

ANNUAL GROSS PRIMARY PRODUCTION AND ABSORPTION OF SOLAR ENERGY BY ARTEMISIA SP. IN ARID AND SEMIARID SHRUBLANDS

MOUSAEI SANJEREHEI, M.

*Department of Plant Protection, Yazd Branch, Islamic Azad University,
Safayieh, Yazd, Iran
(phone: 00 983518211391)*

**Corresponding author
e-mail: mmusaei@yahoo.com*

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Abstract. Gross primary production (GPP), transpiration and conversion efficiency of solar energy by *Artemisia sieberi* and *Artemisia aucheri* in Nodushan shrublands of Yazd, Iran, were determined. GPP was determined through estimates of net primary production (NPP) and respiration (R) of leaf, new branch, stem, coarse root and fine root. Total biomass (g C m^{-2}) of *A.sieberi* and *A.aucheri* was 81.7 and 224.87 respectively. The ratio of below-to-aboveground biomass was 0.4 and 0.56 respectively, for *A.sieberi* and *A.aucheri*. Total NPP, R and GPP (g C m^{-2}) were 32.11, 53.1 and 85.21 for *A.sieberi* and 62.75, 91.56 and 154.31 for *A.aucheri*. The carbon use efficiency (NPP/GPP), R/GPP and Belowground NPP/total NPP were 0.38, 0.62 and 0.29 for *A.sieberi* and 0.41, 0.59 and 0.37 for *A.aucheri* respectively. Based on the estimates of solar energy available in the study sites, the amount of incoming solar energy absorbed in photosynthesis and transpiration was 0.05 % and 0.08 % by *A.sieberi*, and 0.08 % and 0.17 % by *A.aucheri*. *Artemisia* shrublands play an important role as carbon sinks and energy stocks in arid and semiarid ecosystems of the central parts of Iran.

Keywords: *Artemisia sieberi*, *Artemisia aucheri*, Gross primary production, Solar energy, Transpiration

Introduction

Atmospheric CO₂ concentration of twice the preindustrial level will lead to an increase in global mean temperature of 2.5 °C, which in turn may result in losses in the drylands, wetlands, species and ecosystems as well as major changes in agricultural, forestry and fishery sectors and an increase in water demand, air pollution and frequency of natural disasters (IPCC, 1990). Since the main source of absorbing CO₂ is through photosynthesis by vegetation, the study of primary production seems to be of high importance. Estimates of primary production are useful for monitoring ecosystem goods and services (Meyerson et al., 2005), ecosystem function (Schlapfer and Schmid, 1999) and structure, providing resources for herbivores, evaluating the regulation of the global climate through the carbon cycles (Roy and Saugier, 2001), determining variation in wood production as well as studying energy flow in ecosystems (Roxburgh et al., 2004) and ecosystem carbon sequestration. The amount of energy fixed by plants in photosynthesis is referred to as gross primary production (GPP). Annual GPP is defined as the total of all carbon fixed by plants in ecosystems (Ryan, 1991). A portion of the C fixed, is lost through construction (growth) and maintenance respirations by plants. Construction respiration is the amount of C consumed in the processes such as ATP production, transport processes and nutrient uptake (Chiariello et al., 1989) which lead to a net increase in plant dry matter. Construction respiration can be estimated based on the heat of combustion, organic nitrogen and ash content (Williams et al.,

1987), carbon and ash content (Vertregt and Penning de Vries, 1987) or based on the assumption that it consumes carbon equal to 25% of that incorporated into new tissue (Ryan, 1991). Maintenance respiration provides the energy for the plant processes such as maintenance of ion gradients across membranes, protein repair and replacement and translocation-related processes (Penning de Vries, 1975) that do not result in a net gain in biomass, but keep existing phytomass in a healthy state (Amthor, 1989). Maintenance respiration can be calculated from tissue nitrogen and mean annual temperature (Ryan, 1991). The amount of C allocated in plants in a certain period of time after losses due to respiration is known as net primary production (NPP). Another important source of solar energy use by plants is transpiration. Estimates of solar energy used in transpiration can be useful for the study of reduction in air temperature by vegetation through the conversion of solar energy to latent heat (Kurn et al., 1994). Based on increasing population growth and economic prosperity and as a result, a greater demand on production of food and fiber, improving solar energy conversion efficiency will be of critical importance. This requires a complete understanding of the amount of solar energy used by plants in different processes. The objective of this research was to determine (1) gross primary production and (2) the amount of energy absorbed in photosynthesis and transpiration by *Artemisia sieberi* and *Artemisia aucheri* in Nodushan rangelands of Yazd. *A.sieberi* and *A.aucheri* are the most dominant species in Nodushan rangelands of Yazd. These species are two of the most distributed perennial shrubs in central parts of Iran.

Materials and Methods

Site description

NPP, respiration, GPP, transpiration and the amount of solar energy captured by *Artemisia sieberi* and *Artemisia aucheri* species were determined in Nodushan rangelands of Yazd, Iran. Nodushan rangelands are located in the northwest of Yazd province in central parts of Iran (31°46'N, 52°24'E to 32°15'N, 53°47'E) at elevations between 1530 m and 3260 m. Two sites were selected in Nodushan rangelands for sampling. (1) Sadrabad area which is located at an elevation of 2171 m and is dominated by *A.sieberi* (Figure 1). The climate is characterized as arid. The mean annual precipitation and temperature are 89 mm and 13.5 °C respectively. (2) Khood area which is located at an elevation of 2525 m and is dominated by *A.aucheri* (Figure 1). The climate is semiarid. The mean annual precipitation and temperature are 123 mm and 11 °C respectively. The growing season of *A.sieberi* and *A.aucheri* is from early March to mid November, about 260 days. Data of rainfall, temperature, humidity and duration of sunshine on 2011 were collected from synoptic station of Nodushan, Meybod.



Figure 1. *Artemisia sieberi* stand in Sadrabad site (left) and *Artemisia aucheri* stand in Khood site (right)

Preparation of plant samples

To estimate the above and belowground production, 6 individuals of each species with different sizes were totally (shoot and root) harvested every 2 months during the growing season (*Figure 2*). The total biomass was separated into leaf, new and old branch, stem, coarse root (diameter > 2mm) and fine root (< 2mm). Leaf area index was estimated by measuring the area and the weight of a number of leaves and determination of a relationship between leaf area and leaf weight.



Figure 2. Harvesting the whole plant, *Artemisia sieberi* (left) and *Artemisia aucheri* (right)

A total of 10 soil cores were collected randomly below the canopy cover of *A.sieberi* and *A.aucheri* with an auger (10 cm diameter) at a depth of 30 cm (based on the depth of plant rooting) at 2 month intervals during the growing season to determine the fine root production. Dead and live fine roots were separated based on their shape, color and flexibility. To estimate the stem annual growth, 3 plants with different sizes were selected for each species, and the diameter and the length of 5 stems with different sizes for each plant were measured at the beginning and at the end of the growing season. 2 points on each selected stem were wrapped with a piece of metal wire for measuring the diameter and the length. The stems were marked with plastic tags. The annual growth of the stems was determined based on the annual increment in the volume of the sampling

stems and its equivalent weight. The density and the cover of plants were estimated using 40 randomly located $1 \times 2 \text{ m}^2$ quadrats.

Measurement of composition of plant components

Plant components (leaf, new branch, old branch, stem, coarse root and fine root) were dried in oven at $70 \text{ }^\circ\text{C}$ for 48 h. Nitrogen content was measured by the Kjeldahl method. Carbon content was estimated with an elemental analyzer (Costech ECS 4010, Elemental Combustion System). Ash content was determined after heating the dry matter to $550 \text{ }^\circ\text{C}$ for 5 hours.

Total net primary production (Total NPP)

Total NPP (g Carbon m^{-2}) was determined as the sum of the aboveground net primary production (ANPP) and the belowground net primary production (BNPP). ANPP was calculated as the sum of the leaf production and wood production. Maximum value of leaf biomass during the growing season was used as the leaf production. Wood production was considered as the sum of the biomass of new branches at the time of maximum growth and annual increment in the stem biomass. BNPP was determined by measuring coarse root production and fine root production. Coarse root production (NPP_{cr}) was calculated using an equation which assumes that coarse root production is proportional to aboveground NPP (Johnson and Risser, 1974).

$$NPP_{cr} = \frac{ANPP}{AGB} \times B_{cr} \quad (\text{Eq.1})$$

Where NPP_{cr} is coarse root production, ANPP is aboveground net primary production, AGB is aboveground biomass and B_{cr} is coarse root biomass (at the time of maximum growth). Fine root production (NPP_{fr}) was estimated as differences in means of fine root biomass between sampling dates. Positive biomass increments were summed during the growing season (Fogel, 1983). Fine root biomass (g C m^{-2}) was calculated according to the following Equation.

$$B_{fr} = \left[\frac{\text{Mean weight of fine root per core}}{\pi (10)^2 / 4} \right] \times (\text{Percent rooting cover}) \quad (\text{Eq.2})$$

Since the study sites are not totally covered by the plants, and the sampling cores were taken below the canopy cover of the plants, the mean weight of fine root biomass per square was multiplied by the area (%) covered by the plant roots.

Total respiration (Total R)

Total respiration was calculated as the sum of maintenance (R_m) and construction (R_c) respiration. Construction respiration was determined as:

$$R_c = R_{cl} + R_{cw} + R_{ccr} + R_{cfr} \quad (\text{Eq.3})$$

Where R_{cl} , R_{cw} , R_{ccr} and R_{cfr} are respectively, the construction respiration of leaf production, wood production (new branches and increased annual biomass of stems) and coarse root and fine root production. Construction respiration was determined using carbon, nitrogen and ash content of plant materials based on Vertregt and Penning de Vries (1987) method slightly modified by Poorter (1994).

$$R_c = (-1.041 + 5.077 C_{om})(1 - M) + (5.235 N_{org}) \quad (\text{Eq.4})$$

Where R_c is the construction cost (g glucose g⁻¹ dry weight), C_{om} is the carbon content of the organic material (g g⁻¹), and M and N_{org} are the mineral (ash content) and organic N concentration of the total dry matter (g g⁻¹). The carbon equivalent of the glucose used in respiration can be calculated based on the atomic weight of carbon and glucose ($C_6/C_6H_{12}O_6 = 72/180$). Construction respiration is then, equal to the total carbon cost minus carbon incorporated into structure. Maintenance respiration was determined as:

$$R_m = R_{ml} + R_{msw} + R_{mfr} \quad (\text{Eq.5})$$

Where R_{ml} , R_{msw} and R_{mfr} are maintenance respiration of leaf production, sapwood and fine root production respectively. R_{ml} and R_{mfr} were determined using Ryan's (1991) equation,

$$R_m^* = N_t \times D \times 0.059 \times \exp(0.07 T_a) \quad (\text{Eq.6})$$

Where T_a is the average growing season temperature (°C) and D is duration of growing season (number of days). For estimation of R_{ml} , N_t is the total nitrogen content of leaf biomass calculated from N concentration in leaf biomass and average leaf biomass during the growing season (the average leaf biomass was used in the calculation, because the rate of production is low at the beginning of the growing season, March, and peaks around July, then decreases towards the end of the growing season, November). For determination of R_{mfr} , N_t is the total N in fine root biomass calculated from N concentration and average fine root production during the growing season. New branches and coarse roots (diameter > 2mm) were assumed to be 100% of sapwood (Ryan and Waring, 1992). The stem sapwood was determined by separating the bark of a number of stems with different sizes and recognizing the sapwood based on the color. Maintenance respiration of new branches was also obtained using the equation R_m^* , based on the N content in the new branch biomass (sapwood) and the average of new branch biomass during the growing season. Maintenance respiration of coarse roots and stems was determined as (Ryan, 1991):

$$R_m = N_{sw} \times 27 \times \exp(0.07 T_a) \quad (\text{Eq.7})$$

Where T_a is average annual temperature ($^{\circ}\text{C}$) and N_{sw} is N content in sapwood calculated from sapwood biomass and sapwood N concentration.

Gross primary production (GPP)

Annual GPP was calculated from the total net primary production plus the total respiration.

Solar energy capture

The amount of solar energy used by plants was determined as the sum of the energy fixed as GPP and the energy consumed in transpiration. The energy fixed as GPP was determined based on the glucose equivalent of the carbon fixed in plants as GPP ($\text{C}_6/\text{C}_6\text{H}_{12}\text{O}_6 = 72/180$) and the energy required to produce glucose ($3740\text{Cal gr}^{-1}\text{glucose}$).

Energy Used in Transpiration

The amount of energy used in transpiration was determined from the amount of water transpired by *Artemisia* species in the growing season and the amount of energy required for evaporating water at the mean temperature of the growing season. The energy necessary to evaporate water at the mean temperature during the growing season was calculated from Harrison' (1963) equation:

$$\lambda_v = 597.3 - 0.564T \quad (\text{Eq.8})$$

Where λ_v is the latent heat of vaporization (Cal g^{-1}) and T is the mean temperature in the growing season ($^{\circ}\text{C}$). Transpiration (T_R) was estimated by partitioning evapotranspiration into evaporation and transpiration following the approach of Campbell (1985):

$$T_R = AET [1 - \exp(-0.82F)] \quad (\text{Eq.9})$$

Where AET is actual evapotranspiration and F is leaf area index. Actual evapotranspiration (mm) during the growing season was estimated according to Schreiber's (1904) empirical formula:

$$AET = P - \exp\left(\frac{PET}{P}\right) \quad (\text{Eq.10})$$

Where P is mean annual precipitation (mm) and PET is potential evapotranspiration (mm) during the growing season obtained from Thornthwaite's (1948) method.

$$PET = 16 \left(\frac{L}{12}\right) \left(\frac{N}{30}\right) \left[\frac{10T}{I}\right]^a \quad (\text{Eq.11})$$

Where T : average monthly temperature ($^{\circ}\text{C}$) from March to November, L : the average day length (hours) of the month, N : the number of days in the month and I : the heat index calculated as:

$$I = \sum_{i=1}^n \left[\frac{T_i}{5} \right]^{1.514} \quad (\text{Eq.12})$$

Where T_i : average monthly temperature. a is calculated from:

$$a = 0.49239 + 0.0179I - 0.0000771I^2 + 0.000000675I^3 \quad (\text{Eq.13})$$

Determination of solar radiation

To estimate the percentage of the energy used by plants in photosynthesis and transpiration, the annual incoming solar radiation and the net solar radiation were determined. Net radiation (R_n , $\text{MJ m}^{-2}\text{day}^{-1}$) was estimated by the following equations (see FAO, Irrigation and drainage paper, Allen et al., 1998).

$$R_n = R_{ns} - R_{nl} \quad (\text{Eq.14})$$

Where R_{ns} : incoming net shortwave radiation and R_{nl} : outgoing net longwave radiation ($\text{MJ m}^{-2}\text{day}^{-1}$).

$$R_{ns} = (1 - \alpha) R_s \quad (\text{Eq.15})$$

Where α : albedo or canopy reflection coefficient (0.23) and R_s : incoming solar radiation ($\text{MJ m}^{-2}\text{day}^{-1}$).

$$R_s = \left[0.25 + 0.5 \left(\frac{n}{N} \right) \right] \times R_a \quad (\text{Eq.16})$$

Where n : actual duration of sunshine (hour), N : maximum possible duration of sunshine or daylight hours (hour) obtained from:

$$N = \frac{24 \omega_s}{\pi} \quad (\text{Eq.17})$$

Where ω_s : sunset hour angle.

$$\omega_s = \arccos[-\tan(\varphi) \tan(\delta)] \quad (\text{Eq.18})$$

Where φ : latitude (rad) and δ : solar declination (rad).

$$\delta = 0.409 \sin\left(\frac{2\pi}{365} J - 1.39\right) \quad (\text{Eq.19})$$

Where J is the number of the day in the year between 1 (1 January) and 365 or 366 (31 December) and R_a : extraterrestrial radiation ($\text{MJ m}^{-2} \text{day}^{-1}$):

$$R_a = \frac{24(60)}{\pi} G_{sc} d_r [\omega_s \sin(\varphi) \sin(\delta) + \cos(\varphi) \cos(\delta) \sin(\omega_s)] \quad (\text{Eq.20})$$

Where G_{sc} : solar constant ($0.082 \text{ MJ m}^{-2} \text{min}^{-1}$), d_r : inverse relative distance earth-sun.

$$d_r = 1 + 0.033 \cos\left(\frac{2\pi}{365} J\right) \quad (\text{Eq.21})$$

The Outgoing net longwave radiation was determined as:

$$R_{nl} = \sigma \left[\frac{T_{\max,K}^4 + T_{\min,K}^4}{2} \right] (0.34 - 0.14 \sqrt{e_a}) \left(1.35 \frac{R_s}{R_{so}} - 0.35 \right) \quad (\text{Eq.22})$$

Where σ : Stefan-Boltzmann constant ($4.903 \times 10^{-9} \text{ MJ K}^{-4} \text{m}^{-2} \text{day}^{-1}$), $T_{\max,K}$ and $T_{\min,k}$ are daily maximum and minimum absolute temperature ($^{\circ} \text{K}$) respectively, e_a : actual vapor pressure (kPa),

$$e_a = 0.611 \exp\left(\frac{17.27 T}{237.3 + T}\right) \times RH \quad (\text{Eq.23})$$

where T : mean daily temperature ($^{\circ} \text{C}$) and RH : relative humidity. R_{so} : clear-sky solar radiation.

$$R_{so} = (0.75 + 2 \times 10^{-5} z) \times R_a \quad (\text{Eq.24})$$

Where z : elevation above sea level (m).

Results

Incoming and net solar radiation

Based on the calculations, the annual incoming solar radiation (R_s) and the net solar radiation (R_n) were respectively, $1.7045 \times 10^{10} \text{ kcal ha}^{-1}$ ($467 \text{ Cal cm}^{-2} \text{day}^{-1}$) and $7.807 \times 10^9 \text{ kcal ha}^{-1}$ ($213.9 \text{ Cal cm}^{-2} \text{day}^{-1}$) in *A.sieberi* stand and $1.7064 \times 10^{10} \text{ kcal ha}^{-1}$ ($467.5 \text{ Cal cm}^{-2} \text{day}^{-1}$) and $7.944 \times 10^9 \text{ kcal ha}^{-1}$ ($217.6 \text{ Cal cm}^{-2} \text{day}^{-1}$) in *A.aucheri* stand.

Chemical composition

The carbon, nitrogen and ash content in the biomass of plant components for *A.sieberi* and *A.aucheri* are presented in Table 1.

Table 1. Percentage of the carbon, nitrogen and ash in the biomass of *A.sieberi* and *A.aucheri* components

<i>A.sieberi</i>	Leaf	New branch	Stem	Coarse root	Fine root
Carbon	48.1	47.4	46.2	47.3	45.1
Nitrogen	1.9	1.1	1.1	0.7	0.9
Ash	9.5	4.6	6.5	5.6	10
<i>A.aucheri</i>					
Carbon	50.7	47.8	45.4	47.8	47.2
Nitrogen	1.4	0.7	0.7	0.6	0.7
Ash	7.4	5	6.1	4.9	8

Vegetation biomass

The density and the cover of *A.sieberi* were 0.6 (number m⁻²) and 10% respectively. The average dry weight of an *A.sieberi* plant was 291.2 g (total biomass of 174.7 g dry matter m⁻² regarding the density) (Table 2). The average dry matter of leaf, new branch, old branch, stem, coarse root and fine root biomass of an *A.sieberi* plant was 20.5 g (biomass of 12.3 gm⁻²), 49.1 g (29.46 gm⁻²), 60.62 g (36.37 gm⁻²), 77.96 g (46.78 gm⁻²), 79.2 g (47.52 gm⁻²) and 3.82 g (2.29 gm⁻²) respectively. The ratio of below to aboveground biomass for an *A.sieberi* plant was 0.4 (range of 0.29-0.53). The density and the cover of *A.aucheri* were 1 (number m⁻²) and 20.5 % respectively. The average dry matter of an *A.aucheri* plant was estimated to be 483.2 g (total biomass of 483.2g m⁻²) The average dry matter of leaf, new branch, old branch, stem, coarse root and fine root biomass of an *A.aucheri* plant was 14.8 g (total leaf biomass of 14.8 g m⁻²), 30.6 g (30.6 g m⁻²), 53.5 g (53.5 gm⁻²), 210 g (210 gm⁻²), 167.9 g (167.9 gm⁻²), 6.4 g (6.4 gm⁻²) (Table 2). The ratio of below to aboveground biomass was 0.56 (0.38-0.77) for an *A.aucheri* plant.

Net primary production

Total above and belowground biomass (g C m⁻²) of *A.sieberi* was 58.2 and 23.5 respectively (81.7) (Table 2). The total above and belowground NPP (g C m⁻²) of *A.sieberi* was 22.88 (27% of GPP and 71% of total NPP) and 9.23 (11% of GPP and 29% of total NPP) respectively (total NPP: 32.11 g C m⁻²: 38% of GPP). The leaf, new branch, stem, coarse root and fine root NPP (g C m⁻²) of *A.sieberi* during the growing season were 5.92, 13.96, 3, 8.82 and 0.41. Total above and belowground biomass (g C m⁻²) of *A.aucheri* was estimated to be 141.6 and 83.28 respectively (224.88). The leaf, new branch, stem, coarse root and fine root NPP (g C m⁻²) of *A.aucheri* were 7.5, 14.63, 17.4, 22.38 and 0.84 respectively, during the growing season. The total above and belowground NPP (g C m⁻²) of *A.aucheri* was 39.53 (26% of GPP and 0.63% of total

NPP) and 23.22 (15% of GPP and 37% of total NPP) respectively (total NPP: 62.75 g C m⁻²: 41% of GPP).

Table 2. Biomass, net and gross primary production and respiration of *A.sieberi* and *A.aucheri* in the study stands

	<i>Artemisia sieberi</i>						<i>Artemisia aucheri</i>					
	Leaf	New branch	Stem	Coarse root	Fine root	Total	Leaf	New branch	Stem	Coarse root	Fine root	Total
Aver. biomass of an indiv. (g DM)	20.5	49.1	77.96	79.2	3.82	291.2*	14.8	30.6	210	167.9	6.4	483.2*
Biomass (gDMm ⁻²)	12.3	29.46	46.78	47.52	2.29	174.72*	14.8	30.6	210	167.9	6.4	483.2*
Biomass (gCm ⁻²)	5.92	13.96	21.61	22.44	1.03	81.7*	7.5	14.63	95.34	80.26	3.02	224.87*
NPP (gCm ⁻²)	5.92	13.96	3	8.82	0.41	32.11	7.5	14.63	17.4	22.38	0.84	62.75
Rc (gCm ⁻²)	0.82	2.08	0.32	1.03	0.016	4.27	1.34	1.94	1.35	2.9	0.074	7.6
Rm (gCm ⁻²)	8.9	12.1	3.7	23.1	1.03	48.83	6.05	6.25	11	58.75	1.91	83.96
Total R (gCm ⁻²)	9.72	14.18	4.02	24.13	1.05	53.1	7.39	8.19	12.35	61.65	1.98	91.56
GPP (gCm ⁻²)	15.64	28.14	7.02	32.95	1.46	85.21	14.89	22.82	29.75	84.03	2.82	154.31
NPP/GPP	0.38	0.5	0.43	0.27	0.28	0.38	0.5	0.64	0.58	0.27	0.3	0.41
Total R/GPP	0.62	0.5	0.57	0.73	0.72	0.62	0.5	0.36	0.42	0.73	0.70	0.59
ANPP (gCm ⁻²)	22.88								39.53			
ANPP/Total NPP	0.71								0.63			
ANPP/GPP	0.27								0.26			
BNPP (gCm ⁻²)				9.23							23.22	
BNPP/Total NPP				0.29							0.37	
BNPP/GPP				0.11							0.15	

*: Values of biomass for old branches are not presented in table 2, but the total values for biomass are shown regarding the values for old branches (see the text). For *A.sieberi* and *A.aucheri*, the average dry matter of old branches for an individual plant was 60.62 g and 53.5 g, and biomass of old branches was 36.37 g dry matter m⁻² (16.7 g C m⁻²) and 53.5 g dry matter m⁻² (24.12 g C m⁻²) respectively.

Construction and maintenance respiration

For *A.sieberi*, the construction respiration was 4.27 g C m⁻² (Table 2). This was equal to 5% of GPP. The construction respiration of *A.aucheri* was 7.6 g C m⁻² (4.9 % of GPP). The annual maintenance respiration of *A.sieberi* biomass was 48.83 g C m⁻² (57% of GPP). The annual maintenance respiration of *A.aucheri* biomass was 83.96 g C m⁻² (54 % of GPP). 10.36 % of stem biomass of *A.sieberi* and 12.83 % of stem biomass of *A.aucheri* was composed of sapwood. Total respiration was 62% and 59% of GPP for *A.sieberi* and *A.aucheri* respectively.

Gross primary production and conversion efficiency of solar energy to GPP

The annual GPP (g C m⁻²) of *A.sieberi* and *A.aucheri* was estimated to be 85.21 and 154.31 respectively (Table 2). The energy necessary to produce the glucose equivalent of this amount of carbon is 796.7 and 1442.8 kcal m⁻²yr⁻¹ for the two species

respectively. Therefore, the conversion efficiency of the annual incoming solar energy ($R_{incoming}$) and net solar energy (R_{net}) to GPP was 0.047 % and 0.1 % by *A.sieberi*, and 0.084 % and 0.18 % by *A.aucheri* respectively.

Energy used in transpiration

Actual evapotranspiration during the growing season was estimated 88.97 mm and 122.3 mm for *A.sieberi* and *A.aucheri* stands, respectively. The relationship between the leaf weight and the leaf area was found to be as $1 \text{ g} = 28 \text{ cm}^2$ for *A.sieberi* and $1 \text{ g} = 32.9 \text{ cm}^2$ for *A.aucheri*. Based on the leaf biomass of the species, leaf area index (LAI) of *A.sieberi* and *A.aucheri* was determined as 0.034 and 0.049 respectively. The rate of transpiration (Kg water) of *A.sieberi* and *A.aucheri* was estimated 24500 kg ha^{-1} and 48000 kg ha^{-1} during the growing season using the evapotranspiration and LAI. Based on the energy necessary to evaporate water in *A.sieberi* site ($587.8 \text{ Cal gr}^{-1} \text{ water}$) and *A.aucheri* site ($589.2 \text{ Cal gr}^{-1} \text{ water}$), the amount of energy used in transpiration was 1440 kcal m^{-2} (0.08 % of the $R_{incoming}$ and 0.18 % of the R_{net}) by *A.sieberi* and 2828 kcal m^{-2} (0.17 % of the $R_{incoming}$ and 0.36 % of the R_{net}) by *A.aucheri*. Totally, *A.sieberi* consumed 0.13 % of the annual $R_{incoming}$ and 0.28% of R_{net} , and *A.aucheri* consumed 0.25 % of $R_{incoming}$ and 0.54% of R_{net} , in both GPP and transpiration respectively.

Discussion

Desert and semidesert shrublands represent approximately 18 million km^2 of land area worldwide (Whittaker, 1975). The communities of *Artemisia sieberi* and *Artemisia aucheri* are two of the most widespread vegetation covers in arid and semiarid shrublands of central parts of Iran. These communities play an important role in carbon dioxide absorption and carbon sequestration. There is little information on the rate of GPP in arid and semiarid shrublands throughout the world, and no study has been done in this area on *Artemisia* communities in Iran. The total biomass of *A.sieberi* was 36% of *A.aucheri*. This may result form a more favorable climatic condition in *A.aucheri* stand. The total NPP of *A.sieberi* ($32.11 \text{ g C m}^{-2} \text{ yr}^{-1}$) and *A.aucheri* ($62.75 \text{ g C m}^{-2} \text{ yr}^{-1}$) was found to be less than that of forest ecosystems (e.g., $307 \text{ g C m}^{-2} \text{ yr}^{-1}$ for *Picea mariana* in boreal forests, Ryan et al., 1997; $960 \text{ g C m}^{-2} \text{ yr}^{-1}$ for *Pinus radiata* in temperate coniferous forests, Arneeth et al., 1998; $817 \text{ g C m}^{-2} \text{ yr}^{-1}$ for *Betula ermanii*, *B. platyphylla* and *Quercus mongolia* in temperate deciduoud forests, Saigusa et al., 2002, $1560 \text{ g C m}^{-2} \text{ yr}^{-1}$ in tropical forests, Malhi et al., 1999) and temperate grasslands (e.g., 1207 and $1140 \text{ g C m}^{-2} \text{ yr}^{-1}$ in a *Miscanthus sinensis* grassland in Japan over a 2-year period, Yazaki et al., 2004). The amount of NPP for *Artemisia* was found to be approximately close to NPP in some desert grasslands and shrublands (e.g., aboveground NPP: $51.1 \text{ g C m}^{-2} \text{ yr}^{-1}$ in a *Bouteloua eriopoda* grassland and $59.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ in a *Larrea tridentata* shrubland in northern chihuahuan desert, USA, Muldavin et al., 2008). However above ground NPP is reported 224.09 g m^{-2} in a desert shrubland of *Artemisia ordosica* in Mongolia, China, with an annual precipitation of 345.2 mm (Zhao et al., 2007). The low NPP of *Artemisia* species likely relates to a deficiency of rainfall, a short period of favorable climatic condition (rainfall is available only in two months, March through April, during the growing season) and a low LAI. *A.sieberi* NPP was approximately half of the *A.aucheri* NPP. This is a consequence of the lower precipitation in *A.sieberi* site. Studies have highlighted that NPP increases greatly with

increasing precipitation at precipitations below around 4000 mm yr⁻¹ (Lieth, 1975) or 2200 mm yr⁻¹ (Schoor, 2003). The annual GPP (g C m⁻² yr⁻¹) of *A.sieberi* (85.21) and *A.aucheri* (154.31) was low in compared to GPP estimates in temperate grasslands (e.g., 584 and 1112 g C m⁻² yr⁻¹ in a semiarid grassland in Hungary in a dry and wet condition, respectively, Nagy et al., 2007) and forest ecosystems (e.g., 3 kg C m⁻² yr⁻¹ in tropical forests, Chambers et al., 2000; 1.1 kg C m⁻² yr⁻¹ for *Picea mariana* in boreal forests, Ryan et al., 1997; 1.6 kg C m⁻² yr⁻¹ for *Pinus strobes* and *Acer rubrum* in temperate mixed forests, Curtis et al., 2005). The high GPP in forests and temperate grasslands is likely related to year-round growing season, fertile soils and a high LAI (Giardina et al., 2003). The ratio of NPP/GPP referred to as carbon use efficiency (CUE) was 0.38 for *A.sieberi* and 0.41 for *A.aucheri*. This indicates that NPP is approximately proportional to GPP across the different sites (e.g., in different forest types, Waring et al., 1998; DeLucia et al., 2007). The value of CUE in *Artemisia* stands in the arid and semiarid study sites was found to be higher than CUE for old boreal forests (0.31) (Ryan et al., 1997), and lower than CUE in temperate deciduous forests (0.59) and the universal value of 0.47 (Waring et al., 1998). Overall, studies suggest that variation in the climate, ecosystem type, species, edaphic factors (Giardina et al., 2003), stand age and leaf mass-to-total mass (DeLucia et al., 2007) may exert a great influence on the value of CUE. The fraction of total NPP allocated belowground (Belowground NPP/ total NPP), as an important factor influencing nutrient and water uptake, C turnover and species composition (Jackson et al., 2000; Obrist and Arnone, 2003), was 8% greater for *A.aucheri* (0.37) than that for *A. sieberi* (0.29). This is in contrast with the statement that BNPP to total NPP decreases with increasing precipitation (e.g., Runyon et al., 1994; Hui and Jackson, 2005). Hui and Jackson (2005) synthesizing biomass data at 12 grassland sites around the world reported that the ratio of BNPP to total NPP decreases with increasing mean annual precipitation and temperature. Mean annual precipitation in the *A.aucheri* study site is 38% higher than *A.sieberi* study site and mean annual temperature is 19% lower than *A.sieberi* study site. Generally BNPP is strongly influenced by climatic factors (Schoor, 2003). Several studies have shown that there is a positive relationship between BNPP and precipitation (Bradford et al., 2006; Gao et al., 2010), but a negative relationship between BNPP and temperature (Bradford et al., 2006; De Boeck et al., 2007). These results are likely a consequence of the fact that higher precipitation increases water availability whereas higher temperature decreases water availability. It seems that in order to balance the water demand of the transpiring leaf surface with the water uptake capacity of the root system (Gao et al., 2010), a greater amount of NPP was allocated to belowground components in the *A.aucheri* site in a reaction to a higher precipitation and a lower temperature. Respiration was approximately 60% of GPP for both species. This is in line with the statement that partitioning to respiration is constant across a wide range of GPP (Waring et al., 1998; Gifford, 2003) and does not vary with resource availability and competition (Ryan et al., 2004). However, the ratio of belowground respiration to GPP for *A.aucheri* (0.41) was greater than that for *A.sieberi* (0.29). The higher ratio of belowground respiration to GPP for *A.aucheri* results from both a greater allocation of total NPP to BNPP and a higher belowground biomass to total biomass for *A.aucheri*. The percentage of the incoming and net solar energy absorbed in photosynthesis (as GPP) by *A.sieberi* (0.047 %, 0.1 %) and by *A.aucheri* (0.084 %, 0.18 %) showed that the conversion efficiency of solar energy to GPP by shrubs in arid and semiarid climates is low in compared to croplands (e.g., cornfield: 1.6 %; Transeau, 1926; maize field: 1.2

%, Ovington and Lawrence, 1967; rice-barley: 0.89 %, groundnuts-wheat: 0.95 % and maize-*Lolium multiflorum* double cropping agro-ecosystems: 2.4 %, Koizumi et al., 1990), grass communities (e.g., 1.2 %, Golley, 1960; C3 grass:2.4 % and C4 grass: 3.7%, Piedade et al., 1991; Beale and Long, 1995) and forests (e.g., 1%, Droste, 1979). Maximum conversion efficiency of solar energy to biomass is reported 4.6% for C3 and 6% for C4 photosynthesis (Zhu et al., 2008). The causes in the energy loss at the discrete steps of the plant photosynthetic process from interception of radiation to the formation of stored chemical energy in biomass include: outside photosynthetically active spectrum, reflected and transmitted radiation, photochemical inefficiency, photorespiration and respiration (Zhu et al., 2008). The percentage of the incoming and net solar energy used in transpiration by *A.sieberi* and *A.aucheri* was dependant on the amount of both rainfall and temperature. An increase in the amount of both precipitation and temperature may result in a higher evapotranspiration, productivity, LAI and as a result in an increase in the amount of solar energy used in transpiration by plants. To expand the ecosystem services and functions such as carbon dioxide absorption, forage production, climate regulation, etc, in arid ecosystems it is necessary to improve the primary production of species. Establishment and maintenance and of a variety of plant species in arid and semiarid ecosystems, specially a mixture of shrub and grass forms (Mousaei Sanjerehei et al., 2011) may result in a greater aboveground productivity in compared to pure species stands (Forrester et al., 2006; Bessler et al., 2009).

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