 × 1.2 m plots) were established by transplanting seedlings or ramets. This method ensured a standard plant density (100 plants per m^2). After establishment, no water or nutrients were added. Plots were weeded regularly to maintain monoculture status and initial density. The spaces between plots were kept free of vegetation. In autumn 2004, annuals and biennials were re-transplanted into the same plots, with the same spatial arrangement.

Two individuals of the grass *Bromus madritensis*, used as phytometers, were transplanted 40 cm apart in each plot when monocultures were re-established in November 2004. *B. madritensis* was selected as a phytometer since it is a common species from early stages of successional seres from the Mediterranean region around Montpellier (Garnier et al. 2004), and co-occurs with most species selected as neighbours. It is an annual species which grows fast in a large range of environmental conditions and displays a large plastic response of traits under competition (Violle et al. 2006).

Assessing the temporal dynamics of resource depletion

Between November 2004 and the end of June 2005, the leaf area index (LAI) and the fraction of light transmitted to the soil surface through the neighbour plant cover were measured on 11 dates with a "fish-eye" optical sensor (LAI 2000, Plant Canopy analyser; Li-Cor, Nebraska, USA) for all plots. Each measurement was replicated four times within a plot. Similarly, the soil water content of the upper 20 cm was monitored weekly within each plot using a Time Domain Reflectometry system (Trase System Model 6050X1; Soil Moisture Equipment, California, USA).

Resource depletion was modelled by calculating the amount of light and water remaining under each neighbouring community and thus available to phytometers throughout their lifespan. Time-dynamics of resource depletion, i.e. the fraction of light transmitted under plant cover and the fraction of transpirable soil water for the upper 20 cm of soil, were modelled for each plot with a daily time-step over the lifespan of phytometers, from 22 November 2004 to 30 June 2005 (Violle et al. 2007a). The cumulative amount of light transmitted per plot, L_c (J/cm^2) was calculated by summing over the study period the daily fraction of transmitted light per plot, estimated by non-linear adjustments (sigmoid curves) of the 11 records ($R^2 > 0.96$) and the daily total radiation obtained from a nearby meteorological station. The amount of available soil water, W_c, was calculated by summing the daily fraction of transpirable soil water of the upper 20 cm of soil, corresponding to the soil layer that contained more than 80% of root biomass of phytometers during the study period (C. Roumet, unpublished data). The daily fraction of transpirable soil water of each plot was estimated from a water-balance model taking into account daily

Table 1 List of studied species, their characteristics, and related indicators of resource depletion

Neighbouring species	Botanical family	Growth form	Type of root system	L_c (J/cm^2)	W_c (no unit)
Dactylis glomerata (P)	Poaceae	TUS	FIB	120.6 (36.5)	62.2 (0.3)
Brachypodium phoenicoides (P)	Poaceae	TUS	FIB	125.4 (28.8)	47.8 (0.1)
Bromus erectus (P)	Poaceae	TUS	FIB	187.8 (61.4)	52.9 (0.5)
Inula conyza (P)	Asteraceae	SHB	TAP	324.9 (5.5)	68.0 (0.5)
Psoralea bituminosa (P)	Fabaceae	ERL	TAP	883.4 (38.4)	76.9 (3.4)
Teucrium chamaedrys (P)	Lamiaceae	DWS	ADV	1354.9 (87.6)	94.1 (3.8)
Geranium rotundifolium (A)	Geraniaceae	ERL	TAP	1512.2 (95.7)	93.5 (1.8)
Veronica persica (A)	Scrophulariaceae	SEB	TAP	1555.4 (80.0)	87.5 (2.2)
Rubia peregrina (P)	Rubiaceae	DWS	ADV	1648.6 (126.2)	93.8 (2.5)
Calamentha nepeta (P)	Lamiaceae	DWS	TAP	1719.4 (156.7)	62.1 (0.8)
Crepis foetida (A)	Asteraceae	SHB	TAP	1733.7 (50.4)	79.9 (1.1)
Bromus madritensis (A)	Poaceae	TUS	FIB	1804.9 (286.2)	83.2 (1.7)
Arenaria serpyllifolia (A)	Caryophyllaceae	SEB	TAP	1845.0 (49.3)	89.6 (1.3)
Daucus carota (B)	Apiaceae	ERL	TAP	1889.2 (58.8)	82.9 (0.2)
Medicago minima (A)	Fabaceae	SEB	TAP	2161.5 (69.7)	85.1 (1.6)
Trifolium angustifolium (A)	Fabaceae	ERL	TAP	2223.9 (49.8)	83.8 (2.7)
Picris hieracioides (B)	Asteraceae	SHB	TAP	2299.5 (76.8)	82.9 (0.4)
Tordylium maximum (B)	Apiaceae	ERL	TAP	2354.5 (106.3)	84.4 (1.1)

L_c and W_c represent the depleted light and soil water, respectively, under the cover of neighbours over the lifespan of phytometers (from November 2004 to the end of June 2005). Values are mean ± standard deviation in parentheses. Life cycle: *A* annuals, *B* biennials, *P* perennials. Growth forms (classification follows Cornelissen et al. 2003): *DWS* dwarf shrub, *ERL* erect leafy, *SEB* semi-basal, *SHB* short-basal, *TUS* tussock. Root system: *TAP* tap, *FIB* fibrous, *ADV* adventitious. Species were ranked by increasing L_c values

climatic data (precipitation, solar radiation and potential reference evapotranspiration), canopy and root development, and soil water status. A more detailed account of the modelling procedures are given as ESM Method S1 and further developed in Violle et al. (2007a).

Measurements of traits

Neighbours traits

The height of neighbours was assessed from measurements on four plants per plot twice a month from November 2004 to June 2005 (14 records). The maximum rooting depth reached by neighbours was assessed in May (at peak of biomass production) from profiles of belowground biomass sampled every 10 cm between 0 and 70 cm depth (C. Roumet, unpublished data).

Phytometer traits

Phytometers were harvested in June 2005, after flowering; aboveground biomass was measured after drying at 60°C for at least 2 days. Predawn leaf water potential (Ψ_{base}, MPa) was measured on one leaf of each phytometer (8 replicates per neighbouring monoculture) at peak period of biomass production on 23 May 2005 within the 2 h preceding sunrise, using a portable pressure chamber (PMS Instru-

ments, Corvallis, OR, USA). SLA, m^2/kg was measured following a standardised protocol (Garnier et al. 2001), as the ratio of projected leaf area, obtained by the Image Analysis System (Delta-T Devices, UK), and leaf dry mass of one water-saturated mature and healthy leaf of each phytometer (8 replicates per neighbouring monoculture) at peak period of biomass production (May 2005).

Data analyses

Pearson's correlations, linear and non-linear regressions were calculated to relate plant traits, indicators of resource depletion (L_c and W_c) and phytometer biomass. Variables were log-transformed to meet the assumptions of normality when required. Multiple linear regression analyses were used to assess the dependency of phytometer biomass on L_c and W_c. One-way ANOVAs were performed to test for differences in L_c and W_c among neighbour species. All statistical analyses were performed using SAS (SAS Institute, Cary, NC, USA).

Results

The neighbours differed significantly in their effect on L_c and W_c ($F_{17,72} = 230$, $P < 0.0001$ and $F_{17,72} = 240$, $P < 0.0001$, respectively; Table 1). L_c was significantly predicted by the height of neighbours measured on 12 April (Fig. 2a), a time

when neighbour growth rate is at a maximum (Violle et al. 2007a). Interestingly, an increase in neighbour height leads to a comparable decrease in light transmitted, whatever the growth form of the species (Table 1; Fig. 2a). W_c was significantly and negatively correlated to the rooting depth of neighbours measured at peak vegetative biomass in May (23 May) (Fig. 2b) when water becomes limiting in the studied system (Violle et al. 2007a). An increase in rooting depth leads to a comparable decrease in water availability in the upper soil layer, whatever the root system of the species (Table 1; Fig. 2b). Since rooting depth and plant height measured in May (23 May) were allometrically related ($R^2 = 0.63$, $P < 0.0001$), W_c also significantly decreased with neighbour height measured in May (Fig. 2c).

The final above-ground biomass of phytometers was strongly affected by the presence of neighbours (40-fold variation between the different neighbourhoods: $F_{17,72} = 220.2$, $P < 0.0001$), compared to a situation without neighbouring vegetation (46.5 g in average for the biomass of phytometers grown in isolation, data not shown). The biomass of phytometers was positively correlated to both L_c and W_c (Fig. 3a, b) but was more affected by light than by water depletion (multiple linear regression, $R^2 = 0.87$, $P < 0.0001$; $\beta_{L_c} = 0.58$ and $\beta_{W_c} = 0.42$). Thus, among the 14 measurements of neighbour height performed over the season, the height measured on 12 April, as a proxy for light depletion over the season (Fig. 2a), was the best predictor of variation in phytometer biomass (Fig. 3c). Relationships were less significant when using the maximum height reached by neighbours ($R^2 = 0.39$, $P = 0.006$) as commonly done (see "Discussion"), as well as their height or rooting depth measured in May ($R^2 = 0.70$, $P < 0.0001$ and $R^2 = 0.40$, $P = 0.005$, respectively), as a proxies for water depletion over the season (see Fig. 2b and above).

The leaf traits of phytometers used to assess their competitive response changed with resource depletion levels: phytometer SLA decreased with increasing L_c values (Fig. 4a), i.e. when the amount of light intercepted by neighbours was decreasing, whereas phytometer Ψ_{base} increased with increasing W_c values (Fig. 4b), i.e. when the amount of water transpired by neighbours was decreasing. There were significant relationships between phytometer biomass and SLA on the one hand (Fig. 4c), and Ψ_{base} on the other hand (Fig. 4d), suggesting that these two traits play a significant role in the changes in plant performance under competition.

Discussion

Comparative plant ecology is based on the comparison of functional traits across species and the identification of
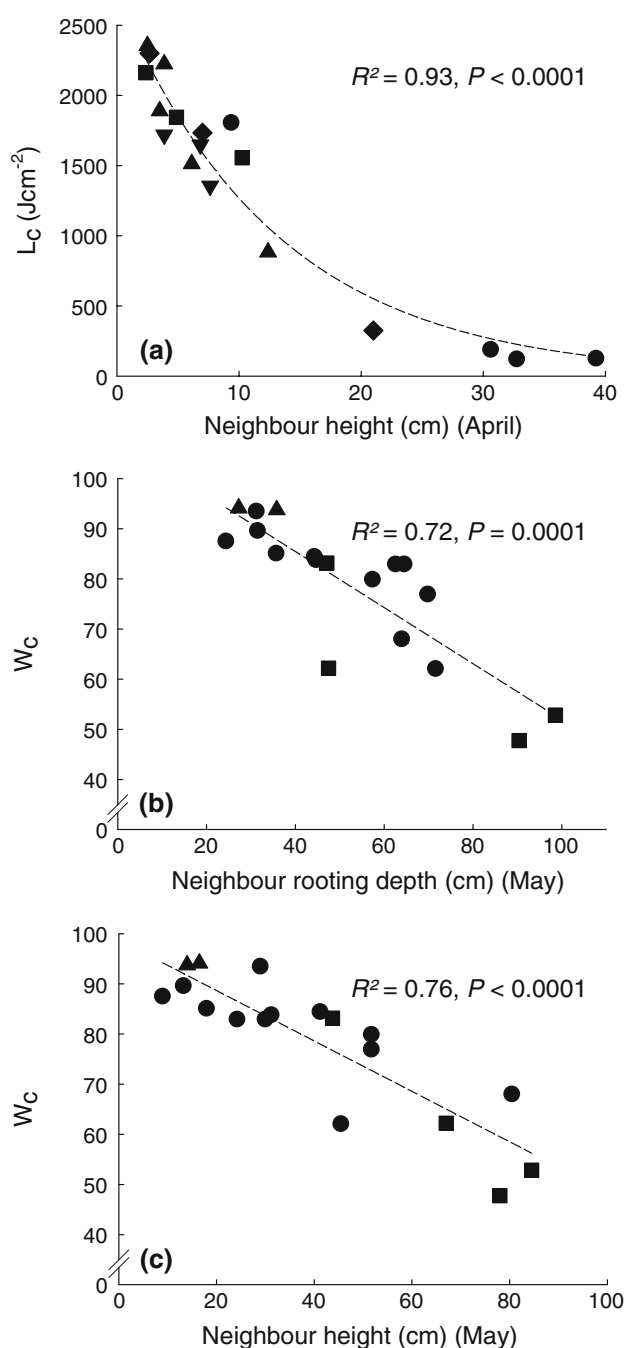

Fig. 2 Resource depletion and competitive effect traits of neighbours. **a** L_c as a function of neighbour height measured during growth shift (12 April) ($L_c = 2705.5 \times \exp(-0.08 \times \text{height})$); **b** W_c as a function of neighbour rooting depth measured at peak of vegetative biomass (23 May) ($W_c = -0.56 \times \text{rooting depth} + 107.8$); **c** W_c as a function of neighbour height measured at peak of vegetative biomass (23 May) ($W_c = -0.50 \times \text{height} + 98.71$). Points are means by neighbour. *Dashed lines* are regression lines. **a** *Symbols* represent growth form of neighbours: SEB (*filled square*), TUS (*filled circle*), ERL (*filled triangle*), DWS (*inverted filled triangle*), SHR (*filled diamond*) (see Table 1). **b,c** *Symbols* represent root system of neighbours: TAP (*filled circle*), FIB (*filled square*), ADV (*filled triangle*) (see Table 1)
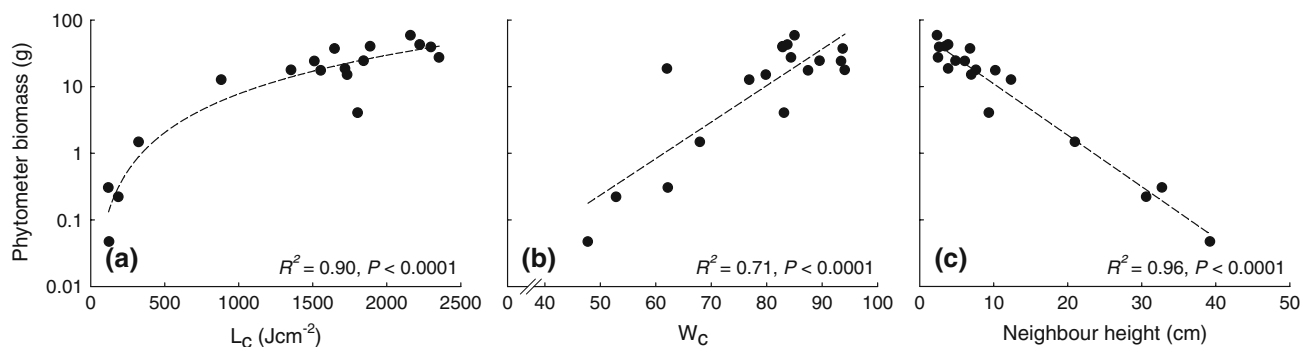
Fig. 3 Response of phytometers to resource depletion and neighbour height. The final biomass of phytometers (log-transformed) was positively correlated with **a** L_c [log(biomass) = 0.84 × log(L_c) – 4.89] and **b** W_c [log(biomass) = 0.05 × W_c – 3.37]. **c** The final biomass of phy-tometers (log-transformed) was negatively correlated with neighbour height measured on 12 April [log(biomass) = –0.16 × height + 5.70]. Points are means by neighbour. Note the log-scale for *y*-axis. *Dashed lines* are regression lines

Fig. 4 Competitive response traits of phytometers and plant performance. Phytometer SLA was directly linked to **a** light depletion [SLA = –4.50 × log(L_c) + 61.07], and, Ψ_{base} to **b** water depletion (Ψ_{base} = 0.03 × W_c + 2.99). The response of the phytometers to change in light and water depletion was related to variation in **c** specific leaf area, SLA [log(biomass) = –0.16 × SLA + 5.70) and **d** predawn water potential, Ψ_{base} [log(biomass) = 1.95 × Ψ_{base} + 2.90]. *Dashed* are means by neighbour. Note the log-scale for *y*-axis. *Dashed line* is the regression line
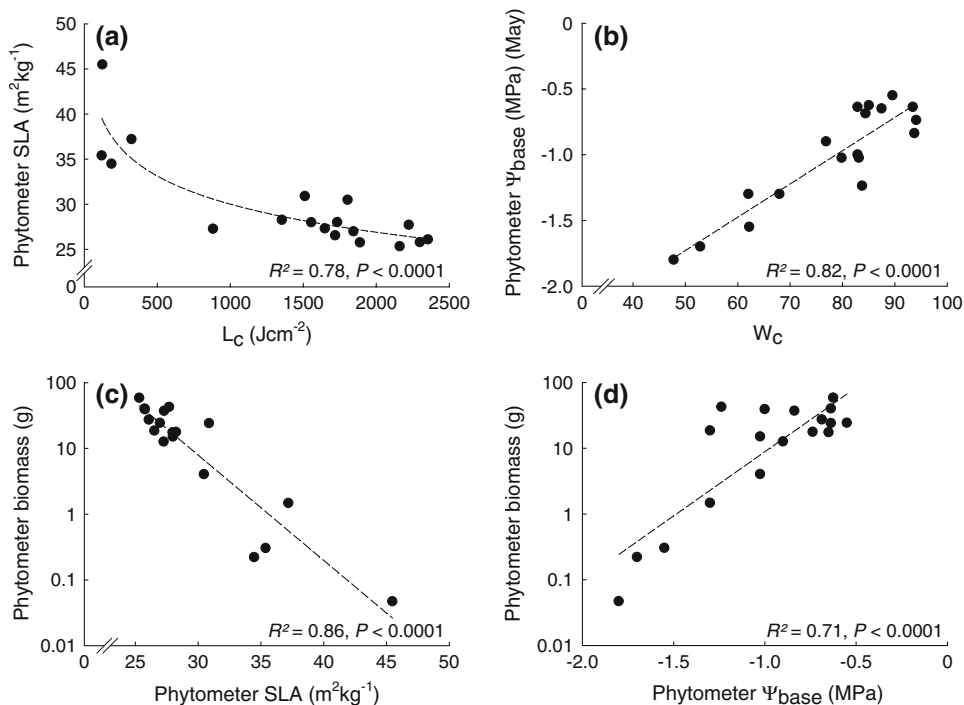
trait–environment relationships (Keddy 1992), in an attempt to develop trait-based predictive models dealing with vegetation dynamics and ecosystem functioning (e.g. van der Valk 1981; van Wijk 2007). Here, the choice of 18 dominant species of contrasted successional stages and growth forms grown in monocultures allowed the simulation of a wide range of resource depletion the temporal variations of which were assessed through resource modelling. Quantitative trait–environment relationships under competition were established: (1) above- and belowground competitive effect traits were correlated with the amount of resources depleted by neighbours over the growing season; and (2) competitive response traits, were significantly linked to the resource depletion levels that phytometers

perceived over their lifespan, the variations of which were related to changes in performance under competition.

Traits of neighbours and resource depletion

We found an exponential negative relationship between light transmission and neighbour height (Fig. 2a) that highlights the asymmetric nature of competition for light (Horn 1971; Schwinning and Weiner 1998). Although the actual mechanism of light interception by the canopy certainly involves more complex traits such as the distribution of leaf area along the stem (Falster and Westoby 2003a; Monsi and Saeki 2005), the strong relationship found here between height and light transmission across species displaying a

wide range of growth forms (e.g. short-basal, tussocks or erect plants; cf. Table 1) is an important step for competition studies investigating simple relationships between traits and resource depletion. Our study demonstrates that when comparisons among widely different growth forms are involved, plant height appears as a primary driver of light extinction down the canopy of herbaceous or small woody species. Size-related traits such as plant height were previously proposed as simple proxies for leaf distribution along the stem to predict light interception (e.g. Berntson and Wayne 2000), but the relationship between traits and light depletion was still remaining mainly qualitative (ESM Table S1). The studies pertaining to light depletion screened for in our literature survey (Supplementary Table S1) were most often theoretical. Empirical studies mainly focused on the efficiency of 'complex' leaf architectural traits (e.g. leaf angle, distribution of position of leaves along the stem) to explain light capture (e.g. Falster and Westoby 2003a), and no generalisation has actually emerged. Here, we advocate that the lack of quantitative relationships may be due to the complexity of predicting the depletion of resources that vary over time from instantaneous measurements of plant features performed at 'standardised' periods (e.g. at peak of biomass production or height growth). Interestingly, we found that the total amount of light intercepted over the growing season was best predicted by instantaneous measures of neighbour height performed at the beginning of canopy closure (Fig. 2a). This result challenges the hypothesis that the outcome of plant–plant interactions is explained by measures of maximum height reached by plants (Westoby et al. 2002), based on the implicit assumption of a time-stability of plant height hierarchy among species. Therefore, a time-integrated quantification of light depletion as well as a measure of resource-capturing traits at a relevant period (i.e. when light becomes limiting; cf. Violle et al. 2007a) should better reveal interspecific predictive relationships from 'easily-measurable' traits.

Strikingly, instantaneous measures of neighbour rooting depth in May, i.e. when water becomes limiting in our system (Violle et al. 2007a), were relevant indicators of water depletion throughout the season (Fig. 2b), in spite of the strong pulsing regime of this resource (Goldberg and Novaplansky 1997). Plants with deeper root systems therefore not only probably extract water from deeper soil layers (Casper and Jackson 1997), but also tend to deplete water to a larger extent in the upper (0–20 cm) soil layer, thereby reducing water available to competitors throughout the season, irrespective of species root system (cf. Table 1). Rooting density in this upper layer was indeed found to be higher for species with deeper root systems [root density $(g\ m^{-3}) = 43 \times$ rooting depth $- 603$, $r = 0.58$, $n = 18$]. This is an important finding, made possible by our experi-

mental design using monocultures: the difficulty of separating belowground species-specific root systems and activities in multi-species communities made it almost impossible to relate traits and water depletion in most studies screened in our literature survey (ESM Table S1). Also, the few existing studies (e.g. Gebauer and Ehleringer 2000; Ho et al. 2005) relating water depletion to root architectural traits (ESM Table S1) ignored aboveground traits as simple surrogates for this aboveground process. Interestingly, we showed that the variation in height among neighbours was related to depletion of both light and water (Fig. 2c). This provided potential explanations for the relationships between neighbour height and performance of phytometers emphasised in the pioneer competition study conducted by Gaudet and Keddy (1988) 20 years ago, which was also found here (cf. Fig. 3c). Therefore, this suggests that plant height could be considered as a generic trait describing both above- and belowground mechanisms of plant–plant interactions in plant communities, extending its current use as a proxy of the sole competition for light (Westoby et al. 2002; Falster and Westoby 2003b; McGill et al. 2006). Hence, analysing the frequency distributions of height in natural dense communities might give an operational quantification of the 'interaction milieu', as suggested elsewhere (McGill et al. 2006).

Phytometer traits in response to resource depletion

The competitive response traits considered were relevant indicators of changes in phytometer performance, in relation to light and soil water availability under neighbour cover (Figs. 3, 4). Phytometer SLA displayed a large range of intraspecific variation among neighbourhoods (2.5-fold), similar to what was found in interspecific comparison for the same successional system in natural conditions (Garnier et al. 2004). This result highlights the interest of applying the trait-based approach at intraspecific level to assess changes in species performance under competition. Phytometer SLA was mostly related to light availability (Poorter and Nagel 2000), increasing with increasing light depletion (Fig. 4a) as expected from ecophysiological studies (e.g. Björkman 1981; Meziane and Shipley 1999; Saldana et al. 2005). Phytometer Ψ_{base}, which is a direct indicator of the soil water status perceived by plants (Boyer 1995), decreased in response to soil water shortage due to competitors, as reported in previous studies (Mitchell et al. 1999; Gebauer et al. 2002). Predawn water potential values lower than -1.0 MPa were recorded in half of the situations (Fig. 4d). Such low values indicate strong water limitation, as shown in Mediterranean (Roy et al. 1987) and other grasslands (Knapp et al. 1993; Colabelli et al. 2004): for example, at -1.0 MPa, the mean leaf elongation rate of five grass species was reduced to approximately 30% of its

value under non-limiting water availability (Colabelli et al. 2004).

Altogether, we demonstrated that instantaneous measures of SLA and Ψ_{base}, performed at peak period of biomass production of phytometers, reflected the amount of light and water perceived by plants throughout their lifespan. These traits thus appear as reliable indicators of resource use at local scales, as needed in competition studies, which stands in complement to their use at broader scales (e.g. Vendramini et al. 2002; Wright et al. 2004, 2005) for detecting plant strategies of resource use.

These results illustrate the trait-based "performance paradigm" (Violle et al. 2007b) for plant–plant interactions with a cascade of relationships between traits (Fig. 1b). In this framework, the cumulative amount of resource depleted by a neighbourhood over the season (i.e. 'R_c' values) stands as a centrepiece of resource-based competition approaches, through links with both competitive effect and response traits. Previously, the 'R^*' indicator, defined as the resource concentration remaining under the plant cover at equilibrium (see Tilman 1980, 1982), has provided valuable results, particularly when relating plant traits (e.g. root biomass or density) and nutrient depletion (e.g. Wedin and Tilman 1993; Fargione and Tilman 2006; see also ESM Table S1). However the R^* concept has proved difficult to generalize across ecosystems (Miller et al. 2005), especially because it does not apply to situations where equilibrium states are not reached. Therefore R_c as modelled here appears as a promising approach to predict the short-term outcome of resource competition in non-steady state situations.

To conclude, instantaneous measurements of plant traits appear to be relevant tools to predict the dynamics of species effects/responses on/to resource availability under competition. This validates the use of plant traits as sensors of resource availability, particularly at the local scale at which plant–plant interactions operate, or as indicators of the effects of environmental filters involved in the structuring of plant communities along environmental gradients (McGill et al. 2006; Shipley et al. 2006).

References

Aarssen L, Keogh T (2002) Conundrums of competitive ability in plants: what to measure? Oikos 96:531–542

Berntson GM, Wayne PM (2000) Characterizing the size dependence of resource acquisition within crowded plant populations. Ecology 81:1072–1085

Björkman O (1981) Responses to different quantum flux densities. In: Lange OL, Nobel PS, Osmond CB, Ziegler H, Zimmermann MH (eds) Encyclopaedia of plant physiology. Springer, Berlin, pp 57–107

Boyer JS (1995) Measuring the water status of plants and soils. Academic Press, San Diego

Casper BB, Jackson RB (1997) Plant competition underground. Annu Rev Ecol Syst 28:545–570

Colabelli M, Assuero S, Durand J-L (2004) Water status and leaf elongation of C3 and C4 grasses of flooding Pampa grassland. J Veg Sci 15:817–822

Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust J Bot 51:335–380

Craine JM (2005) Reconciling plant strategy theories of Grime and Tilman. J Ecol 93:1041–1052

Dybzinski R, Tilman D (2007) Resource use patterns predict long-term outcomes of plant competition for nutrients and light. Am Nat 170:305–318

Falster DS, Westoby M (2003a) Leaf size and angle vary widely across species: what consequences for light interception? New Phytol 158:509–525

Falster DS, Westoby M (2003b) Plant height and evolutionary games. Trends Ecol Evol 18:337–343

Fargione J, Tilman D (2006) Plant species traits and capacity for resource reduction predict yield and abundance under competition in nitrogen-limited grassland. Funct Ecol 20:533–540

Garnier E, Shipley B, Roumet C, Laurent G (2001) A standardized protocol for the determination of specific leaf area and leaf dry matter content. Funct Ecol 15:688–695

Garnier E, Cortez J, Billès G, Navas M-L, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint J-P (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology 85:2630–2637

Gaudet CL, Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. Nature 334:242–243

Gebauer RLE, Ehleringer JR (2000) Water and nitrogen uptake patterns following moisture pulses in a cold desert community. Ecology 81:1415–1424

Gebauer RLE, Schwinning S, Ehleringer JR (2002) Interspecific competition and resource pulse utilization in a cold desert community. Ecology 83:2602–2616

Goldberg DE (1990) Components of resource competition in plant communities. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, San Diego, pp 27–49

Goldberg DE (1996) Competitive ability: definitions, contingency and correlated traits. Phil Trans R Soc B 351:1377–1385

Goldberg DE, Fleetwood L (1987) Competitive effect and response in four annual plants. J Ecol 75:1131–1143

Goldberg DE, Novaplansky A (1997) On the relative importance of competition in unproductive environments. J Ecol 85:409–418

Grime JP (1973) Competition exclusion in herbaceous vegetation. Nature 242:344–347

Grime JP (1979) Plant strategies and vegetation processes. Wiley, Bath

Gutschick VP, Wiegel FW (1988) Optimizing the canopy photosynthetic rate by patterns of investment in specific leaf mass. Am Nat 132:67–86

Ho MD, Rosas JC, Brown KM, Lynch JP (2005) Root architectural tradeoffs for water and phosphorus acquisition. Funct Plant Biol 32:737–748

Horn HS (1971) The adaptative geometry of trees. Princeton University Press, Princeton

Joffre R, Morales MJL, Rambal S, Ales RF (1987) Root-growth and water-uptake by Mediterranean annual and perennial grasses. Act Oecol 8:181–194

Keddy PA (1992) A pragmatic approach to functional ecology. Funct Ecol 6:621–626

Knapp AK, Fahnestock JT, Hamburg SP, Statland LB, Seastedt TR, Schimel DS (1993) Landscape patterns in soil–plant water relations and primary production in tallgrass prairie. Ecology 74:549–560

MacArthur RH (1972) Geographical ecology: patterns in the distribution of species. Princeton University Press, Princeton

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends Ecol Evol 21:178–185

Meziane D, Shipley B (1999) Interacting determinants of specific leaf area in 22 herbaceous species: effects of irradiance and nutrient availability. Plant Cell Environ 22:447–459

Miller PC (1981) Resource use by Chaparral and Matorral: a comparison of vegetation function in two Mediterranean-type ecosystems. Springer, Berlin

Miller TE, Burns JH, Munguia P, Walters EL, Kneitel JM, Richards PM, Mouquet N, Buckley HL (2005) A critical review of twenty years' use of the resource-ratio theory. Am Nat 165:439–448

Mitchell RJ, Zutter BR, Gjerstad DH, Glover GR, Wood CW (1999) Competition among secondary-successional pine communities: a field study of effects and responses. Ecology 80:857–872

Monsi M, Saeki T (2005) On the factor light in plant communities and its importance for matter production. Ann Bot 95:549–567

Newman EI (1973) Competition and diversity in herbaceous vegetation. Nature 244:310

Poorter H, Nagel O (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Aust J Plant Physiol 27:595–602

Rosenzweig ML (1968) Net primary productivity of terrestrial communities: prediction from climatological data. Am Nat 102:67–74

Roy J, Garnier E, Jackson LE (1987) Responses of two perennial grasses to water availability in different habitats related to successional change under Mediterranean climate conditions. In: Tenhunen JD, Catarino FM, Lange OL, Oechel WC (eds) Plant response to stress-functional analysis in Mediterranean ecosystems. NATO ASI Series. Springer, Berlin, pp 175–190

Saldana A, Gianoli E, Lusk CH (2005) Ecophysiological responses to light availability in three *Blechnum* (Pteridophyta, Blecnaceae) of different ecological breadth. Oecologia 145:252–257

Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. Science 148:339–346

Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113:447–455

Shipley B, Vile D, Garnier E (2006) From plant traits to plant communities: a statistical mechanistic approach to biodiversity. Science 314:812–814

Tilman D (1980) A graphical-mechanistic approach to competition and predation. Am Nat 116:362–393

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton

Valladares F, Martinez-Ferri E, Balaguer L, Perez-Corona E, Manrique E (2000) Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? New Phytol 148:79–91

van der Valk AG (1981) Successions in wetlands: a Gleasonian approach. Ecology 62:688–696

van Wijk MT (2007) Predicting ecosystem functioning from plant traits: results from a multi-scale ecophysiological modeling approach. Ecol Model 203:453–463

Vendramini F, Díaz S, Gurvich DE, Wilson PJ, Thompson K, Hodgson JG (2002) Leaf traits as indicators of resource-use strategy in floras with succulent species. New Phytol 154:147–157

Violle C, Richarte J, Navas M-L (2006) Effects of litter and standing biomass on growth and reproduction of two annual species in a Mediterranean old-field. J Ecol 94:196–205

Violle C, Lecoeur J, Navas M-L (2007a) How relevant are instantaneous measurements for assessing resource depletion under plant cover? A test on light and soil water availability in 18 herbaceous communities. Funct Ecol 21:185–190

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007b) Let the concept of trait be functional!. Oikos 116:882–892

Wedin D, Tilman D (1993) Competition among grasses along a nitrogen gradient—initial conditions and mechanisms of competition. Ecol Monogr 63:199–229

Westoby M, Falster DS, Moles A, Vesk P, Wright I (2002) Plant ecological strategies: some leading dimensions of variation between species. Annu Rev Ecol Syst 33:125–159

Wilson SD, Tilman D (1991) Components of plant competition along an environmental gradient of nitrogen availability. Ecology 72:1050–1065

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin FS III, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Garnier E, Hikosaka K, Lamont BB, Lee W, Oleksyn J, Osada N, Poorter H, Villar R, Warton DI, Westoby M (2005) Assessing the generality of global leaf trait relationships. New Phytol 166:485–496