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Allocation of photoassimilates to biomass, resin and carbohydrates in *Grindelia chiloensis* as affected by light intensity

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Abstract

Grindelia chiloensis (Asteraceae) is a shrub native to Patagonia, Argentina, and can accumulate as much as 25% resin (on a dry weight basis) in leaves. The resin can be used in applications similar to those of pine resins. Reductions in available radiation are thought to decrease both the plant C:N ratio and resin production. The objective of this study was to assess the effect of light availability on the allocation of photoassimilates to biomass, resin (terpenes) and carbohydrates in *G. chiloensis*. To examine this, three radiation treatments were applied to field grown plants: (i) 100% radiation (full-sun), (ii) 50% radiation and (iii) 25% photon flux density radiation. Changes in available radiation resulted in significant changes in above ground biomass accumulation, carbon based secondary metabolites (resin), non-structural carbohydrate (TNC) content, and relative growth rate (RGR). At low radiation levels, above ground biomass accumulation, RGR, resin, TNC content and CO₂ assimilation rate were highly reduced (from 150 to 80 g per plant, from 16 to 7%, and from 30.2 to 8.6 g per plant, for biomass, resin content, and resin production, respectively). The responses to low radiation found in *G. chiloensis* would limit productivity and the distribution of this species when grown under cultivation. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Biomass production; C:N ratio; Terpenes; Radiation availability

1. Introduction

Some members of the Asteraceae adapted to arid conditions, produce diterpene resin acids that can be used as alternatives to pine resins (Hoffmann et al., 1984; Timmermann and Hoffmann, 1985). *Grindelia chiloensis* (Corn.) Cabr. (Asteraceae), is a shrub native to the Patagonia and Monte regions of Argentina. It can accumulate as much as 25% resin by weight in its leaves, with net primary productivity between 90 and 170 g per plant per year when growing in native stands

(Ravetta et al., 1996a). Under cultivation in Arizona, USA, up to 67.4 g of resin per plant has been produced (about 2.24 Mg ha⁻¹; Ravetta et al., 1996b). In Patagonia similar yields have been achieved after appropriate agronomic practices were developed for this area (Ravetta and Soriano, unpublished data). Spring is the regular transplanting season in northern Patagonia, and to harvest to maximise yields. The first is at full bloom, the second around the date of the first frost (approximately 6 months after transplanting). The use of selected accessions tested for the local conditions allowed for a near 100% increase in resin production per plant, reaching those levels found in Arizona (changing from 30 to 70 g per plant). With the

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aid of a cloning protocol, resin production should increase (Wassner and Ravetta, 2000) since large phenotypic variation in related traits has been found (Ravetta et al., 1996a). After 6–7 months, plants can attain from 0.40 m to about 1 m in height, and may cover a projected area of up to 1.60 m in diameter, depending on growth conditions.

Arid and semiarid lands of the world occupy around one-third of the world's land area (Heathcote, 1983) and are underutilized, although in many cases there are clear signs of over-exploitation and degradation due to unsustainable agricultural practices. These same areas contain many indigenous species with potential to be domesticated as renewable sources of specialty chemicals or other compounds that confer adaptability to harsh environments and are of considerable economic importance (Timmermann and Hoffmann, 1985). Such crops have the additional advantage that they would not compete with conventional food and fiber crops, that require more productive land. McLaughlin (1985) proposed four criteria for the selection of new crops for arid environments. He concluded that the target species should have environmental/biological limitations to grow in mesic environments, where production costs tend to be lower than in arid lands due to the lower need for supplementary water. It has also been suggested that the production of such speciality compounds is promoted (increased harvest index) by the environmental conditions of arid lands, by high radiation and dry environments (Hoffmann et al., 1984), which limit plant productivity (Ravetta and Soriano, 1998). On the other hand, mesic environments tend to have lower radiation levels than arid lands due to their greater cloudiness (Ravetta and McLaughlin, 1996). These conditions could limit productivity of some plant species, restricting their cultivation to arid environments. In *Grindelia* surface resins are believed to protect the plant reducing transpiration, by increasing leaf reflectance. Support for this hypothesis comes from the work with *Beyiera viscosa* (Euphorbiaceae), a shrub native to the arid regions of Western Australia, which accumulates terpenoids as a major leaf resin (Dell, 1977).

In general, the resource availability hypothesis (Bryant et al., 1983), predicts a decline in allocation to carbon-based secondary metabolites (Bryant et al., 1985; Bryant, 1987) when carbon gain is limited relative to nutrient availability, as during periods of

low irradiance. This prediction is based on the effects of environmental conditions on carbon–nutrient balance (C:N). Among terpenoid-bearing herbs, high irradiance (photon flux density) conditions generally stimulate increases in monoterpene concentration (Gershenzon, 1994). However, little is known about the effect of irradiance on other carbon-based secondary metabolites, like the diterpene resins found in *Grindelia* species.

Environmental factors (e.g. water stress; Zavala and Ravetta, 1977) affect resin production in *Grindelia* through changes in C:N and biomass partition. We hypothesize that consequently, reductions in available radiation will decrease both the C:N ratio and resin production. Such responses would limit productivity and the distribution of this species when grown as a crop.

The objective of this study was to assess the effects of different levels of irradiance on the allocation of photoassimilates to biomass, resin (terpenes) and carbohydrates in *G. chiloensis*, grown under otherwise normal field conditions in Patagonia, Argentina.

2. Materials and methods

2.1. Experiment

The experiment was carried out in Trelew, Patagonia, Argentina (43°12'S, 65°16'W) during the summer of 1996–1997.

Seeds were collected from a native population of *G. chiloensis* from Chubut in northeastern Patagonia (43°16'S, 56°21'W). They were placed in germination trays filled with local top soil in a glasshouse. In October 1996, approximately 4 weeks after germination, plants (6–8 leaves) were selected and transplanted to 12 plots of 10 m² (2 m × 5 m). Each plot consisted of six rows of six plants, with the 12 plots assigned (36 plants per plot). The 12 plots were assigned randomly to three light environments (four replicates each): 100% radiation (full-sun), 50% radiation (50%-sun), and 25% radiation conditions (25%-sun). Treatments were imposed immediately after transplanting by covering the top (not the sides) of the plots with 10 m² of shade cloth. Plots were furrow-irrigated with 10 plants per plot harvested by hand from the center of the plot on 8 January (63 days after

transplanting 63 DAT) and another 10 plants harvested on 15 May 1997 (180 DAT). Roots were extracted by digging them out and then washing them with tap water. Temperature, carbon dioxide assimilation and photosynthetic photon flux density (PPFD) were recorded for 24 h periods under the shade cloths (50%-sun and 25%-sun) and control (full-sun) with a Li-Cor 6200 (Li-Cor Inc., Lincoln, NE, USA) immediately before both harvests. Instantaneous net CO₂ uptake and PPFD values were integrated for 24 h periods. Average canopy temperatures under both types of shade cloth and full-sun treatment were always within <0.8°C of each other, and in no case were consistent differences in temperature detected between treatments.

Harvested plants, including roots, were oven-dried at 60°C for 72 h and whole plant dry mass was determined. Relative growth rate (RGR) was calculated using the dry mass from both harvests, 63 DAT and 180 DAT. Resin content was determined separately for leaves and stems. Content of non-structural carbohydrates (TNC) and nitrogen (N) were determined in leaves, stems, capitula and roots. The carbon–nitrogen ratio (TNC:N) was calculated by computing TNC and N content, respectively.

2.2. Methods of analysis

Samples (5 g) were extracted with 150 ml of dichloromethane (DCM) in a Soxhlet apparatus for 8 h. The crude extracts were evaporated until dryness and the plant's total resin determined as the percentage of dry biomass (Timmermann and Ravetta, 1990).

After resin extraction, biomass samples (50 mg) were autoclaved (0.1 MPa, 15 min) with 100 ml of distilled water. Samples were homogenized in 100 ml of water and the content of solubilized sugar as determined by the Anthrone method (Yem and Willis, 1954).

Nitrogen analysis was based on the Kjeldahl method. A protein digester together with a nitrogen determinator (Kjeltec System 1002 Tecator, Höganäs, Sweden) were used.

2.3. Estimation of energy (gram of glucose)

The energy cost of different plant fractions (resin, protein, TNC, fiber) was determined by computing the

amount of glucose required to provide all the substrates and cofactors consumed in the biosynthesis of plant diterpenoids, protein, non-structural carbohydrates and fiber, according to published data (Gershenzon, 1994). Glucose is a suitable compound for such calculations, since non-structural carbohydrates are the usual storage and transport forms of fixed carbon in plants and can be readily respired to generate ATP and NADPH (Gershenzon, 1994). Here “resin” refers to a combination of non-volatile terpenoids, C₂₀ diterpenoids, and “fiber” refers to the rest of the biomass left after the extraction of protein, non-structural carbohydrates and resin. The results are presented as the amount of glucose (in g) needed to produce a gram of each product.

Energy in resin: grams of resin (in leaves + stems + capitula) × 3.26 g glucose per gram of resin (Gershenzon, 1994).

Energy in protein: grams of N (in leaves + stems + capitula + roots) × 6.25 × 1.62 g glucose per gram of protein (Loomis and Connor, 1996).

Energy in non-structural carbohydrates: grams of TNC (in leaves + stems + capitula + roots) × 1.21 g glucose per gram of TNC (Loomis and Connor, 1996).

Energy in fiber: grams of fiber (in leaves + stems + capitula + roots) × 1.32 g glucose per gram of fiber (Loomis and Connor, 1996).

2.4. Statistical analysis

One way analysis of variance (ANOVA) was conducted. Percentage values were arcsine($x^{1/2}$) transformed to correct non-normality in proportions, prior to statistical analysis. Mean separation was done using Honestly Significant Difference (Tukey's; *T*-method).

3. Results

Peak instantaneous PPFD for plants under the full-sun treatment were 1980 and 1820 μmol m⁻² s⁻¹ for the January and May measurements, respectively. Because of the difference in peak PPFD and day-length (15:10 h for the January measurements and 10:45 h for the May measurements), the total available

Table 1

Above ground biomass (g per plant) and resin content (%) for the first (63 DAT) and second (180 DAT) harvest of *G. chiloensis* grown in Argentina under three radiation treatments: full-sun, 50%-sun and 25%-sun^a

Treatment	Above ground biomass (g per plant)		Resin content (%)	
	63 DAT	180 DAT	63 DAT	180 DAT
Full-sun	30.0 a	155.6 a	16.2 a	16.3 a
50%-sun	22.6 ab	95.9 b	17.2 a	12.1 b
25%-sun	18.2 b	80.5 b	12.6 b	7.3 c

^a Means followed by different letters within a column are significantly different at $P < 0.05$ (Tukey's; *T*-method).

daily PPFD in the full-sun treatment was halved between January (54 mol m⁻² per day) and May 1997 (25.3 mol m⁻² per day). Integrated PPFD in the other two treatments yielded about 50 and 25% PPFD of that of the full-sun treatment, in accordance with the manufacturer's specification for the shading fabric. For the first measurement date (08/01/1997) maximum, minimum, and mean temperatures were 26.2, 13.5 and 19.8°C, respectively. For the second measurement temperatures were 13.8, 9.3 and 11.5°C, respectively.

At 63 DAT plants under full sun had relatively little growth and no significant differences in above ground biomass were found among treatments (Table 1). Resin content was only reduced in plants grown under 25%-sun ($P < 0.01$; Table 1). Far more growth took place in the period between harvests (63 to 180 DAT), and at the second harvest above ground biomass was markedly reduced by lower radiation, being highest for full-sun and lowest for 25%-sun treatment ($P < 0.01$; Table 1). Resin content decreased from the first (63 DAT) to the second (180 DAT) harvest for

plants growing under 50%-sun and 25%-sun treatments ($P < 0.01$; Table 1). Total resin production (above ground biomass × resin content) was significantly affected by radiation availability. For both harvests the total resin production was highest for the full-sun treatment ($P < 0.01$; Table 2) and was similar to previous resin yield for this unselected accession (Ravetta and Soriano, unpublished data).

Differences in RGR, plant height and number of capitula associated with radiation availability, were found. RGR was higher in the full-sun treatment than in the 50%-sun and 25%-sun treatments ($P < 0.01$; Table 2). Plant height decreased and number of capitula increased with light availability ($P < 0.01$; Table 2).

Net CO₂ assimilation rate was significantly reduced in plants under 50%-sun and 25%-sun treatments both in January and May ($P < 0.01$; Fig. 1). The highest instantaneous CO₂ uptake values were found for full-sun plants 63 DAT ($P < 0.05$; Fig. 1). An interaction between light level and season on net CO₂ uptake was found (best illustrated when instantaneous values were integrated throughout 24 h periods; Fig. 2). For all treatments, integrated net CO₂ assimilation was reduced in May (autumn; 180 DAT), compared to that found in January (summer; 63 DAT; $P < 0.01$; Fig. 2). No differences were found in May for integrated net CO₂ assimilation between full-sun (26 mol m⁻² per day) and 50%-sun (12 mol m⁻² per day) treatments (Fig. 3, open symbols).

Both the analysis of biomass partitioning between organs and energy content was done only for the final biomass harvest (May). Relative dry matter partitioning between organs was affected by radiation availability ($P < 0.05$; Fig. 3). Plants growing under the 25%-sun treatment had the highest proportion of root biomass (21%; $P < 0.01$; Fig. 3). Relative dry matter

Table 2

RGR (RGR for the period from 63 DAT to 180 DAT), and plant height, number of capitula and total resin (R) production (g per plant) at the first (63 DAT) and second (180 DAT) harvests for *G. chiloensis* plants grown under three radiation treatments: full-sun, 50%-sun and 25%-sun in Argentina^a

Treatment	RGR (g g ⁻¹ per day)	Height (cm)		Number of capitula		Total resin (g per plant)	
		63 DAT	180 DAT	63 DAT	180 DAT	63 DAT	180 DAT
Full-sun	0.006 a	21.0 a	47.8 b	0	20.0 a	4.9 a	25.3 a
50%-sun	0.005 b	22.3 a	66.3 a	0	13.6 b	3.9 b	11.6 b
25%-sun	0.005 b	24.5 a	73.1 a	0	7.2 c	2.4 c	6.2 c

^a Means followed by different letters within a column are significantly different at $P < 0.05$ (Tukey's; *T*-method).

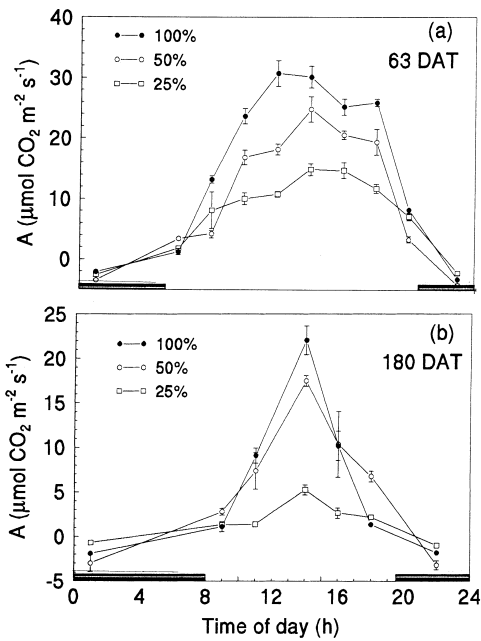


Fig. 1. Daily patterns of instantaneous net CO₂ assimilation for *G. chiloensis* plants growing in three radiation treatments: full-sun (100%), 50%-sun (50%) and 25%-sun (25%) in Argentina: (a) 5 January 1997, 63 DAT; (b) 15 May 1997, 180 DAT. Error bars represent ±1 S.E. of the mean; *n* = 5. The dark bar on the abscissa stands for the night period.

partitioning to stems and green leaves was significantly higher in plants under full-sun and 50%-sun treatment (28 and 34%, respectively) than in the 25%-sun treatment (26 and 27%, respectively; *P* < 0.05;

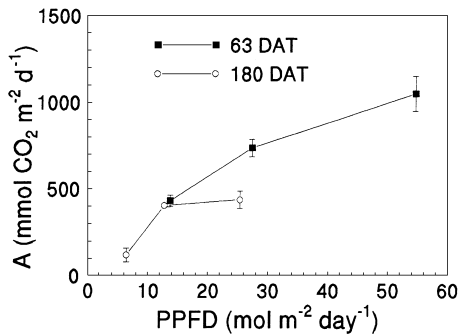


Fig. 2. Net CO₂ assimilation integrated through 24 h as a function of integrated PPFD available in a horizontal plane for *G. chiloensis* plants at the first (63 DAT) and second (180 DAT) harvest growing in three radiation treatments: full-sun (100%), 50%-sun (50%) and 25%-sun (25%) in Argentina. Error bars represent ±1 S.E. of the mean.

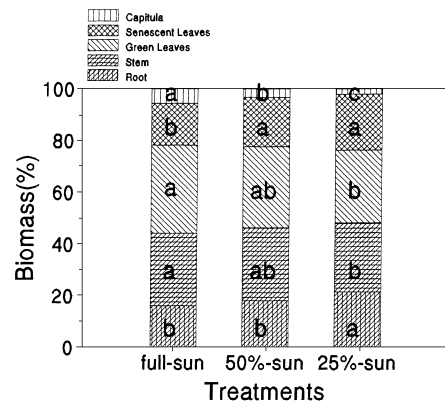


Fig. 3. Relative dry matter partitioning between organs for *G. chiloensis* at 180 DAT grown in Argentina under three radiation treatments: full-sun, 50%-sun and 25%-sun. Within each organ bars with the same letter are not significantly different at *P* < 0.05 (Tukey's; *T*-method).

Fig. 3). The proportion of senescent leaves was lowest for plants in the full-sun treatment (16%; *P* < 0.01; Fig. 3). Partitioning to capitula dry matter increased significantly with radiation availability (2% for 25%-sun, 3% for 50%-sun and 6% for full-sun; *P* < 0.01; Fig. 3).

The proportion of energy partitioned to resin increased significantly with radiation availability (17% in 25%-sun, 19% in 50%-sun and 29% in full-sun treatments; *P* < 0.01; Fig. 4). The energy

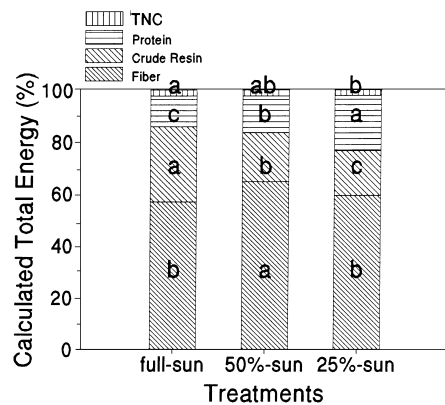


Fig. 4. Total energy partitioning between fiber, resin, protein and TNC for *G. chiloensis* at 180 DAT grown in Argentina under three radiation treatments: full-sun, 50%-sun and 25%-sun. Within each fraction bars with the same letter are not significantly different at *P* < 0.05 (Tukey's; *T*-method).

in fiber was highest in the 50%-sun (65%) and lowest in the full-sun and 25%-sun treatments (57 and 60%, respectively; $P < 0.01$; Fig. 4). The energy stored in TNC increased and protein decreased with increased light availability ($P < 0.01$; 2 and 21% in 25%-sun to 2 and 12% in the full-sun treatment for TNC and protein, respectively; Fig. 4).

The carbon–nitrogen ratio (TNC:N) was increased by the decrease in radiation. It was 1:0.8 in full-sun plants, 1:0.9 in 50%-sun plants and 1:1.6 in 25%-sun plants.

4. Discussion

A reduction in leaf biomass and number of capitula per plant, and an increase in leaf senescence and plant height were found under diminished light availability, in accordance with observations in other plant species (e.g., Evans and Hughes, 1961; Rice and Bazzaz, 1989).

Radiation availability was positively correlated with above ground biomass accumulation, carbon-based secondary metabolites (resin), and RGR (Tables 1 and 2). This positive correlation between growth and carbon-based secondary metabolism, was stimulated by the increase in CO₂ assimilation rate found in plants under the full-sun treatment (Fig. 1). Since it is considered that carbon-based secondary metabolites and growth compete for assimilated carbon (Herms and Mattson, 1992), an increase in carbon assimilation rate creates the possibility of concomitant increases of growth and secondary metabolism despite a potential competition for a common energetic resource base (van Noordwijk and de Jong, 1986). The proportion of energy partitioned to resin and TNC was highest in the full-sun treatment (Fig. 4). This build up of carbohydrates is believed to provide additional substrate for the production of non-nitrogenous secondary metabolites (Gershenson, 1994), or be available for re-growth.

At low radiation levels, above ground biomass accumulation, RGR and CO₂ assimilation rate were highly constrained (Figs. 1 and 2 and Tables 1 and 2). When plant growth is limited by the availability of fixed carbon, carbohydrate reserves are expected to decline, leading in turn, to a reduction in terpenoids synthesis (Gershenson, 1994). Essential primary

metabolic processes and base line maintenance may receive priority use of limited carbon (Herms and Mattson, 1992), and carbon conservation is generally enhanced (Koch, 1996). In our experiment, the energy partitioned to the synthesis of resin was lower in the shaded treatments (50%-sun and 25%-sun; Fig. 4) than under full-sun conditions. It is expected that under low light conditions increased allocation to chlorophyll protein complexes, which are involved in the use of low PPFD, will have an advantage (Hikosaka and Terashima, 1996). Normally, more than half of the leaf nitrogen is allocated to photosynthetic proteins (Makino and Osmond, 1991; Evans, 1989). The energy partitioned to the synthesis of proteins was higher in the shaded treatments (50%-sun and 25%-sun; Fig. 4) than under full-sun conditions. The decrease in TNC and the increase in N and protein in shaded plants resulted in a reduction in the TNC:N ratio (Fig. 4). This kind of response agrees with the C:N theory (Bryant et al., 1983).

Available PPFD clearly affected instantaneous and integrated CO₂ assimilation rate in *G. chiloensis*, but the degree of this effect was altered at different times in the growing season. The lowest CO₂ assimilation rate was found during May (autumn), when reduced PPFD availability clearly limited integrated CO₂ assimilation rate (Fig. 2). During May, for plants grown under conditions of full-sun (PPFD = 25 mol m⁻² per day), limitations to CO₂ assimilation rate, other than light availability, seemed to have occurred. This conclusion is based on the changing slope of the curve (Fig. 2 and Table 2).

G. chiloensis should achieve higher biomass productivity and, consequently, higher total resin per plant in high radiation environments, and with high number of hours of bright sunshine. The response found in *G. chiloensis* to radiation would set limits to the productivity and agro-ecological distribution of this species grown under cultivation. For the commercial cultivation of *Grindelia* the elucidation of the mechanisms that result in reductions in resin production at low ambient irradiance will be of importance.

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