Effect of the Hierarchical Position of Individuals in a *Medicago sativa* Stand on Shoot Respiration

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EFFECT OF THE HIERARCHICAL POSITION OF INDIVIDUALS IN A *MEDICAGO SATIVA* STAND ON SHOOT RESPIRATION

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Abstract

The influence of the hierarchical position on the relationship between C gains and C losses (respiration) of individuals was investigated in a alfalfa (*Medicago sativa*) stand. The hierarchical position that an individual occupied was defined by its height relative to the stand height. Stands were established by arranging potted individual plants at a density of 400 plants m^{-2}. Stands were grown in growth cabinets. ^{13}C steady-state labelling was used to assess C fixation (C_{new}) by individuals during a photoperiod of 16 h. Respiration of shoots was measured during the following 8 h dark period. The amount of C_{new} used in shoot respiration ($C_{new,R}$) was calculated from the rate of respiration and the isotopic composition of respiratory CO_2. The rate of $C_{new,R}$ of each individual was proportional to the product of C_{new} and the hierarchical position of the individual. For individuals in high hierarchical positions, $C_{new,R}$ was about 10 % of C_{new}. This proportion decreased with decreasing hierarchical position. Conversely, the amount of C respired by the consumption of other substrates ($C_{old,R}$) was about 0.5 % of the shoot C mass. This was true for all plants, independent of their hierarchical position. It was concluded that plants getting into low hierarchical positions had to invest increasingly more carbohydrates from reserves to sustain maintenance needs.

Keywords: Photosynthesis, *Medicago sativa*, respiration, size hierarchy, stable isotopes

Introduction

The size often varies considerably among individual plants within a stand. These size differences may be the result of genetic differences in growth rate and shoot elongation rate. Initial small differences can be amplified by competition for light. As a dense stand develops, the growth rate of the smallest individuals will become zero and they will eventually die due to the suppression by larger individuals. This self-thinning process is well documented on the basis of shoot mass and plant density (e.g. Matthew *et al*. 1995, Nie *et al*. 1997). However, plants may change allometry and show physiological adaptations when they get into lower hierarchical positions within a stand. Yet, little is known about the physiological adaptations which occur as a function of the hierarchical position in a stand. Adaptations to the light environment are manifested in the gas exchange which reflects carbon (C) gains and losses (respiration) of the plants. In the present study we investigated the influence of the hierarchical position on the relationship between C gains and C losses of individuals.

Material and Methods

One week after germination, alfalfa (*Medicago sativa*) seedlings were transplanted into pots (5 cm diameter, 35 cm long) filled with sand and transferred to four growth cabinets. Plant stands were formed by placing the pots in eight containers (76 cm long, 56 cm wide, 32 cm high), two per growth cabinet. Each container held 165 pots resulting in a density of 400 plants m^{-2}. Conditions in the growth cabinets were: 22/18°C day/night temperature, 375 µmol m^{-2} s^{-1} photosynthetic photon fluence rate, 16 h photoperiod and 70 % relative humidity. Plants were irrigated twice a day with a complete nutrient solution containing 7.5 m*M* nitrate (pH 6.5). The growth cabinets were part of a steady-state $^{13}CO_2$/$^{12}CO_2$ labelling system. In this system, atmospheric CO_2 was exchanged with CO_2 of known ^{13}C composition (ä). Growth cabinets received CO_2 with ä –2.4 ‰ or ä –46.8 ‰ (two cabinets each). After four weeks, the stands were cut to a stubble height of 5 cm. During a regrowth period of four weeks, 16 to 24 individuals per week were randomly selected and transferred between cabinets of differential ä. Thus, all photosynthates fixed during one photoperiod were labelled. At the end of the photoperiod, half of the labelled plants were harvested, whereas the other plants were enclosed in a respiration cuvette to measure shoot and root respiration for 8 h. Air flows were recorded (mass flow meters, Tylan, CA, USA) and CO_2 was continuously analysed for concentration (Infrared gas analyser, LI-COR 6262, NE, USA) and C-isotopic composition (IRMS, Delta plus, Finnigan, Germany). Afterwards, shoot height (h_i) and leaf area (leaf area meter, LI-COR 3100, NE, USA) were measured and plants were harvested. Plant material was analysed for total C and C-isotopic composition using an elemental analyser (Carlo Erba NA1108, Italy) interfaced to a IRMS. The amount of C fixed during the labelling photoperiod (C_{new}) was calculated from total C mass and isotopic composition in the plant material. Use of C_{new} in respiration ($C_{new,R}$) was assessed from the rate of respiration and the isotopic composition of respiratory CO_2.

Results and Discussion

During the fourth week of regrowth, maximum plant height (h_{max}) increased from 0.54 to 0.65 m. Leaf area index was about 5 and more than 90 % of the incident radiation was absorbed by the stand. The amount of recently fixed C (C_{new}) increased exponentially with increasing shoot height and linearly with shoot mass of the individuals (Fig. 1). Some individuals in low hierarchical positions showed a relatively high shoot mass. Yet, their C gain (C_{new}) was low when compared with similar-sized plants (same mass) in higher hierarchical positions.

The rate of nocturnal respiration of non-labelled C ($C_{old,R}$, g plant^{-1}; i.e. C respired using substrate fixed prior to labelling including reserve C) was proportional to shoot C mass (C, g plant^{-1}):

$C_{old,R} = 0.0049 * C$; $r = 0.95$; $p < 0.001$.

Conversely, the rate of nocturnal respiration of C originating from recently fixed photosynthates ($C_{new,R}$, g plant^{-1}) was proportional to the product of C fixation during labelling (C_{new}, g plant^{-1}) and shoot height (h_i, m):

$C_{new,R} = 0.165 * C_{new} * h_i$; $r = 0.98$; $p < 0.001$. (1)

Equation (1) can also be written using relative shoot height ($h_i * h_{max}^{-1}$) as a measure of the hierarchical position that an individual plant occupied in the stand:

$$C_{new,R} = k * C_{new} * \frac{h_i}{h_{max}}. \quad (2)$$

Equation (2) implies that the amount of new C respired during the dark period depends on the amount of C fixed during the previous photoperiod and on the hierarchical position of the individual (Fig. 2). When individuals occupied a high hierarchical position ($h_i * h_{max}^{-1} = 1$; $k = 0.096$), $C_{new,R}$ was equivalent to almost 10 % of the C fixed in the previous photoperiod (C_{new}). This proportion decreased with decreasing hierarchical position. For example, an individual that reached a fifth of the stand's height ($h_i * h_{max}^{-1} = 0.2$) respired only 2 % of the C_{new}.

The amount of C fixed during labelling (C_{new}) reflects the instantaneous growth rate of an individual in the stand. Respiration of new C was high when the growth rate was high. In low hierarchical positions, the instantaneous growth rate was low due to the low availability of light. In such a situation respiration of new C was low and gross respiration depended mainly on the mass of the individual. Also, individuals of short stature with relatively high mass respired mainly 'old' C. These results indicate that plants getting into low hierarchical positions had to invest increasingly more carbohydrates from reserves to sustain maintenance needs. These costs were particularly high for plants with a relatively high mass in relation to their height.

References

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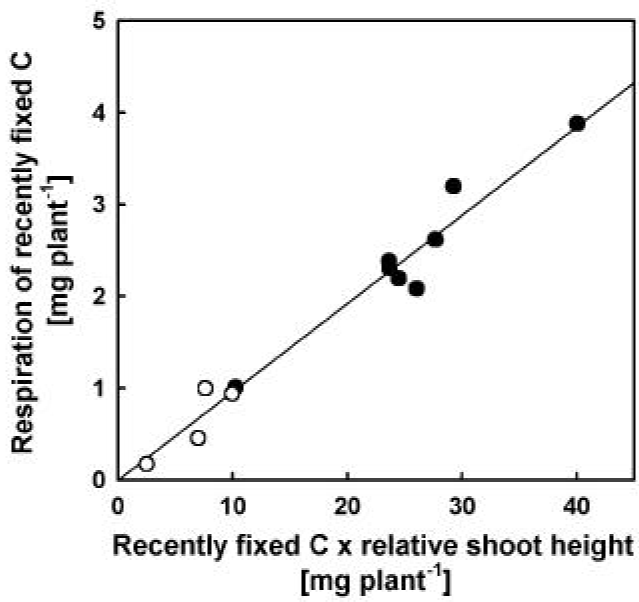
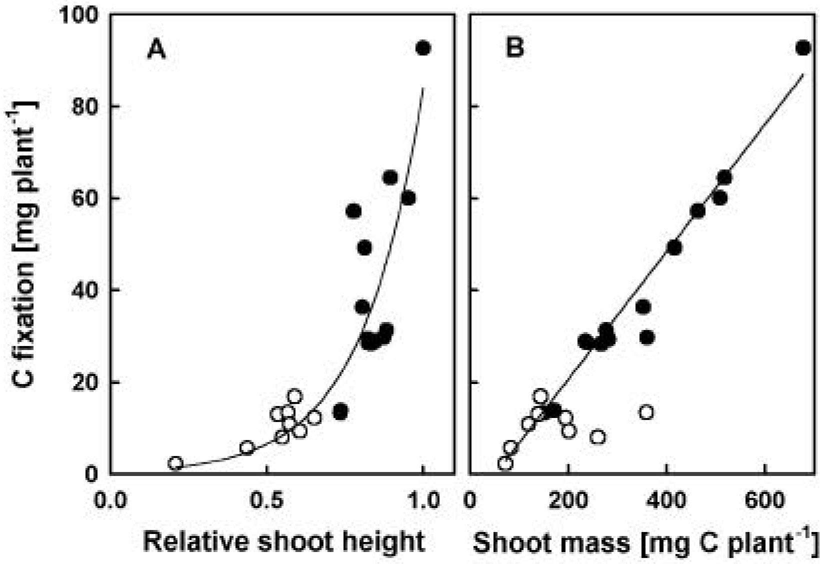
Legends

Figure 1 - Carbon fixation (C_{new}) during a 16 h photoperiod as related to shoot height (A) and shoot mass (B) of alfalfa individuals growing in a stand. Data are from the fourth week of regrowth. Shoot height of an individual is given relative to the height of the stand. Closed circles denote dominant individuals which had a height of more than 70 % of stand height, open circles denote subordinate individuals with a height of less than 70 % of the stand height.

Figure 2 - Respiration of recently fixed C ($C_{new,R}$) in relation to the product of C fixation and hierarchical position of the individual (see equation 2 in the text). Respiration was measured throughout the 8 h dark period. Hierarchical position was defined as the height of the individual relative to stand height. $Y = 0.096\ X$; $r = 0.98$; $p < 0.001$. Description of symbols see Fig. 1.


Respiration of recently fixed C
[mg plant⁻¹]
0
1
2
3
4
5
0
10
20
30
40
Recently fixed C x relative shoot height
[mg plant⁻¹]


100
80
60
40
20
0
C fixation [mg plant^{-1}]
A
0.0
0.5
1.0
Relative shoot height
B
0
200
400
600
Shoot mass [mg C plant^{-1}]