

Growth, Dry Matter Partitioning and Photosynthesis in North American Ginseng Seedlings

John T. A. Proctor^{1*}, John W. Palmer², and John M. Follett³

¹Department of Plant Agriculture, University of Guelph, Guelph, ON N1G 2W1, Canada

²Nelson Research Centre, Plant and Food Research Ltd., Motueka 7198, New Zealand

³Ruakura Research Centre, AgResearch Ltd., Hamilton 3240, New Zealand

North American ginseng seedlings (*Panax quinquefolius* L.) were grown in pots in heated greenhouses, in a cool greenhouse, or in the field, in 11 experiments at various times over 16 years. Crop establishment, dry matter partitioning, photosynthesis, radiation use efficiency and carbon budget were measured and/or calculated in some years. Once the seedling canopy, of about 20 cm² per seedling, and a leaf area index of 0.37, was established, about 40 days after germination, full canopy display lasted about 87 days. Only 16.6% of the incoming solar radiation was intercepted by the crop, the remainder falling on the mulched soil surface. Total and root dry matter accumulations in the cool greenhouse and in the field were about double that in the heated greenhouses. Partitioning of dry matter to roots (economic yield or harvest index) in the cool greenhouse and in the field was 73% whereas it was 62.5% in the heated greenhouses. The relationship between root dry matter and radiation interception during the full canopy period was linear with growth efficiencies of 2.92 mg MJ⁻¹ at 4.8% of incoming radiation and 0.30 mg MJ⁻¹ at 68% of incoming radiation. A photosynthetic rate of 0.39 g m⁻² h⁻¹ was attained at light saturation of about 150 μmol m⁻² s⁻¹ (7.5% of full sunlight); dark respiration was 0.03 g m⁻² h⁻¹, about 8.5% of maximum assimilation rate. Estimates of dry matter accumulation by growth analysis and by CO₂ uptake were similar, 6.21 vs. 7.62 mg CO₂, despite several assumptions in CO₂ uptake calculations.

Keywords: Light interception, Medicinal herbs, *Panax quinquefolius*, Photosynthesis, Radiation use efficiency

INTRODUCTION

Medicinal and aromatic plants are important to the healthcare programs of people around the world, particularly in developing countries [1]. About 2,500 species of medicinal and aromatic plants worldwide are involved in international trade. The two major species of ginseng, the Asian, *Panax ginseng* C. A. Meyer, and the North American, *Panax quinquefolius* L. [2] are very valuable commercially [1].

Ginseng is native to the understory of deciduous and mixed forests in eastern Asia and eastern North

America. In commercial cultivation of ginseng an attempt is made to emulate the environmental conditions of the forest. Proctor and Bailey [3] have pointed out that although ginseng has been cultivated for a long time, only recently has the necessary detailed research on the growing environment of North American ginseng been initiated. This report is part of our continuing research with emphasis on the shade requirements, photosynthesis and dry matter partitioning particularly in the first year (seedling/crop establishment) growth phase [4-6].

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*Corresponding author

E-mail: jtprocto@uoguelph.ca

Tel: +1-519-824-4120, Fax: +1-519-767-0755

The necessary artificial shade for ginseng cultivation in North America permits about 30% of the incident light to reach the plants [3,7]. In the Asian culture of ginseng the shade permits only diffuse light to reach the plants and measured values range as low as 1 to 2% of incident light [8]. The effect of low light intensities on the growth and development of North American ginseng seedlings is unknown. Within the ginseng literature there is confusion and debate about the light response curve for photosynthesis of mature ginseng plants (for a review see Proctor and Bailey [3]). Also, we have found no information on photosynthesis and dry matter distribution of one-year-old (seedling) plants although Bailey and Stathers [9] addressed growth of seedlings.

Yield data for ginseng are scarce. Some root (economic) yield from research plots, e.g. Proctor *et al.* [10] and Fiebig *et al.* [11], and from industry sources, e.g. British Columbia Ministry of Agriculture, Fisheries and Food [12], exist. Also, little is known about the environmental factors that influence yield. Stathers and Bailey [13] characterized energy receipt and partitioning in a ginseng shade canopy, and the associated root environment, but did not couple them with root yield. Subsequently, Proctor *et al.* [14] reported the dry matter yield of components of 2, 3, 4 and 5-year-old plants, and root respiration but did not relate them to light interception. Fournier *et al.* [5] showed that in mid-season, shoot and root growth, and leaflet area of 2-year-old forest-grown ginseng were correlated with under-story light amount and light quality, accounting for up to 88% of the variation. Most recently Proctor [6] showed that 90% of the variation in seedling dry root weight was accounted for by leaf area once the canopy was established. The quantitative relationship between accumulated plant and crop dry matter and intercepted light has been developed [15] and reviewed [16]. As 90 to 95% of a plant's dry weight is derived from photosynthesis [17] understanding the partitioning of assimilates within a plant is vital to the improvement of crop yield. The ginseng root is a very strong sink for assimilates, accumulating about 50% of a reproductive plant's total dry weight [14]. Inflorescence dry weight is about 15% and its removal increases root yield by 25% [10].

The objectives of this study were to measure growth, dry matter partitioning, photosynthesis and light interception of North American ginseng seedlings in various regimes and years, and to assess crop performance by determining radiation use efficiency.

MATERIALS AND METHODS

All experiments were carried out at Guelph (43° 33' N, 80° 13' W), or nearby commercial ginseng farms, except for one, Expt.4, Table 1, which was carried out in 1989 (March to August) at the Institute of Horticultural Research, East Malling, England (51° 18' N, 0° 26' E).

Seed propagation and planting

Seedlings were grown from seeds which had been harvested in September of one year and stratified until October of the next year [18]. They were then seeded into the field [19], or were mixed with moistened sand (3:1, v/v, sand/seed) in plastic containers and put in cold storage at $4 \pm 2^\circ\text{C}$ and $50 \pm 5\%$ relative humidity, and held until the start of experiments in February or March of the following year. The same seed lot was used for Expts 3 and 4, Table 1.

For pot experiments ten seeds were planted equidistant within each wide (21 cm diameter) and deep (21 cm) pot. Average seedling population was 289 seedlings m^{-2} . Growing media for the seedlings are given in Table 1. Light transmission of the greenhouses was measured with a quantum, or line quantum, sensor (LI-COR, Lincoln, NE, USA). For greenhouse experiments 30% of the incident light at the top of the seedlings was established by suspending different thicknesses of knitted black polypropylene shade cloth above the pots. Likewise, for the two shade experiments (Table 1, Expts 3 and 4) shade thickness was varied to supply the required amount of incident light. For each experiment there was a minimum of 4 pots per treatment in a completely randomized design.

For the field experiments (Table 1, Expts 5 to 10) seedlings were established at a seeding rate of 112 kg ha^{-1} (about 215 seeds m^{-2} or 46.5 cm^2 space per seedling) and grown following standard cultural methods for North American ginseng [20]. Briefly, seeds were planted on raised soil beds and covered with 5 to 10 cm of straw mulch. Woven black polypropylene shade was placed 2 m above the beds to reduce solar radiation to an optimal 20 to 30% of full sunlight. Standard commercial practices for pest control were followed [19].

Plant sampling

In the pot experiments seedling emergence was recorded daily and at about ten day intervals seedlings were harvested. Stem length was measured and then leaf area of each seedling was determined using a LI-3100 leaf area meter (LI-COR). Each seedling was then

Table 1. Experimental and published data for annual above-ground and root dry matter production and growth rate of ginseng seedlings grown in different years in a range of environments. All experiments were carried out in Canada except for Expt. 3 which was carried out in England

Expt. No. year and details	Growing medium	Duration of growth		Final dry wt (mg)		Root:shoot ratio	Growth rate (mg day ⁻¹)	
		Above ground (d)	Above ground ¹⁾	Root	Total		Above ground	Root
Experimental greenhouse								
1. 1988, heated, in pots, top removal	Vermiculite	104	39.0	62.5	101.5	1.60	0.37	0.84
2. 1988, heated, in pots Light: 22%	Vermiculite	116	--	76.1	--	--	--	0.88
3. 1989, cool, in pots, shade Light: 7%	Peat moss/sand	136	79.0	193.0	272.0	2.45	0.58	2.25
15%		136	95.0	234.0	329.0	2.46	0.72	2.72
30%		136	115.0	339.0	453.0	2.95	0.84	3.94
100%		136	130.0	318.0	448.0	2.45	0.95	3.70
Mean % of total		136	104.7	271.0	375.5	2.58	0.77	3.15
			27.9	72.1	100			
4. 1989, heated, in pots, shade Light: 5%	Promix-BX	132	73.0	99.0	172.0	1.35	0.55	0.97
10%		132	83.0	92.0	175.0	1.11	0.63	0.90
15%		132	76.0	158.0	234.0	2.07	0.58	1.55
22%		132	101.0	181.0	282.0	1.80	0.76	1.78
Mean % of total		132	83.3	132.5	215.7	1.59	0.63	1.30
			38.6	61.4	100			
Field								
5. 1986 A	Fox sandy loam soil	138	141	384	525	2.72	1.02	3.55
B	Fox sandy loam soil	138	88	256	344	2.91	0.64	2.37
6. 1987	Fox sandyloam soil	117	80	222	302	2.77	0.68	2.55
7. 1988	Fox sandy loam soil	149	98	284	382	2.90	0.66	2.39
8. 1989	Fox sandy loam soil	112	102	243	345	2.38	0.91	2.96
9. 2003	Fox sandy loam soil	108	129	317	446	2.45	1.19	4.06
10. 2004	Fox sandy loam soil	125	107	417	524	3.89	0.86	4.39
Mean % of total		126.7	106.4	303.3	409.7	2.85	0.85	3.18
			26.0	74.0	100			
Published								
11. Lee <i>et al.</i> , 1986 [22]	Greenhouse soil beds, 18°C	108	74	143	217	1.90	0.68	1.32
	% of total		34.1	65.9	100			
	Vermiculite in pots in a growth chamber	81	53	87	140	1.60	0.65	1.07
	% of total		37.9	62.1	100			

¹⁾The start of root weight was estimated to have occurred 30 days after 50% of the seedling tops had emerged through the straw mulch.

separated into leaves with petioles, stem and root, and dried to constant weight at 80°C.

In the field experiments (Table 1, Expts 5 to 10) seedlings growing under typical Ontario conditions [19], were dug at about ten day intervals. At each sampling date four replications each of ten plants were selected randomly and dug. Sample size was considered representative [21]. The dug plants were placed in plastic bags and taken to a constant temperature room held at 20±1°C. Plant measurements were made as for seedlings harvested in the pot experiments as outlined above.

Light interception and absorption

Daily incoming radiation was measured and recorded with a LI-190SA quantum sensor attached to a LI-1000 data logger (LI-COR) located about 2 km from the experimental plantings. The quantum sensor measures photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$). Light interception above and below the crop canopy (absorption) was measured with a 1m long line quantum sensor (LI-191SA) attached to a LI-1000 data logger. Measurements were made at intervals during the growing seasons prior to solar noon under clear sky conditions. Measurements were made by taking readings

for 5 minutes above, and then below the crop canopy and then repeating this procedure 3 times. The sensor was inserted randomly below the canopy which had grown from broadcast seed. Seasonal light absorption was calculated from incoming PAR and fractional interception over approximately 10-day intervals (plant sampling dates) throughout the growing seasons.

Radiation use efficiency (mg MJ^{-1}) was calculated as the ratio of total dry matter production (g m^{-2}) including leaf, stem and root weight, or just root weight, to the cumulative absorbed PAR (MJ m^{-2}) within the same period [17]. Harvest index (HI) was calculated as the ratio of root dry matter harvested (g m^{-2}) to total matter (g m^{-2}) and expressed as a percentage.

Photosynthesis

A photosynthesis (P_n) light response curve of mature central leaflets on ginseng seedlings was measured on two dates, June 8 and July 12, 1989. A preliminary experiment showed no differences in P_n rates between the three leaflets of the seedling. A leaf cup, which allowed insertion of 2 cm^2 of a leaflet, connected to an infrared gas analyzer (Type 225 Mark 3; Analytical Development Company, Hoddesdon, UK) was used. The carbon dioxide concentration was 361 ppm and the flow rate 90 mL min^{-1} on June 8 and 53 mL min^{-1} on July 12. To simultaneously measure stomatal conductance dry air was introduced to the cup and the humidity of the outlet air measured with a Vaisala sensor (Vaisala Oyj., Helsinki, Finland). Leaf temperature was sensed with a 38 gauge thermocouple appressed to the adaxial surface of the leaflet and recorded at each measurement. A range of light intensities (0 to $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$) for developing a response curve were obtained using a 12V 75W tungsten halogen dichroic lamp (Thorn type M60) and different density fine wire screens. Light intensity at the leaflet was measured with a LI-COR 180S quantum sensor. The statistical analyses of the data were carried out in three steps. Firstly, there were no differences between the two measuring dates. Secondly, the pooled data were fitted to a negative exponential asymptotic curve of the form $Y=a(1-e^{-bx})$ detailed in the Statistical Analysis System (SAS Institute, Cary, NC, USA) users guide. Thirdly, in order to overcome the limitation imposed by the fitted curve going through the origin (Fig. 3) a linear regression was performed on data close to the origin and the light compensation point, dark respiration and initial slope calculated. Where appropriate data were analyzed using the Statistical Analysis System package.

RESULTS AND DISCUSSION

Canopy establishment

Leaf area increased exponentially with time (Fig. 1A). The rapid increase of leaf area from emergence of the hooked epicotyl (stage 009) [4] around day 150 (May 29) to full canopy display (stage 109) of about 20 cm^2 leaf area occurred around day 190 (July 9), a rate of 0.5 cm^2 per day. This canopy establishment period of about 40 days varies from year to year and is influenced by prevailing soil and air temperatures [22]. Growers of the crop estimate, from visual observations, that this canopy establishment takes about one month, the month of June.

Leaf and stem dry weight increased quickly to about 0.12 g by day 200 in agreement with leaf area (see above), and then increased very slowly for the remainder of the growing season (Fig. 1B). Root dry weight started to increase by day 205, at about the time of full canopy development, and thereafter increased linearly to over 0.30 g by day 260.

In Expts 5 to 10 (Table 1) the duration of the above-ground canopy was about 127 days so full canopy display was about 87 (127-40) days. Given the variability in the canopy establishment phase, 30 to 40 days, a general

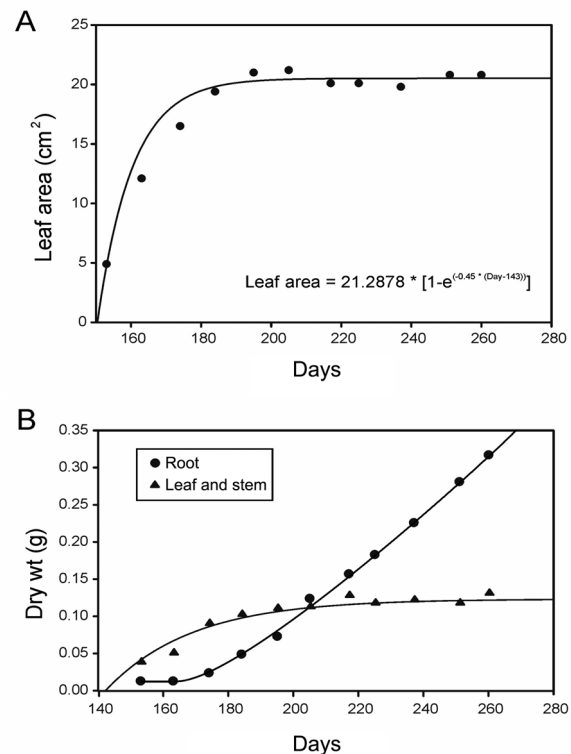


Fig. 1. Leaf area (A) and root and leaf plus stem dry weight (B) per seedling throughout the 2003 growing season in a field environment.

Table 2. Plant age, plant density, leaf area per plant, leaf area index, and light absorption for field-grown ginseng plantings in their first (seedling), second, third, and fourth years. Measurements were taken in the middle of the growing season. As the data for the two years, 2003 and 2004 were not significantly different they were combined and are presented below

Planting age (yr)	Plant density (plants/m ²)	Leaf area per plant (cm ²)	Leaf area index	Light absorption (%)
1	206	18	0.37	16.6
2	133	160	2.54	82.4
3	93	481	4.47	91.7
4	62	788	4.88	93.1

canopy duration period could be taken as 100 days – see below.

If the leaf area of a pot grown seedling is taken as 20 cm² and there were 289 seedlings m⁻² (see Materials and Methods above) then the leaf area index (LAI) was 0.58. This is comparable to field grown seedlings where the LAI was 0.37 (Table 2).

In the calculation of unit leaf rate (ULR), also known as the net assimilation rate, the assumption is made that leaf area and weight are linearly related. For the 2003 field data regression analysis of leaf weight and leaf area gave an R² of 0.85. Such a good relationship allows accurate determination of ULR and an estimate of the carbon-assimilatory capacity of the leaves.

Dry matter accumulation

Total plant dry weight accumulation over the growing season varied considerably from a low of 101.5 mg in Expt. 2 to a mean of 409.7 mg in the field, Expts 5 to 10 (Table 1). In the heated greenhouse experiments (Expts 1,4,11) mean total dry weight was 168.5 mg whereas in the field experiments (Expts 5 to 10) and in the cool greenhouse (Expt. 3) it was over double that at 409.7 and 375.5 mg, respectively. Mean root weights were similarly affected with 100.2 mg in heated greenhouses (Expts 1,2,4,11) and 303.3 mg in field experiments (Expts 5 to 10) and 271 mg in the cool greenhouse (Expt. 3).

In the two shade Exps, 3 and 4 (Table 1), the same seed lot was used but the seedlings were grown in Canada (Expt. 3) and England (Expt. 4). At 15% light (85% shade) in both experiments root yield was 48.1% higher in England; similar differences were found at the other shade levels. The slopes of the regression lines of root dry weight vs. % light in Expts 3 and 4 were similar with 5.29 mg/1% increase in light over the 5 to 22% light levels in Expt. 3 and 4.82 mg/1% light in Expt. 4. The higher root yield in England is likely a reflection of the

more favorable growing environment of a cool rather than a warm greenhouse; the cool greenhouse more adequately mimics the native habitat of ginseng which is in the understory of the deciduous hardwood forest [3,5].

The root to shoot ratio of greenhouse-grown seedlings was lower (Table 1; range, 1.35 [Expt. 4] to 2.07 [Expt. 4]) than for field-grown (Table 1; range, 2.38 to 3.89; Expts 5 to 10). The lower greenhouse-grown root to shoot ratios are in agreement with previously reported ratios for ginseng seedlings grown in growth chambers (0.20 to 1.60) and in greenhouses (1.40 to 1.80) [22]. The root to shoot ratio for seedlings grown in a cool (unheated) greenhouse (Table 1; range, 2.45 to 2.95; Expt. 3) were similar to those for field-grown seedlings (Table 1; range, 2.38 to 3.89; Expts 5 to 10). This is likely a reflection of the greenhouse growing temperature which was allowed to vary with the outside temperature. Partitioning of dry matter to the roots, equivalent to harvest index and partitioning efficiency, in the cool greenhouse (Table 1, Expt. 3) and in the field (Expts 5 to 10) was 72.1 and 74 % respectively; in the heated greenhouses it was 61.6% (Expt. 1), 61.4% (Expt. 4) and 65.9 and 61.2% (Expt. 11). The partitioning within and between the two environments was remarkably consistent and shows the more favorable field environment having about a 10% better allocation of dry matter to the roots. In other root crops, e.g. sweet potato (*Ipomoea batatas* L.), the ratio between storage root dry matter and the total dry matter is used to indicate dry matter partitioning efficiency to storage roots [23]. Further, in sweet potato partitioning efficiency can range from 11 to 85% depending on cultivar; in ginseng seedling used here it was high, ranging from 61 to 74%. This high partitioning efficiency is encouraging in relation to potential yield as cultivated North American ginseng was taken from woodland habitats and is genetically diverse [24].

The daily growth rate for the above-ground portion of the seedling varied from a low of 0.37 mg per day (Expt. 1) to 0.85 mg per day in the field experiments (Expts 5 to 10) (Table 1). Daily root growth also varied similarly with the greatest growth being 3.15 mg per day in the cool (unheated) greenhouse (Expt. 3) and 3.18 mg per day in the field (Expts 5 to 10).

Light interception and absorption

In the field experiments the seedlings had a LAI of 0.37 and intercepted only 16.6% of the incoming light allowing 83.4% of the incoming solar radiation to pass through it (Table 2). The radiation not intercepted by the canopy fell on the mulched soil surface where it was

likely dissipated as convective heat and used to evaporate mulch and soil water and warm the soil. Stathers and Bailey [13] have addressed the partitioning of radiation and its use in a two-year-old ginseng planting but not in a seedling planting. As our seedling planting had a LAI of 0.37 (Table 2) and their two-year-old planting a LAI of 1.6 it is likely that in the seedling planting decoupling of the soil and moisture regimes from the atmospheric environment, as found by Stathers and Bailey [13], would not have been as strong. Therefore, there would have been more evapotranspiration from the seedling planting, occurrence of disease infections would have been reduced, and irrigation was necessary. In the second, third and fourth years the canopies were fully developed, light interception was 82 to 93% so only about 12% of the light was not intercepted by the canopies (Table 2).

Radiation use efficiency

From emergence of the seedlings the relationship between dry matter accumulation and cumulative radiation received at the canopy was linear. For example, in Expt. 3 (Table 1 and Fig. 2) regression analysis accounted for about 90% (range, 88 to 95%) of the variance. Ayaz *et al.* [25], working with four grain legumes (chickpea, lentil, lupin and pea), showed that seed yield was correlated with total intercepted PAR with regression accounting for 78 to 98% of the variance. The slope of the line relating ginseng seedling root weight increase to intercepted radiation changed with shade treatment (Fig. 2). These slopes establish the growth efficiency for the conversion of radiant energy to dry matter. The growth efficiencies ranged from a high of 2.92 mg MJ⁻¹ at 7% light on the crop

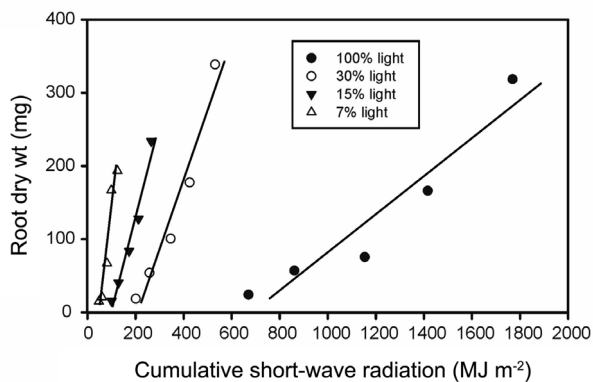


Fig. 2. The relationship between root dry weight at five harvest dates and cumulative short-wave solar radiation incident on the crop under four shade treatments. Regression analysis for the four shade treatments gave R² as follows: Δ, 7% light, R²=0.89; ▽, 15% light, R²=0.95; ○, 30% light, R²=0.92; and ●, 100% light (no shade), R²=0.88.

(4.8% of outside light) to 0.30 mg MJ⁻¹ in greenhouse light (68% of outside light).

These growth efficiency values are much lower than those of other field-grown root crops, e.g. potato, 1.45 to 1.7 g MJ⁻¹ [16], and sugar beet, 1.44 to 1.52 g MJ⁻¹ [26]. However, our growth efficiencies were calculated using root yield in the seedling year whereas the crop is harvested for economic yield in the third year. This analysis in terms of interception of solar radiation, the efficiency of conversion of intercepted radiation into dry matter, and the distribution of the latter to competing sinks, particularly the root, is a first attempt at such an integration with a plant of this type.

Photosynthesis

The light response curves for North American ginseng seedling leaves, previously unreported, are shown in Fig. 3. Light saturation was reached at about 150 μmol m⁻² s⁻¹ which is similar to that reported for leaves of 3-year-old plants [3].

If full sunlight is estimated at 2,000 μmol m⁻² s⁻¹ then ginseng seedlings are light saturated at about 7.5% of full sun. The light compensation point was about 5 μmol m⁻² s⁻¹ (Fig. 3B) more characteristic of C₄ than C₃ plants; it indicates that these seedlings are very photosynthetic efficient even at relatively low irradiances. The maximum assimilation rate was 0.39 g CO₂ m⁻² h⁻¹ (Fig. 3A) which is higher than that reported for leaves of 3-year-old plants but comparable to data for Asian ginseng (*Panax ginseng* C. A. Meyer) [8], and similar to that for a representative sample of shade plants [27]. Dark respiration was 0.03 g CO₂ m⁻² h⁻¹ (Fig. 3B) which is about 8.5% of maximum assimilation rate.

Carbon budget for field-grown plants

Ginseng, being a perennial plant, requires the storage of carbon and other nutrients to support initial growth in the spring. In ginseng seedlings initial support comes from the seed reserves [4]; in older plants roots respire and root dry weight decreases by 30 to 50% as shoots emerge and become the primary source of carbon [14]. Once the canopy was established root dry weight gain increased linearly (Fig. 1) and accounted for about 70% total dry weight at final harvest; conversely, leaf dry weight increased minimally and accounted for about 30% dry weight at final harvest (Fig. 1 and Table 1). These accumulations of dry matter by growth analysis can be used to provide comparisons of carbon assimilation derived from calculations of CO₂ uptake shown in the section above entitled "Photosynthesis".

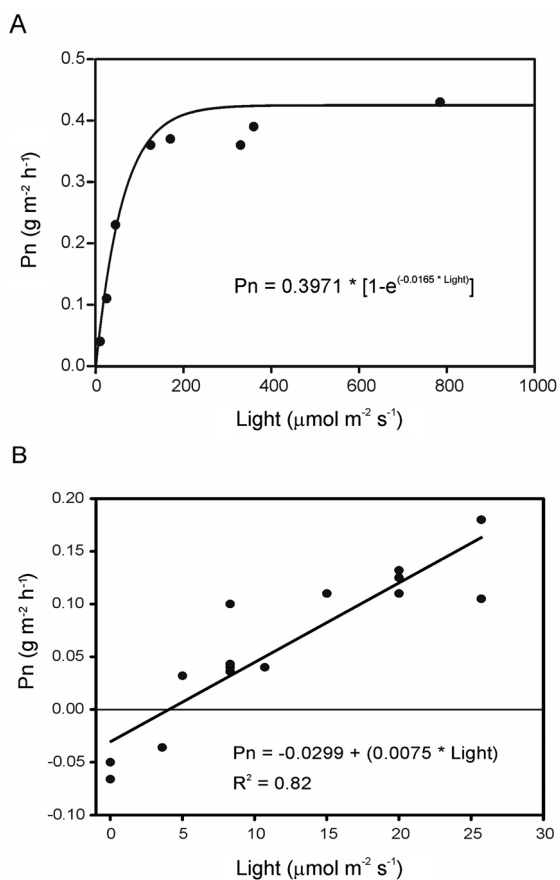


Fig. 3. The effect of light on the rate of photosynthesis (Pn) of ginseng seedlings. (A) shows a statistically fitted curve with a steep initial response to light followed by a maximum Pn rate. (B) shows a fitted linear portion of the response curve below 2.0 g m⁻¹ h⁻¹ and 30 μmol m⁻² s⁻¹ showing the light compensation point and the estimated dark respiration value.

Mean daily dry matter increase derived from the 6 field experiments (Expts 5 to 10, Table 1) gave a total value of 4.03 mg or 6.21 mg CO₂ (Table 3).

To compare with this dry matter increase, net hourly uptake of CO₂ on four days in July and August 2003 was calculated using the equation in Fig. 3A and measured hourly light interception. The mean hourly photosynthesis was 9.36 mg CO₂ which when corrected for dark respiration of 0.80 (8.5% of total) gave 8.56 mg CO₂ (Table 3). If it is assumed that soil respiration was a further 10% of total photosynthesis (as suggested by Amthor [28]) then the CO₂ assimilation is reduced by 0.94 to 7.60 mg CO₂. Data for soil respiration of ginseng do not exist.

Therefore, the two methods of calculating dry matter increase are reasonably close, 6.21 vs. 7.62 mg CO₂ and encouraging. Assuming that the growth analysis of 6.21 mg CO₂ is 100% then the overestimate by CO₂ uptake is about 22%. The CO₂ uptake approach is subject to a lot of variation in measurements and several assump-

Table 3. Comparison of daily growth analysis and CO₂ assimilation data for field-grown ginseng seedlings

Variable	Dry weight increase (mg)	mg CO ₂ ³⁾
Growth analysis ¹⁾	4.03	6.21
CO ₂ assimilation ²⁾		
Mean total photosynthesis		9.36
Dark respiration correction (8.5%)		-0.80
Dark respiration correction (8.5%)		8.56
Less soil respiration (10%)		-0.94
		7.62

Mean leaf area per seedling 20 cm².

¹⁾Data from Table 1, Expts 5 to 10, mean values, 0.85+3.18=4.03.

²⁾Mean for 4 days in July and August 2003.

³⁾Dry weight converted to g CO₂ using a conversion factor of 1.54 [29].

tions, and needs refinements to reduce the overestimate.

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