

Leaf Photosynthesis, Growth, and Seed Chemicals of Sacha Inchi Plants Cultivated Along an Altitude Gradient

Z. Q. Cai,* D. Y. Jiao, S. X. Tang, X. S. Dao, Y. B. Lei, and C. T. Cai

ABSTRACT

Sacha inchi (*Plukenetia volubilis* L.) is known to naturally grow under a wide range of elevational gradients in South America. We assessed the combined effects of altitude (560, 900, 1200, and 1490 m asl) and season on leaf- and whole-plant traits and seed chemicals of sacha inchi plants in Xishuangbanna, Southwest China, to explore the optimum altitudinal zone for its cultivation. Leaf maximum net photosynthetic rate (A_{\max}), stomatal conductance (g_s), and dark respiration (R_d) were greatest in the wet season and lowest in the cool season. With similar values in the wet season between altitudes, the reduction in A_{\max} and g_s was greater in plants growing in higher elevations than in lower elevations in the cool season. Plant biomass and fruit production were highest at lower altitudes and dramatically decreased above 900 m, which can primarily be attributed to a C source limitation. Sacha inchi could be useful for cropping in cooler regions because the reproductive growth is adapted to high elevations. The oil and protein content and linolenic and unsaturated fatty acid (UFA) concentrations in seeds were highest in the cool season. With an increase in elevation, the linolenic and UFA concentrations in seeds increased. We concluded that lower altitudes (<900 m) could be the optimum zone for growth and yield of sacha inchi plants whereas seeds collected from plants growing at higher altitudes (>900 m) and in the cool season appear to have better quality.

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Abbreviations: A_{\max} , maximum net photosynthetic rate; g_s , stomatal conductance; N_{mass} , nitrogen concentration; P_{mass} , phosphorus concentration; R_d , dark respiration; SFA, saturated fatty acid; UFA, unsaturated fatty acid.

SACHA INCHI (*Plukenetia volubilis* L.) is a promising oilseed crop indigenous to the rain forests of the Andean region of South America. It is a woody twining vine yielding mostly tetralobular capsules with 4 to 7 lenticular oleaginous seeds inside. Sacha inchi seed contains high protein and oil content (Hamaker et al., 1992; Cai et al., 2011; Gutiérrez et al., 2011) and have shown high economic value. In recent years, sacha inchi seed has become increasingly important for human health and nutrition because of its high concentration of omega fatty acids (especially high linoleic and linolenic) and the beneficial health effects that arise from its consumption (Cai, 2011a). Sacha inchi plants flower about 5 mo after being planted and can be flowering and fruiting continuously throughout the growing season. In the original regions, sacha inchi plants occur in rainforest environment at a range of altitudes from near sea level to about 1700 m elevation depending on availability of water and good drainage (Semino et al., 2008). Therefore, the plant is well adapted to different environments. Successfully introduced from South America, sacha inchi plants are being grown in Xishuangbanna, southwest Yunnan, China, where 95% percent of the land is covered by mountains. With increasing population and development of social economics in China, the developmental

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potential of land resources is mainly dependent on the exploitation of mountainous areas.

Although the composition and properties of sacha inchi seeds are relatively well known, to date there is a lack of detailed information about cultivation potential. Intensive research on this species can contribute to future implementation of sacha inchi into the agricultural systems of South China as an alternative crop that can reduce local farmers' dependence on cultivation of rubber trees. Therefore, our objective is to develop a comparative analysis on leaf physiology, growth, and seed chemicals of sacha inchi plants due to the combined effects of altitude and season. Based on these results, conclusions were made concerning the optimum altitudinal zone for the cultivation of this species based on seed yield and quality.

MATERIALS AND METHODS

Study Site and Plant Materials

The study was performed in Xishuangbanna, southwest Yunnan, China. The climate of Xishuangbanna is dominated by the southwest monsoon with three distinct seasons (a wet season from May to October, a cool season from November to January, and a dry season from February to April; Cao et al., 2006).

Seeds of *P. volubilis* were sown in the Xishuangbanna Tropical Botanical Garden (21°56' N, 101°15' E, 560 m asl), Chinese Academy of Sciences, in June 2009. When the seedlings were approximately 20 cm tall, uniform seedlings (180–300 individuals in each site) were selected and were cultivated in four open sites at intra- and interrow spacing of 2.0 and 2.0 m in Xishuangbanna mountain areas: site A (21°56' N, 101°25' E), B (22°11' N, 100°55' E), C (21°48' N, 101°19' E), and D (21°13' N, 101°20' E) at altitudes of 560, 900, 1200, and 1490 m, respectively. At site A, mean precipitation is 1500 mm and minimum and maximum air temperatures varied from 8 to 30°C in the cool season, from 15 to 32°C in the dry season, and from 20 to 35°C in the wet season, respectively. Because it is a liana species, *P. volubilis* plants were supported by steel wires with a height of 1.6 m. All plants at each site received a compound fertilizer with 1–1–1 (N–P–K) that was spread in an approximately 2 m-wide zone around the plants in June 2010 and 2011, respectively (150 g per plant corresponding to 375 kg ha⁻¹).

Leaf Physiology and Whole-Plant Morphological Traits Measurements

Gas exchange measurements were made between 0900 and 1100 h with a portable infrared gas analyzer in open system mode (LI-6400XT, Li-Cor) in January (cool season), April (dry season), and August (wet season), respectively, over two successive years. Six to eight plants per site were selected for photosynthetic measurements in each season; one leaf per plant was measured. Photosynthetic parameters were measured on fully expanded, recently matured sun canopy leaves. We measured maximum net photosynthetic rate (A_{\max}) and stomatal conductance (g_s) under a light saturating irradiance (photon flux density = 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ provided by an internal red and blue light-emitting diode light source, LI6400-02B [Li-Cor Inc.]). Light-response curves showed that this was sufficient to saturate photosynthesis for all plants (results not shown).

The CO₂ concentration in the cuvette was held at 400 $\mu\text{mol mol}^{-1}$ by a 6400–01 CO₂ injector (Li-Cor Inc.), and leaf temperature and vapor pressure deficit in the cuvette were kept at 25 to 26°C and less than 1 kPa, respectively. We also measured dark respiration (R_d) in the leaf chamber, allowing several minutes for the leaves to stabilize before recording data. Leaf N concentration was measured by semi-micro Kjeldahl analysis using a wet digestion procedure, and leaf P concentration was measured by atomic absorption spectrum-photometry.

Six to eight plants were harvested for each site in late August 2010. The plants were separated into leaves, stems, coarse roots (diameter ≥ 1 mm), fine roots (diameter < 1 mm), flowers (both male and female parts), and fruits and were dried to a constant mass and weighed. Then the biomass fraction of each component was calculated. Fruit biomass was used to assess the yield. The total plant biomass was calculated to evaluate the growth rate.

Determination of Crude Protein, Total Fat, and Fatty Acid Composition

Mature seeds of sacha inchi plants were collected from four different altitudinal regions in January, April, and August in 2010, respectively. Immediately after the collection, seeds were dried at 50°C and stored at 4°C. Specimens of seed samples were submitted to the Kunming Center for Inspection and Testing for Quality and Safety of Agricultural Products, Ministry of Agriculture, China, for the analysis of seed chemical composition (lipid, protein, and fatty acids).

Total N concentration of the seed samples was determined by a standard micro-Kjeldahl method and was converted to crude protein content using a 6.25 conversion factor (Chang, 1994). Total lipids were extracted and converted into fatty acid methyl esters using the IRAM 5–560II method (Instituto Argentino de Racionalizacion de Materiales, 1982). Fatty acid methyl esters were separated and quantified by an automated gas chromatograph (Model 6890, GC; Hewlett-Packard Co.) equipped with flame ionization detectors and a 30 m \times 530 μm i.d. capillary column, as described previously (Cai et al., 2011). The total lipid and protein contents were expressed on dry weight basis per seed while fatty acid concentration was expressed as percentage of weight of the total fatty acids.

Statistical Analyses

As leaf photosynthetic traits had not a significant interyear variation, data were analyzed by two-way ANOVA for each morphological and physiological variable with elevation and season as main fixed factors. Before analysis, data were checked for normality and homogeneity of variance and were \log_{10} -transformed when necessary to satisfy the assumption of ANOVA. Mean treatment differences were separated by the least significant difference (LSD_{0.05}) test if *F* tests were significant ($p < 0.05$) (Fisher's protected test).

RESULTS AND DISCUSSION

Seasonal and Altitudinal Patterns in Leaf Nutrient

There was no significant altitude \times season interaction for leaf N and P concentration (N_{mass} and P_{mass} ; Fig. 1),

indicating that seasonal variation showed a similar and modest increase in leaf nutrients with an increase in elevation. Season had a significant effect on leaf N_{mass} and P_{mass} , with the highest values in the wet season and the lowest values in the cool season. Irrespective of soil substrate due to the fertilization in our study, the lowest leaf nutrient concentration in the cool season may be mainly attributable to generally lower air temperatures and long periods of low solar irradiance (Cai et al., 2007).

Leaf nutrient concentrations did not increase with elevation indicated by the not significant altitude effect, which was in line with the results from the conifers [*Picea rubens* Sarg. and *Abies balsamea* (L.) Mill.] in the mountains of the northeastern United States (Richardson, 2004). That also gives weak support for the hypothesis that nutrient limitation plays an important role in determining plant growth in high elevations. However, results for both trees (Oleksyn et al., 2002; Li et al., 2009) and a wide range of alpine plant species (Körner, 2003) support the idea that nutrient accumulation and conservation of plants growing in high elevations are adaptive responses that enhance metabolic capacity in energy limited systems. Our gradient was established in a tropical area where intra-annual

temperature differences are much smaller than in most other studies (whereas most other studies have been conducted in temperate regions). Temperature differences between low and high elevation sites in our study may have been insufficient to trigger enhanced leaf nutrient accumulation.

Seasonal and Altitudinal Patterns in Leaf Photosynthetic Traits

In general, it has been assumed that a low CO_2 partial pressure has a negative effect on photosynthesis at high altitudes (Sakata and Yokoi, 2002). However, several observations have suggested that alpine plants have a higher photosynthetic capacity than lowland plants (James et al., 1994; Koh et al., 2009). Although there were lots of reports on altitudinal trends in leaf photosynthesis, many studies focused on the measurements only for a certain period of time, and no clear consensus on effects of altitude on photosynthesis has been reached (Koh et al., 2009). In our study, the responsiveness to elevation differed among the seasons, which was indicated by the significant altitude \times season interactions for all gas exchange parameters (Fig. 2). Such interactions may indicate that their response to elevation differed in magnitude, significance, or direction of the responses to season. For example, during the dry season, large decreases were recorded in leaf A_{max} of plants grown at higher altitudes (>900 m) whereas no significant changes were detected at lower altitudes (<900 m). In the dry season, plants at high altitude are exposed to greater irradiance, large diurnal fluctuations of temperature, reduced partial pressure of CO_2 gases, and limited water for growth and development as compared to low altitude, which may reduce leaf photosynthetic rate (Cai et al., 2007; Gesch and Forcella, 2007). Maximum net photosynthetic rate in general decreased with an increase in elevation in the cool season, but it had similar values between altitudes in the wet season (Fig. 2). Compared to the wet season, the magnitude of decrease in A_{max} was much greater in the highest elevation than that in the lowest elevation in the cool and dry seasons. The lower A_{max} in the cool and dry seasons for plants growing at high altitudes may be attributed to their lower leaf-level C gain throughout the growing season. Season significantly affected all photosynthetic variables whereas altitude affected A_{max} and g_s but not respiration rate (R_d).

Most plants grow year round in the tropics but are particularly vulnerable to low temperatures (Allen and Ort, 2001). Maximum net photosynthetic rate was highest in sacha inchi plants during the wet season when environmental conditions (water, temperature, and light) were closest to optimal and leaves were in peak physiological condition. The lowest A_{max} observed in the cool season at high altitudes may be partially attributable to generally lower air temperatures and long periods of low solar irradiance (Liu et al., 2004) whereas water stress and

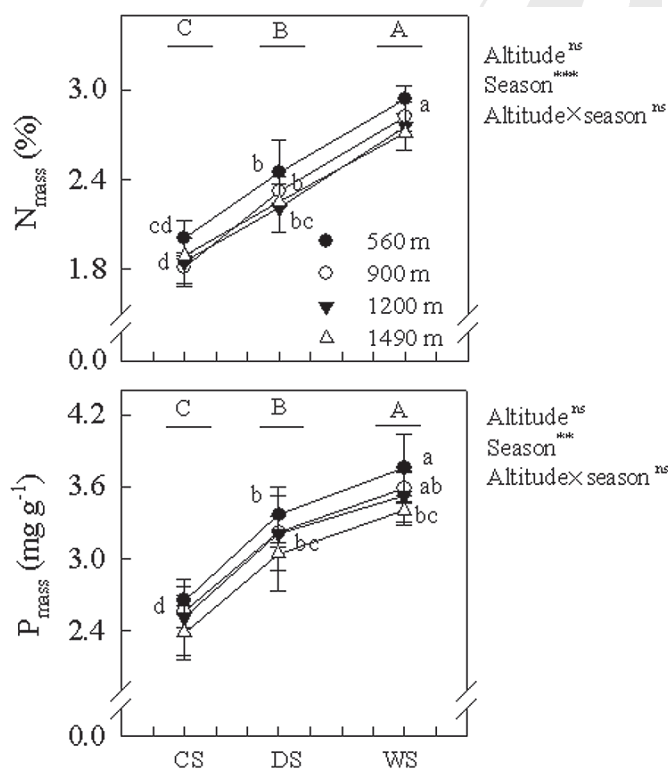


Figure 1. Seasonal variations in leaf nutrients (mean \pm SD, $n = 4$ to 5) in *Plukenetia volubilis* plants cultivated along an altitude gradient in 2010. CS, cool season; DS, dry season; WS, wet season; N_{mass} , N concentration; P_{mass} , P concentration; ns, not significant at $p > 0.05$; **, significant at the 0.01 probability level; ***, significant at the 0.001 probability level. Different capital letters above horizontal lines indicate significant differences between seasons, and different small letters denote significant differences among different environments, respectively, at $p < 0.05$ level.

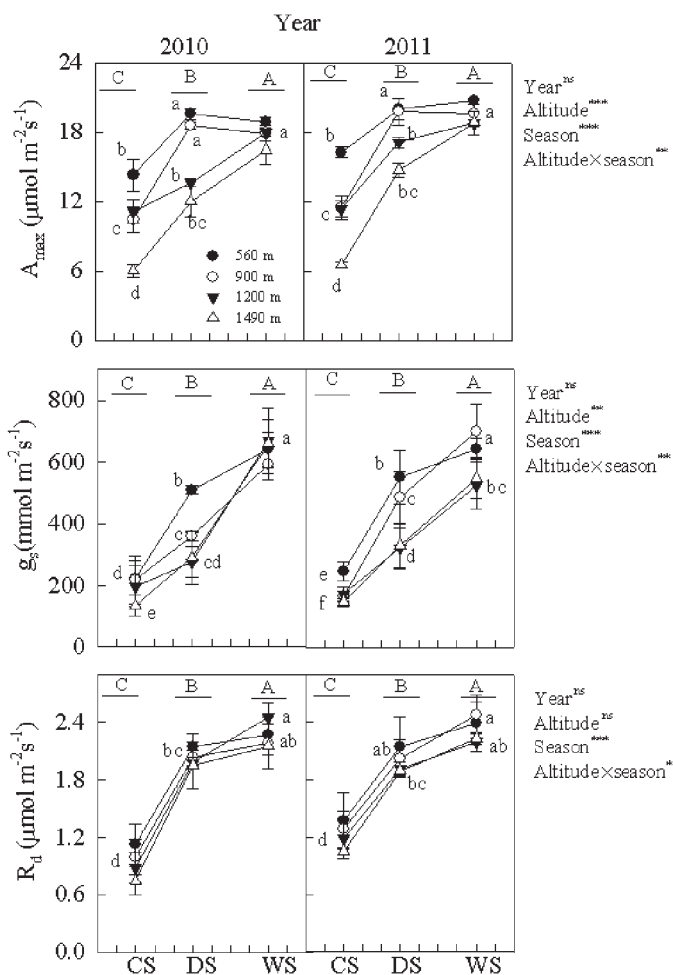


Figure 2. Seasonal variations in photosynthetic variables (mean \pm SD, $n = 6$ to 8) in *Plukenetia volubilis* plants cultivated along an altitude gradient over two successive years. A_{max} , maximum net photosynthetic rate; R_d , dark respiration; g_s , stomatal conductance; CS, cool season; DS, dry season; WS, wet season; ns, not significant at $p > 0.05$; *, significant at the 0.05 probability level; ***, significant at the 0.001 probability level. Different capital letters above horizontal lines indicate significant differences between seasons, and different small letters denote significant differences among different environments, respectively, at $p < 0.05$ level.

intermittent high solar irradiance causing photoinhibition reduced A_{max} in the dry season (Cai et al., 2007). However, some plant species do acclimate to lower seasonal temperatures by increasing photosynthetic capacities (Koh et al., 2009). This adaptive upregulation of photosynthetic capacity presumably represents an investment to counteract the lowering of enzyme activity at lower temperature by increasing the overall capacity of photosynthesis and/or size of the photosynthetic apparatus (Adams et al., 2002).

The stomatal conductance exhibited a similar response to A_{max} with altitude and season. Compared to the wet season, the magnitude of decrease in g_s was much greater in the highest elevation than that in the lowest elevation in the dry season, indicating that high altitude determined a greater g_s downregulation due to water stress. Maximum net photosynthetic rate was significantly correlated to g_s ,

across all environments ($r = 0.86$, $p < 0.001$); therefore, this indicated g_s to be a significant parameter to influence A_{max} (Cabrera et al., 1998).

Altitudinal Trend in Plant Biomass and Biomass Allocation

Total biomass per plant decreased significantly as the elevations rose from 560 to 1200 m but had a slight reduction in the uppermost location at 1490 m (Fig. 3A and 3B). In many other mountain forests, tropical and temperate, tree biomass and productivity tends to decrease with altitude toward the alpine tree line (James et al., 1994; Moser et al., 2011). This indicates that wood production is increasingly limited by environmental constraints or assimilate shortage when approaching the uppermost limit of tree growth. With the increase in elevation, the leaf, stem, and flower biomass fraction generally decreased whereas coarse root and fruit biomass fraction increased and fine-root biomass fraction remained constant (Fig. 3C). The decreased plant biomass and leaf biomass fraction resulted in lower leaf areas along the altitude gradient. Lower stem biomass fraction of plants that thrive at high altitudes is an adaptive strategy to avoid the damaging mechanical effect of strong winds (Körner, 2003).

Sacha inchi plants increased biomass allocation to the reproductive organs (mainly fruit biomass fraction) at higher altitudes at the expense of a lower allocation to vegetative parts. This result corroborated that reproductive growth is adapted to lower temperatures during the reproductive period (Dierig et al., 2006; Gesch and Forcella, 2007) and suggests that this species could be useful for cropping in cooler regions. However, the greater allocation to the reproductive organs under high elevation conditions did not result in increased fruit biomass and, therefore, higher yields. High fruit production of sachu inchi plants at lower altitudes involved a high resource availabilities for the reproductive period (Gesch and Forcella, 2007; Cai, 2011b)—an increased current photosynthetic input because they received high canopy C gain throughout the growing season—and plant total biomass (storage of photosynthetic products) increased with decreasing elevation.

Plant biomass productivity decreased continuously with elevation, which may likely be directly influenced by air temperature, because indirect limitation via soil processes was not apparent in our study. This trend could have different reasons: (i) a reduction in C source strength, that is, decreased canopy C gain at higher elevations, and/or increased C consumption by plant respiration or (ii) reduced C sink strength, that is, environmentally induced reductions in plant growth at higher elevations despite sufficient carbohydrate supply. In our study, although A_{max} in the wet season did not change significantly among the elevation levels, canopy C gain undoubtedly decreased with elevation along the

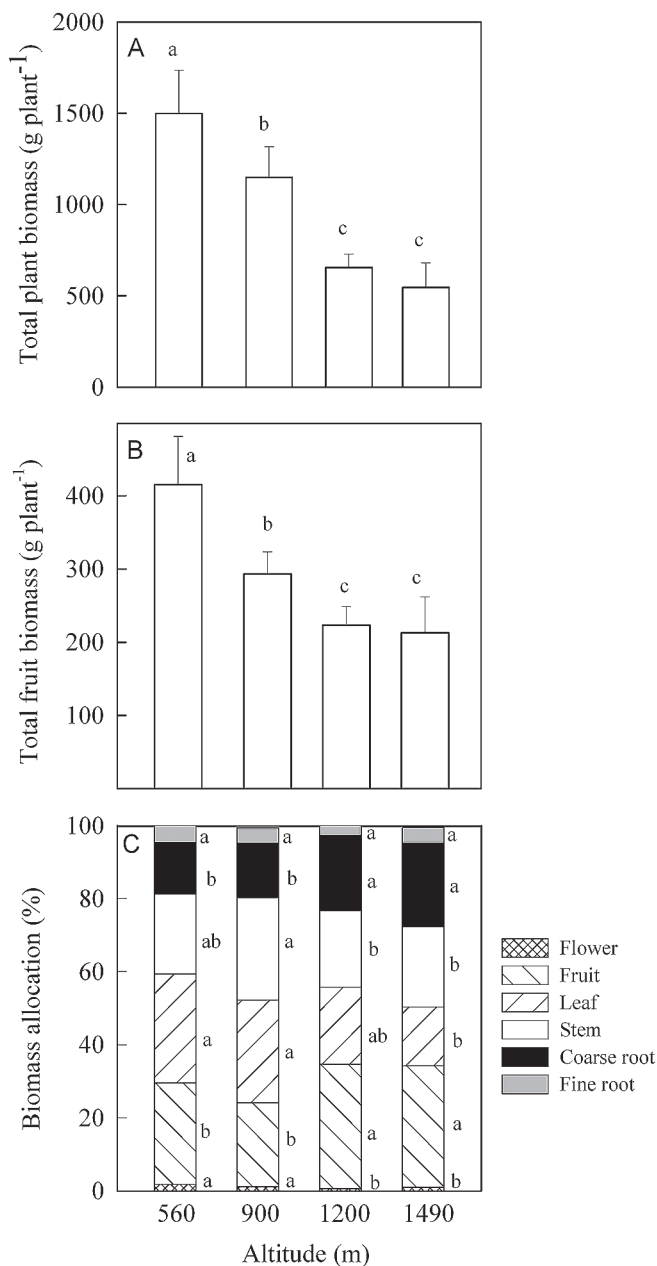


Figure 3. The whole-plant traits measured in the wet season in 2010 of *Plukenetia volubilis* plants cultivated along an altitude gradient. Different letters indicate significant differences for each trait between elevations at $p < 0.05$ level.

altitude gradient. This was indicated by the decline of annual canopy assimilation (resulted from total leaf area and leaf photosynthetic rate) between 560 and 1490 m. The possibility of plant respiration losses increasing with elevation can also be excluded because altitude did not significantly affect leaf respiration rate. In addition, a rough extrapolation of wood respiration measurements at the stand level indicated that mean daily CO_2 release from stems greatly decreased with increasing elevation, and mean daily CO_2 release from coarse roots also decreased, although not significantly (Zach et al., 2008). Whether sink limitation of growth, that is, reduced meristematic activity of high-elevation plants, is responsible for the

reduction in plant biomass may ultimately be decided on the basis of physiological studies in the laboratory. Indirect evidence from a tropical mountain rain forest seems to indicate that stem wood cambial activity is reduced with elevation independently of carbohydrate supply (Zach et al., 2008). In our study, the C sink strength increased with elevation, which is indicated by the higher fruit biomass fraction at higher altitudes. Moreover, we observed no significant variation of fine root fraction along the altitude gradient, which contradicts the assumption that the C sink caused by tree meristematic activity is reduced from low to high elevation due to the temperature reduction. Therefore, we conclude that the reduction in plant total biomass between 560 and 1490 m cannot primarily be attributed to a C sink limitation of plant growth. A much more plausible explanation is that C source limitation is the predominant cause (Li et al., 2008). The elevational decrease in annual canopy C gain limits plant growth toward higher elevation, although at different intensities in the aboveground and belowground compartments.

Seasonal and Altitudinal Patterns in Seed Protein and Fatty Acids

Among the different locations and seasons, the oil and protein content and unsaturated fatty acid (UFA) (oleic, linoleic, and linolenic combined) concentration varied within the range of 404 to 508 g kg⁻¹, 242 to 305 g kg⁻¹, and 90 to 93%, respectively (Table 1). The overall seed chemical concentrations in this study were comparable to our previous reports and from the original Peruvian Amazon (Hamaker et al., 1992; Cai et al., 2011; Gutiérrez et al., 2011). The oil content did not correlate with protein content across all environments for sacha inchi seeds (Fig. 4A), contrasting with literature data regarding such a relationship in soybean [*Glycine max* (L.) Merr.] and rape seed (*Brassica napus* L.) (Wilcox and Shibbes, 2001; Peltonen-Sainio et al., 2011). This result may partly be explained by the fact that (i) the biosynthesis of storage protein and oil in developing oil-storing seeds are independent processes (Voelker and Kinney, 2001), and a decrease in the amount of protein or oil in seeds does not generally lead to a compensating increase in other major storage compounds (Borek et al., 2009), and (ii) genes controlling oil and protein contents are differently expressed during the individual stages of the developmental period (Variath et al., 2009). There was a negative relationship between UFA and saturated fatty acid (SFA) (calculated as the sum of palmitic and stearic acids) (Fig. 4B), supporting the hypothesis from the micro-evolutionary studies that early seed germination and seedling growth are the selective agents affecting the balance between SFA and UFA in seed triacylglycerols (Linder, 2000; Agrawal and Thelen, 2006).

There were significant altitude \times season interactions for oil and protein content and fatty acid components

Table 1. Means and standard deviations of seed protein content, oil content, and fatty acid profile of sachu inchi plants grown in different environments.

Season [†]	Altitude (m)		Lipid (g kg ⁻¹)	Protein (g kg ⁻¹)	Palmitic (%)	Stearic (%)	Oleic (%)	Linoleic (%)	Linolenic (%)	SFA [‡] (%)	UFA [‡] (%)
CS	560	Mean	462.8	303.0	3.64	2.90	8.56	40.57	43.20	6.53	92.33
		SD	17.1	11.2	0.15	0.29	0.45	2.62	3.21	0.43	0.39
	900	Mean	501.4	295.5	4.04	3.06	9.28	36.85	45.91	7.10	92.04
		SD	15.8	11.1	0.23	0.05	0.30	1.30	1.26	0.27	0.21
	1200	Mean	50.78	27.73	3.88	2.52	8.43	37.23	46.91	6.40	92.56
		SD	22.8	24.1	0.28	0.15	0.52	1.00	1.17	0.43	0.28
	1490	Mean	485.4	299.0	3.59	2.29	7.61	38.84	46.14	5.88	92.59
		SD	11.7	9.5	0.23	0.39	1.21	1.53	1.26	0.59	0.99
DS	560	Mean	507.7	242.3	4.33	4.01	9.77	41.82	38.55	8.34	90.14
		SD	8.7	7.8	0.27	0.37	0.69	0.91	1.47	0.57	1.01
	900	Mean	462.3	304.8	3.65	3.23	7.92	38.37	45.49	6.89	91.77
		SD	6.8	5.0	0.25	0.12	0.65	3.14	3.66	0.35	0.36
	1200	Mean	463.2	298.5	3.55	2.71	7.62	41.89	42.97	6.26	92.48
		SD	3.5	5.4	0.17	0.34	0.62	2.96	3.51	0.47	0.46
	1490	Mean	462.5	290.8	3.52	2.07	6.96	37.69	48.57	5.59	93.22
		SD	9.8	6.3	0.18	0.17	0.97	0.77	1.35	0.33	0.38
WS	560	Mean	419.1	247.8	4.04	3.22	8.86	37.46	45.21	7.26	91.53
		SD	27.6	19.7	0.07	0.12	0.35	0.55	0.98	0.11	0.16
	900	Mean	449.4	274.2	3.79	2.68	7.32	35.82	49.25	6.47	92.39
		SD	6.0	7.7	0.28	0.38	0.80	1.11	2.61	0.65	0.71
	1200	Mean	437.1	281.1	3.89	3.11	8.74	37.41	45.72	7.01	91.88
		SD	42.3	21.4	0.16	0.19	0.53	0.65	1.58	0.35	0.48
	1490	Mean	403.6	279.2	3.82	2.69	7.45	35.91	48.95	6.51	92.31
		SD	10.9	12.1	0.22	0.42	1.10	0.96	2.78	0.64	0.73
Two-way ANOVA (p-value)											
Altitude			0.041	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Season			<0.001	<0.001	0.32	0.011	0.25	<0.001	<0.001	0.11	0.072
Altitude × season			<0.001	<0.001	<0.001	<0.001	0.01	0.091	0.042	<0.001	<0.001
Means											
Season CS			489.3a [§]	293.7a	3.79a	2.69a	8.47a	38.37a	45.54b	6.48a	92.38a
DS			473.9a	284.1a	3.76a	3.00b	8.07a	39.94b	43.89b	6.76a	91.9b
WS			427.3b	270.6b	3.89a	2.93ab	8.09a	36.65c	47.28a	6.82a	92.02ab
Altitude 560 m			463.2a	264.3b	4.00a	3.37a	9.06a	39.95a	42.32b	7.37a	91.33c
900 m			471.0a	291.5a	3.83b	2.99b	8.17bc	37.01ab	46.88a	6.82b	92.06bc
1200 m			469.4a	285.6a	3.78b	2.78b	8.26b	38.85b	45.20a	6.56b	92.31ab
1490 m			450.5a	289.6a	3.64b	2.35c	7.34c	37.48b	47.89a	5.99c	92.71a

[†]CS, cool season; DS, dry season; WS, wet season.

[‡]SFA, saturated fatty acid; UFA, unsaturated fatty acid.

[§]Different letters denote significantly between seasons and elevations, respectively, at $p < 0.05$ level.

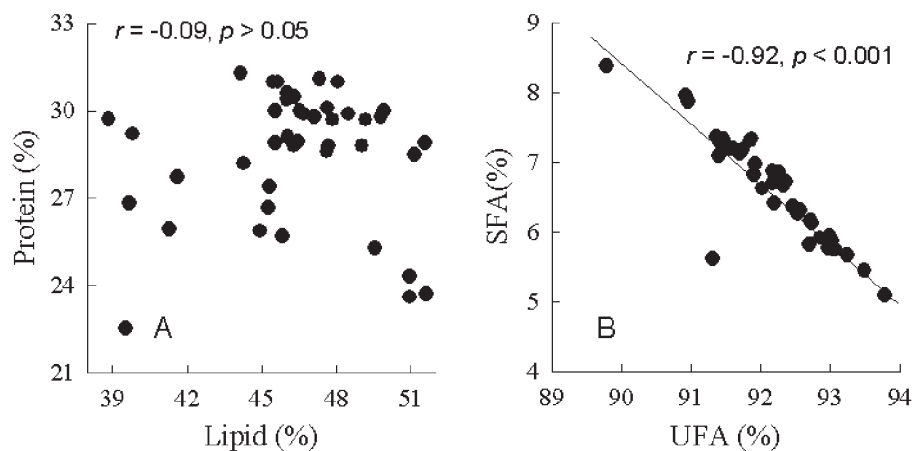


Figure 4. Relationships (A) between lipid and protein content and (B) between saturated fatty acid (SFA) and unsaturated fatty acid (UFA) concentrations.

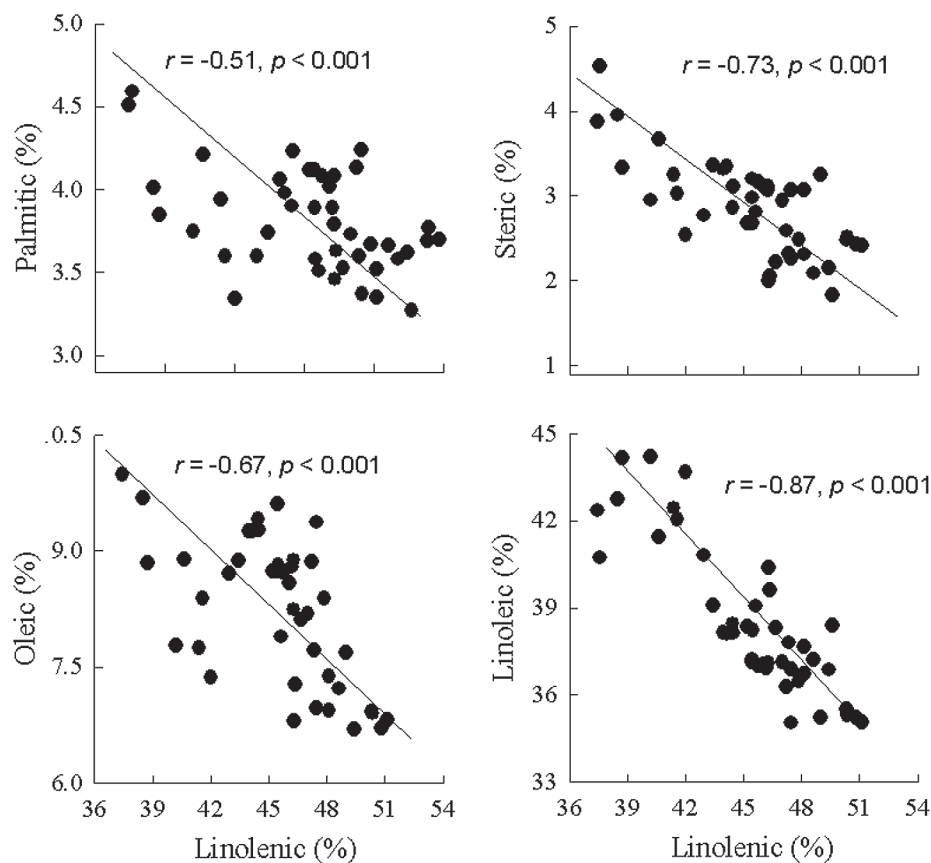


Figure 5. Relationships between linolenic and palmitic, steric, oleic, and linoleic acid concentrations.

except for linoleic (Table 1), implying that the response to altitude differed among seasons. Oil and protein content and linoleic and UFA concentrations were highest in the cool season and lowest in the wet season across altitude gradients. On the other hand, oil content showed no significant differences among the elevation gradients whereas it was significantly affected by altitude. With an increase in elevation, the seeds had, on average, higher UFA concentrations but lower oleic, linoleic, and SFA concentrations. Although the negative relationship between elevation and temperature is often mitigated by a number of other factors, air temperature generally decreased 0.56°C per 100 m (Körner, 2003). Temperature has been identified as the main factor affecting oil quality (Piper and Boote, 1999; Dierig et al., 2006). The general trend between elevation, season, and fatty acid composition and oil saturation found for sacha inchi seed most probably is related to a spatial and temporal variation in air temperature. Unsaturated fatty acid and SFA tended to significantly increase and decrease, respectively, as growing temperature decreased at high altitudes and in the cool season, which is consistent with the fact that oilseed plants produce a higher proportion of UFA for incorporation into phospholipids at colder temperatures (Thomas et al., 2003; Kumar et al., 2006; Ayerza and Coates, 2011). Cool temperatures strongly increased the level of UFA of sacha inchi seeds, as is

the case for sunflower (*Helianthus annuus* L.) and olive (*Olea europaea* L.) (Lajara et al., 1990; Issaoui et al., 2010), although the influence of the temperature on the proportion of UFA is weak in safflower (*Carthamus tinctorius* L.) (Esteban et al., 2004) and moderate in soybean and rape seed (Wolf et al., 1982; Deng and Scarth, 1998). The linolenic fatty acid concentration was negatively correlated with its precursors—palmitic, steric, oleic, and linoleic fatty acids, respectively (Fig. 5). These results are in agreement with observations made in other crops such as almond [*Prunus dulcis* (Mill.) D. A. Webb], rape seed, and chia seeds (*Salvia hispanica* L.) (Yaniv et al., 1995; Abdallah et al., 1998; Ayerza and Coates, 2011). The linolenic fatty acid concentration of sacha inchi seed is controlled by the processes of desaturation and elongation of the fatty acid complex, probably as a result of the enzymatic activity, which then appears to be regulated by temperature.

CONCLUSIONS

Elevation and season effects were pronounced on traits such as leaf photosynthesis, biomass, and seed yield and quality of sacha inchi plants. With similar values in the wet season among the elevation gradients, leaf maximum photosynthetic rate decreased with increasing elevation in the cool and dry season. Plant biomass production and fruit yield were highest at lower altitudes and

dramatically decreased above 900 m, which can primarily be attributed to a C source limitation of plant growth due to lower annual canopy assimilation. However, with an increase in elevation, the seeds had higher linolenic and UFA concentrations. Sacha inchi could be useful for cropping in cooler regions because the reproductive growth is adapted to high elevations. The trends for seed quality also changed over the season, with oil and protein content and linoleic and UFA concentrations having the highest values in the cool season. These results suggest that sachá inchi plants can grow well and had high yield at lower altitudes (<900 m), but sachá inchi seeds with high nutritious value could partially compensate for the low yield at higher altitudes (>900 m). Additional studies should be conducted to determine the environmental factors that affect plant growth and development to predict and simulate yield and oil quality interactions.

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