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Vegetative Growth Analysis of *Schoenoplectus californicus* (Totora): Dynamics and Physiological Mechanisms in High-Altitude Andean Lakes

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Abstract

Schoenoplectus californicus (Totora) is a wetland plant of cultural and ecological importance, traditionally used for handicrafts and habitat conservation in Andean lakes. This study investigates its vegetative growth in two Andean lakes in Imbabura, Ecuador (Yahuarcocha and Imbacocha), which present contrasting chemical and biological conditions (total nitrogen, total phosphorus, and chlorophyll *a*). Vegetative growth analysis, using indices, provides tools for understanding Totora growth dynamics within a cultivation cycle. By quantifying biomass accumulation and other parameters, it is possible to infer how the plant responds to its environment and to guide its production and management. Our objective was to evaluate how physiological and morphological traits influence growth under differential nutrient conditions. A 210-day field trial was conducted with periodic sampling and analysis of physiological indices, combining classical and functional growth approaches. Key growth indices—relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR)—were calculated from photosynthetic surface area and dry biomass. Results show that plants in Yahuarcocha, a hypertrophic lake, exhibited greater biomass production (up to 2380 g m^{-2}) and photosynthetic area (8.68 m^2), reaching peak growth at 150 days. In contrast, plants in Imbacocha, a eutrophic lake, reached maximum growth at 180 days, with a greater dependence on NAR. Strong correlations among RGR, NAR, and LAR were observed in Yahuarcocha, highlighting the influence of higher nutrient concentrations and harvesting pressure on growth dynamics. These findings underscore the importance of considering lake trophic status when planning sustainable harvesting and cultivation strategies for Totora in Andean wetlands.

Keywords: Andes; biomass yield; eutrophication; Lake Imbacocha; Lake Yahuarcocha; net assimilation rate; plant physiology; relative growth rate; trophic status; wetlands

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1. Introduction

Totora, scientifically known as *Schoenoplectus californicus* (C.A. Meyer) Sójak, a member of the Cyperaceae family, is a plant used since before the arrival of the Spanish in the Americas [1,2]. Due to its significant cultural and practical value, various social groups have employed it for both functional and symbolic purposes, many of which continue to the present day [3,4]. Economically, it is the most important Cyperaceae species in countries such as Argentina, Bolivia, Ecuador, Guatemala, Mexico, Peru, and the United States [5,6],

as its fibers are utilized to craft a variety of handicrafts (Figure 1) and the traditional reed boats known as caballitos de totora.



Figure 1. (**Left**): Totora grower and artisan from the parish of San Miguel de Yahuarcocha. (**Right**): Handicrafts made from woven Totora stems.

Beyond its economic and cultural significance, Totora plays crucial ecological roles. It contributes to the restoration and stabilization of altered or degraded wetlands, aids in the removal of heavy metals and nutrients in treatment systems, and provides food and shelter for wildlife, among other ecosystem services [7,8]. Despite these benefits, a key gap exists: studies integrating Totora's vegetative growth with nutrient availability in high-Andean lakes are lacking. This gap limits the development of predictive models and sustainable management strategies for this keystone species in lacustrine ecosystems.

Although Totora is biologically, economically, and culturally important, it has received less scientific attention than it deserves, particularly concerning its biology and physiology. Most research on *Schoenoplectus californicus* has been conducted in laboratories or artificial wetlands under controlled conditions [3,9], while studies in natural environments remain scarce [9,10].

The present research aims to generate scientific knowledge in Yahuarcocha and Imbacocha lakes to better understand Totora's development and provide technical guidance for the sustainable management of ecosystems, while also supporting its cultural and economic uses in local communities. Specifically, this study seeks to analyze the growth dynamics of Totora (*Schoenoplectus californicus*) in relation to nutrient availability in these lakes, with the goal of elucidating the mechanisms that regulate its productivity and its role in Andean lacustrine ecosystems.

The genus *Schoenoplectus*, particularly *Schoenoplectus californicus*, has been the subject of numerous studies across diverse ecological and cultural contexts in the Americas. Research in Peru, Mexico, and the United States has explored ethnobotanical, ecological, and applied aspects of this species and related members of the genus.

In Peru, *S. californicus* is a vital cultural and ecological resource in Huanchaco and the Altiplano (Lake Titicaca). Indigenous communities have traditionally woven its dried stems to produce handicrafts, construct boats, mats, and housing, thereby preserving traditional conservation practices [6]. The species is highly efficient in phytoremediation, capable of removing heavy metals from contaminated waters [11], and its thermal and mechanical properties—low thermal conductivity and fire resistance—make it suitable for

sustainable construction [12]. Despite this, its traditional use in the Altiplano is declining due to modernization and environmental pollution [2].

In Mexico, *S. californicus* has mainly been documented in floristic inventories and botanical collections, while detailed studies on its genetics or population dynamics remain limited [13]. Culturally, research on related aquatic species, such as *Typha domingensis* in Lake Pátzcuaro, has highlighted their significance in indigenous artisanal production, as well as conflicts arising from their dual role as both an economic resource and an invasive species [14].

In the United States, particularly in California and Texas, *S. californicus* has been studied for its resilience in wetlands and its application in ecological restoration. Mature plants exhibit higher tolerance to prolonged flooding than seedlings, and they show greater survival rates compared to *Schoenoplectus acutus* under inundation conditions [15]. Its capacity to remove nutrients, salts, and heavy metals makes it an ideal species for constructed wetlands used in wastewater treatment [15,16], emphasizing its crucial role in restoration projects [15,17]. Culturally, *S. californicus* has historically been used by Indigenous peoples for basketry, construction, and food, underlining its importance in traditional wetland management [6].

Collectively, these studies highlight the ecological significance of *S. californicus* in phytoremediation and wetland restoration, as well as its cultural value to Indigenous communities [18]. However, its vulnerability to environmental change and socioeconomic pressures underscores the need for integrated strategies to ensure its sustainable management and conservation [19].

Schoenoplectus californicus occurs throughout the Northern Hemisphere, primarily in Mexico and the United States, and is also present in parts of South America. In the United States, it has been recorded in California, Arizona, Texas, and Florida, where it forms an integral component of marsh and wetland ecosystems [20]. In Mexico, its range extends from the northern regions to the central and western states, including Baja California, Sonora, Jalisco, and Michoacán, where it inhabits high-altitude wetlands [21].

In Ecuador, Totora primarily grows in the Andean region at altitudes above 2000 m above sea level [22]. Specifically, in the province of Imbabura, located in the northern Ecuadorian Andes, this plant is found in lakes bearing Kichwa names such as Yahuarcocha and Imbacocha (Figure 2). Among these, Lake Imbacocha stands out as the oldest and most extensive Totora production area both nationally and regionally [23]. These lakes, associated with diverse socio-geographic areas, exhibit different nutrient conditions that may strongly influence plant productivity and ecological functions [24–26]. Thus, analyzing how trophic conditions affect Totora growth is critical to understanding its dynamics and ensuring sustainable management [27–29].

Totora is a hydrophilic plant that thrives in soils that remain permanently or temporarily flooded, exhibiting notable resistance to inundation [30]. It is characterized by rhizomatous growth and erect, tall, conical, and triangular aerial stems that grow in dense clusters. The leaves are reduced to sheaths at the base of the stems, and the terminal inflorescence consists of numerous spikelets [5].

The longevity of *Schoenoplectus californicus* (Cyperaceae) is influenced by several factors, including hydrological regimes, nutrient dynamics, and anthropogenic pressures [31]. This species sustains population persistence through vegetative resprouting, facilitated by extensive underground rhizome networks [32]. Under optimal conditions—characterized by stable hydrology, adequate nutrient availability, and minimal anthropogenic disturbance—its longevity is estimated to range from 5 to 10 years [19,31]. However, precise data on the longevity of *S. californicus* remain limited, as studies have primarily focused on its ecological functions and phytoremediation potential [16]. En-

vironmental variables, such as salinity gradients, flood duration, and agricultural practices, may affect its longevity [33]. Additionally, experimental evidence suggests that local communities harvest *S. californicus* approximately twice per year across various cultivation zones.



Figure 2. Lakes of Imbabura Province, Ecuador. (**a**) Lake Yahuarcocha (2192 m a.s.l.), Ibarra City, Ecuador. (**b**) Lake Imbacocha (2650 m a.s.l.), Otavalo City, Ecuador.

Vegetative growth analysis is a quantitative approach that enables the understanding of the development of a plant or plant population under both natural and controlled environmental conditions [34]. This technique has been widely employed to investigate the factors influencing plant growth and performance by monitoring the accumulation of dry matter over time [35,36]. Vegetative growth represents a fundamental biological process extensively studied across a broad range of scientific disciplines, from physiology to community dynamics [37]. There are two main approaches for conducting growth analysis. The first, known as the classical approach, involves analysis at the level of individual plants, although it has also been adapted for use with non-isolated plants. Its application has been reported in basic ecological and physiological studies and is widely used in extensive cropping systems [38]. The second approach, referred to as integrated analysis, evaluates both the production of biomass by the plant in relation to essential environmental resources and the allocation of that biomass to the production of the agronomically relevant organ [36,38]; in the case of *Schoenoplectus californicus* (totora), the organ of interest is the aerial stem.

Studies with *Schoenoplectus californicus* in constructed wetlands have applied allometric and classical growth analysis methods to assess biomass accumulation and nutrient uptake

dynamics [30,39,40]. However, there is a lack of knowledge on how these methods can be applied in natural highland lakes with differing trophic conditions.

The relevance of studying Totora growth under natural conditions lies in the fact that most physiological studies have been developed in artificial wetlands. Limited research has explored how nutrient enrichment, water quality, and anthropogenic pressures such as harvesting history affect its productivity in highland ecosystems [30,39,40]. Understanding these dynamics is particularly important in trophically contrasting lakes such as Yahuarcocha, which is nutrient-rich, and Imbacocha, with lower nutrient availability. These differences provide a natural framework to test how environmental conditions shape growth responses, biomass accumulation, and photosynthetic efficiency.

The fundamental concept in vegetative growth analysis is the relative growth rate (RGR), defined as the increase in biomass relative to the existing biomass over a given period of time. In the early stages of plant development, growth typically follows an exponential pattern, with notable differences observed among species [41,42]. RGR is influenced by both environmental and genetic factors [43,44] and helps to determine the types of habitats a species can colonize [45–47]. Furthermore, RGR can be understood as the result of the interaction between parameters that reflect the morphology and physiology of growth—factors that may be critical to a species' survival within a plant community [36,42,48–50]. Other indices, such as the leaf area ratio (LAR), which represents the ratio between leaf area and total plant mass [51], and the net assimilation rate (NAR), which reflects photosynthetic efficiency per unit leaf area [36,52,53], are also essential for explaining differences in plant performance.

Therefore, investigating the vegetative growth of Totora under natural conditions is highly valuable for researchers, farmers, and traditional cultivators, as it can help optimize natural fiber production, improve the craftsmanship process, and increase the economic returns derived from its cultivation. At the same time, it offers insights into how trophic status and human pressures shape the productivity of Andean wetland systems.

It is hypothesized that the growth dynamics of *Schoenoplectus californicus* are regulated by distinct physiological components in each lake. In Yahuarcocha, strong positive correlations among relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR) are anticipated, reflecting the integrated effects of nutrient availability and morphological traits on plant performance. Conversely, in Imbacocha, growth is expected to rely predominantly on NAR due to lower nutrient concentrations and the additional limitation imposed by chronic harvesting pressure. This differentiation in growth regulation may provide insights into the adaptive strategies of *S. californicus* under contrasting trophic and management conditions.

2. Materials and Methods

Totora is cultivated in Lakes Yahuarcocha and Imbacocha as raw material for handicraft production. Lake Imbacocha stands out as the oldest Totora cultivation area in the country and region (for over 500 years), highlighting the plant's significance in the study area [1]. Within this lake, the cultivation area selected for analysis was Araque (Imb 1). In Lake Yahuarcocha, the study area was located at the site known as the treatment plant (Yah 1). This pilot plant has been out of operation for more than a decade, as the water that was once treated is now discharged directly into the sewer system of the San Miguel de Yahuarcocha parish. Both Imb 1 and Yah 1 are located along parallel orientations to the edges of the aforementioned lakes, with the purpose of avoiding potential effects associated with hydrological factor gradients.

Experimental Area and Sampling Strategies

At each site, a 14 × 2 m area (28 m^2) was demarcated, and seven subplots of 2 × 2 m (4 m^2) were established. Each subplot was further subdivided into four 1 m^2 replicates. Data were collected at 30-day intervals, starting with the first subplot at 30 days and continuing up to 210 days (seven months after the beginning of the evaluations). The selection of a 1 m^2 area as the experimental unit, with four replicates (totaling 4 m^2) for sampling, was appropriate, as this surface concentrates a sufficient and representative amount of plant material. Working with larger areas would have complicated sample handling without improving data representativeness. Similar studies on factors limiting the growth and expansion of *totora* on Freedom Island in California, USA, were conducted using 1 m^2 plots in each study zone [26]. These replicates within each subplot were used to capture potential temporal variability, ensuring the independence of measurements (Figures 3 and 4) [54].

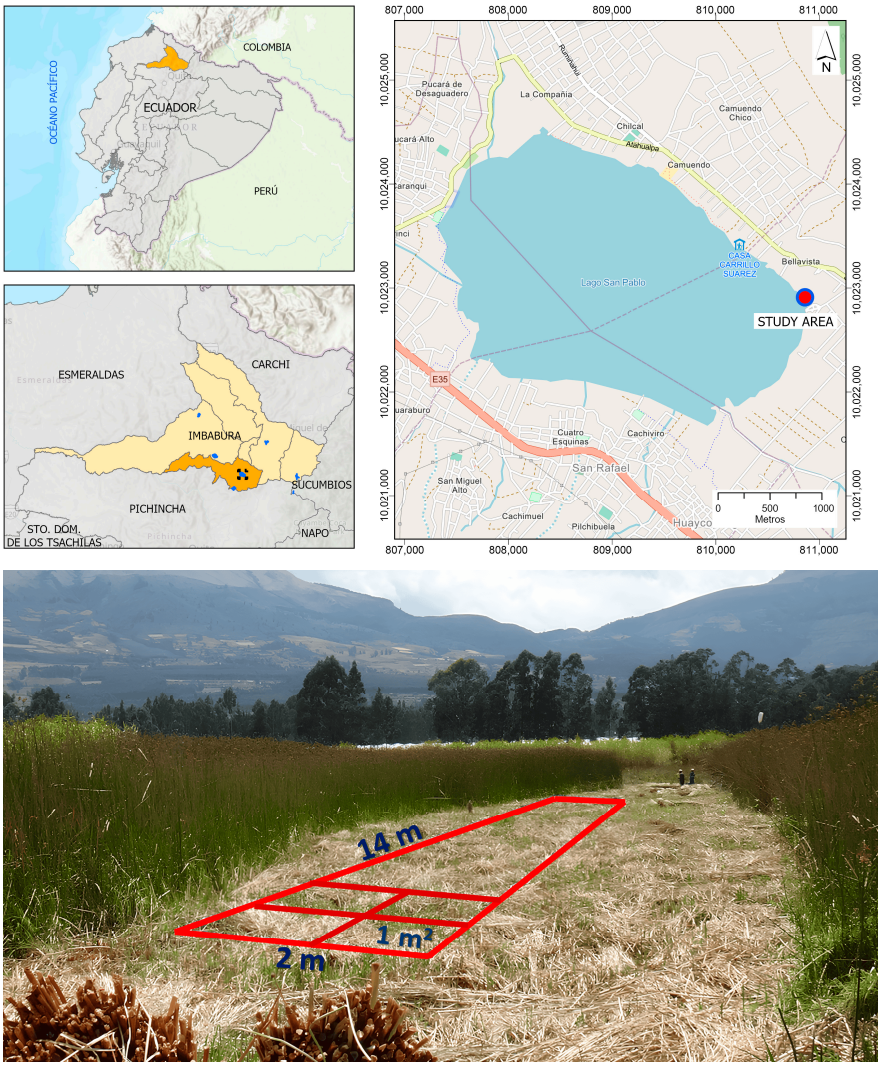


Figure 3. Geographical location of the experimental site in Lake Imbacocha (Imb 1), indicated by its UTM coordinates (x: 810,860; y: 100,229,100; zone 17 South, WGS84) (above). The lower panel shows a schematic projection of the experimental plot (14 × 2 m; 28 m^2), subdivided into seven subplots of 2 × 2 m (4 m^2) assigned to sequential harvests every 30 days. Each subplot was further divided into four quadrants of 1 × 1 m, which represented the experimental units and served as replicates (n = 4).

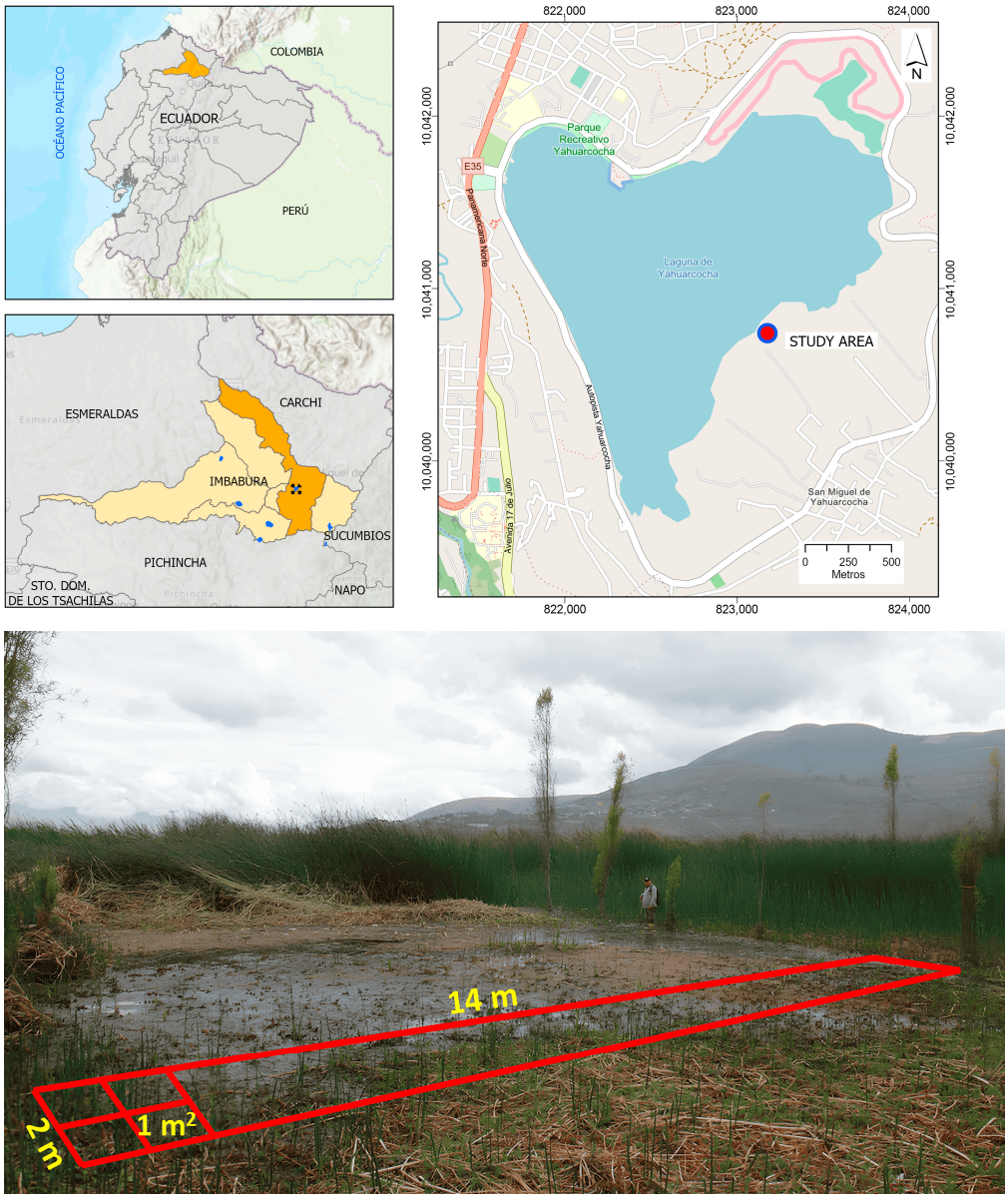


Figure 4. Geographical location of the experimental site in Lake Yahuarcocha (Yah 1), indicated by its UTM coordinates (x: 823,175; y: 10,040,741; zone 17 South, WGS84) (above). The lower panel illustrates the layout of the experimental plot (14 × 2 m; 28 m^2), subdivided into seven subplots of 2 × 2 m (4 m^2) for destructive sampling at 30-day intervals. Within each subplot, four quadrants of 1 × 1 m were established as experimental units, providing four independent replicates per sampling date.

The research was performed during the period from November 2024 to May 2025, encompassing a full growth cycle of Totora in the study sites.

The following variables were measured [4,54]:

(a) Photosynthetic stem area (defined as the total photosynthetic surface area of aerial stems in one square meter of the plant growth zone);
(b) Dry mass of the stems;
(c) Dry mass of the roots.

Photosynthetic stem area was estimated by calculating the lateral surface area of a cone, as Totora stems exhibit an elongated conical shape. Measurements of stem height and basal diameter were used to determine the lateral surface area for each stem, and values were then summed to obtain the total photosynthetic surface per replicate.

The lateral area of a cone is calculated using Equation (1).

$$A_{lateral} = \pi rl \quad (1)$$

where r is the radius of the stem base, l is the generatrix (the slant height from the base to the tip of the stem), and π is the mathematical constant (3.14159). The lateral areas of all stems within a replicate were summed to obtain the total photosynthetic surface per 1 m^2.

The quantitative interpretation of growth was based on classical and functional analysis approaches [55], for this purpose, periodic measurements (every 30 days) were carried out on all plants that grew within 1 m^2 and its replicates (totaling 4 m^2). The following indices were calculated (Table 1): Relative Growth Rate (RGR), Absolute Growth Rate (AGR), Net Assimilation Rate (NAR), Leaf Area Ratio (LAR), Leaf Weight Ratio (LWR), Specific Leaf Area (SLA), Leaf Area Index (LAI), Harvest Index (HI), and Crop Yield (R) [36,56–58]. For indices related to leaf structure (LAR, LWR, SLA, LAI), data were collected from aerial stems as the primary photosynthetic structure, since true leaves are inconspicuous.

Table 1. Growth indices used in the present study, with their symbols, calculation formulas, and units of expression. Adapted from [35].

Growth Index	Symbol	Average Value over a Time Interval (t_2–t_1)	Units
Relative Growth Rate	RGR	$RGR = \frac{(lnW_2 - lnW_1)}{(t_2 - t_1)}$	g g^{-1} day^{-1}
Absolute Growth Rate	AGR	$AGR = \frac{(W_2 - W_1)}{(t_2 - t_1)}$	g day^{-1}
Net Assimilation Rate	NAR	$NAR = \frac{(W_2 - W_1)}{(t_2 - t_1)} \frac{(lnA_2 - lnA_1)}{(A_2 - A_1)}$	g m^{-2} day^{-1}
Leaf Weight Ratio	LWR	$LWR = \frac{W_h}{W_t}$	g g^{-1}
Leaf Area Index	LAI	$LAI = \frac{A}{S}$	Dimensionless
Harvest Index	HI	$\mathrm{HI} = \frac{HB}{TB}$	Dimensionless $\times$ 100 = %
Crop Yield	R	$R = Total\ biomass \times HI$	g m^{-2}

Symbols: W = weight; t = time; A = leaf area; S = soil surface; HB = Harvestable Biomass; TB = Total Biomass.

The growth indices calculated for the two cultivation areas of Yahuarcocha and Imbacocha were:

- Relative Growth Rate (RGR): Increase in plant material per unit of existing plant material per unit of time [57].
- Absolute Growth Rate (AGR): Increase in dry mass of plant material per unit of time [36].
- Net Assimilation Rate (NAR): Estimates the plant's photosynthetic capacity; represents the rate of increase in plant mass per unit of leaf area [58].
- Leaf Area Ratio (LAR): Ratio of leaf area to total plant mass [56].
- Leaf Area Index (LAI): Instantaneous measurement that relates the assimilable leaf area (A) per unit of soil Surface (S) [36].
- Harvest Index (HI): Ratio between the yield of the harvestable organ and the plant biomass [36].
- Crop Yield (R): Product of biomass and the harvest index (HI) [36].

For the indices referring to leaf structure (Leaf Area Ratio, Leaf Weight Ratio, Specific Leaf Area, and Leaf Area Index), data were collected from the aerial stem as the structure responsible for photosynthesis (since true leaves are not conspicuous). The acronyms used to identify each index correspond to their English abbreviations. Definitions of the

growth indices were taken from Villar et al. (2008) [42] and Di Benedetto and Tognetti (2016) [38]. Calculations were performed following the methodology proposed by Hunt et al. (2002) [36]. Table 1 presents the calculation formulas and the units in which the results are expressed.

The relationships between Relative Growth Rate (RGR), Net Assimilation Rate (NAR), and Leaf Area Ratio (LAR) were analyzed through linear regression, using the Coefficient of Determination (R^2) to assess the strength of the fit [59–61], as it more accurately reflects the explanatory capacity of the model under field conditions. It is also important to note that field data, unlike laboratory experiments (or studies conducted under controlled conditions), may exhibit high variability inherent to their nature, which could magnify errors and lead to misinterpretations of model performance. The data obtained did not meet the assumptions of normality and homogeneity of variance; therefore, parametric statistical tests such as ANOVA were not applied. Instead, the use of vegetative growth analysis as an alternative quantitative method allowed for the interpretation of growth dynamics and the comparison of patterns between Yahuarcocha and Imbacocha lakes without requiring these assumptions. All data analyses and graph generation were conducted using Microsoft Excel 2024 (subscription version with continuous updates: Microsoft 365).

3. Results

The geographic area where Imbacocha and Yahuarcocha lakes, selected for this study, are located does not experience seasonality due to its equatorial location. It records relatively constant mean annual temperatures, ranging from 14.1 °C to 15.8 °C. Precipitation shows fluctuations: maximum between March and May (>75 mm/month), minimum in July and August (<30 mm/month), with transitional periods from October to February. The historical mean annual precipitation in Yahuarcocha and Imbacocha lakes is 676.8 mm. Yahuarcocha and Imbacocha have been classified as eutrophic lakes [24]. However, the high nutrient levels (particularly total phosphorus and total nitrogen), along with elevated chemical oxygen demand (COD) and biological oxygen demand (BOD_5) values in Yahuarcocha compared to Imbacocha, classify Yahuarcocha as a hypertrophic lake, while Imbacocha remains in the eutrophic category according to the Trophic State Index (TSI) of Carlson and Simpson, proposed in 1996 (author's unpublished data). Contamination parameters and primary productivity in the studied lakes, consistent with those reported by [54], are presented in Table 2.

Table 2. Contamination parameters and primary productivity in the studied lakes. No relevant differences were detected between the rainy and dry seasons for the same lake; therefore, each value represents the average of measurements taken during the rainy season (19 April 2024) and the dry season (23 August 2024).

Lake	Chemical Oxygen Demand (COD) (mg L^{-1})	Biological Oxygen Demand (BOD_5) (mg L^{-1})	Total Phosphorus (TP) (µg L^{-1})	Total Nitrogen (TN) (µg L^{-1})	Chlorophyll *a* (µg L^{-1})
Yahuarcocha	103	16	272	4125	71.1
Imbacocha	24	7	149	1558	23.4

This study on vegetative growth analysis was conducted in Lakes Yahuarcocha and Imbacocha, where Totora is cultivated and commercially exploited. The averaged values of the traits—photosynthetic area (stems present in 1 m^2), stem dry mass, and total plant dry mass—corresponding to Yahuarcocha (Yah 1) and Imbacocha (Imb 1) are presented in Table 3. Total plant dry mass includes stems, roots, and rhizomes, while photosynthetic area values reflect the cumulative lateral surface area of all aerial stems within 1 m^2,

accounting for the conical shape of the stems. To clarify, total plant dry mass encompasses the combined biomass of aerial stems, roots, and rhizomes, which explains the higher values (e.g., 4390 g m^{-2} in Yahuarcocha) compared to stem dry mass alone (e.g., 2380 g m^{-2}). Similarly, the photosynthetic area (e.g., 8.68 m^2 in Yahuarcocha) represents the total lateral surface area of all conical stems within a 1 m^2 plot, not the ground area occupied, which may result in values exceeding 1 m^2 due to the cumulative surface of multiple stems.

Table 3. Values of the main traits used for the vegetative growth analysis of Totora from Yahuarcocha (Yah 1) and Imbacocha (Imb 1), recorded at 30-day intervals. Means ± standard deviations (n = 4) are shown.

***Schoenoplectus californicus* in Lakes Yahuarcocha and Imbacocha**						
Days	**Photosynthetic Area PA (m^2)**		**Stem Dry Mass (g m^{-2})**		**Total Plant Dry Mass (g m^{-2})**	
	Yah 1	**Imb 1**	**Yah 1**	**Imb 1**	**Yah 1**	**Imb 1**
30	1.01 ± 0.51	0.60 ± 0.15	280 ± 88	110 ± 47	508 ± 19	223 ± 18
60	2.75 ± 0.59	1.33 ± 0.28	682 ± 121	214 ± 63	1283 ± 55	448 ± 29
90	6.37 ± 0.70	2.18 ± 0.42	1575 ± 206	397 ± 115	3005 ± 23	837 ± 59
120	8.38 ± 0.83	4.11 ± 0.45	2228 ± 188	745 ± 148	4222 ± 54	1537 ± 62
150	8.68 ± 0.85	5.37 ± 0.66	2380 ± 116	977 ± 103	4390 ± 253	2038 ± 123
180	8.32 ± 0.70	5.77 ± 0.77	2240 ± 100	1050 ± 99	4253 ± 81	2068 ± 177
210	7.44 ± 0.52	5.47 ± 0.62	2234 ± 108	1026 ± 69	4168 ± 86	2061 ± 165

Note: "Total dry mass" refers to the accumulated dry biomass of the stem per plant (g), and "photosynthetic area" refers to the total surface area of photosynthetically active tissue (cm^2).

In general, Totora plants from Lake Yahuarcocha showed higher growth values than those from Imbacocha. Yahuarcocha plants reached maximum photosynthetic surface area (8.68 m^2), stem dry mass (2380 g m^{-2}), and total plant dry mass (4390 g m^{-2}) at 150 days, marking the peak of vegetative growth. In contrast, Imbacocha plants peaked at 180 days (photosynthetic area = 5.77 m^2; stem dry mass = 1050 g m^{-2}; total plant dry mass = 2068 g m^{-2}), indicating a 30-day growth delay. Total plant dry mass includes the biomass of stems, roots, and rhizomes, which explains the higher values compared to stem dry mass alone. Similarly, the photosynthetic area corresponds to the cumulative lateral surface of all aerial stems within a 1 m^2 plot, considering their conical shape. This metric reflects the total photosynthetic surface available rather than the ground area occupied. The growth dynamics of photosynthetic area and stem dry mass are illustrated in Figure 5. Vertical bars represent standard deviations (n = 4) to indicate variability across replicates. The Yahuarcocha plants exhibited an exponential growth phase up to 90 days, followed by linear growth between 90 and 120 days, deceleration from 120 to 150 days, and the onset of senescence at 150 days. Imbacocha plants showed similar phases, but delayed by ~30 days, with the senescence phase beginning at 180 days.

In the Imbacocha plants, all growth phases were delayed by approximately 30 days. Consequently, the exponential growth phase extended up to 120 days, with the maximum expansion of the photosynthetic area occurring between days 90 and 120. The senescence phase began at 180 days—one month later than in the Yahuarcocha plants. The maximum stem photosynthetic area for the Yahuarcocha plants was 8.68 m^2 at 150 days, whereas the Imbacocha plants reached only 5.77 m^2 at 180 days.

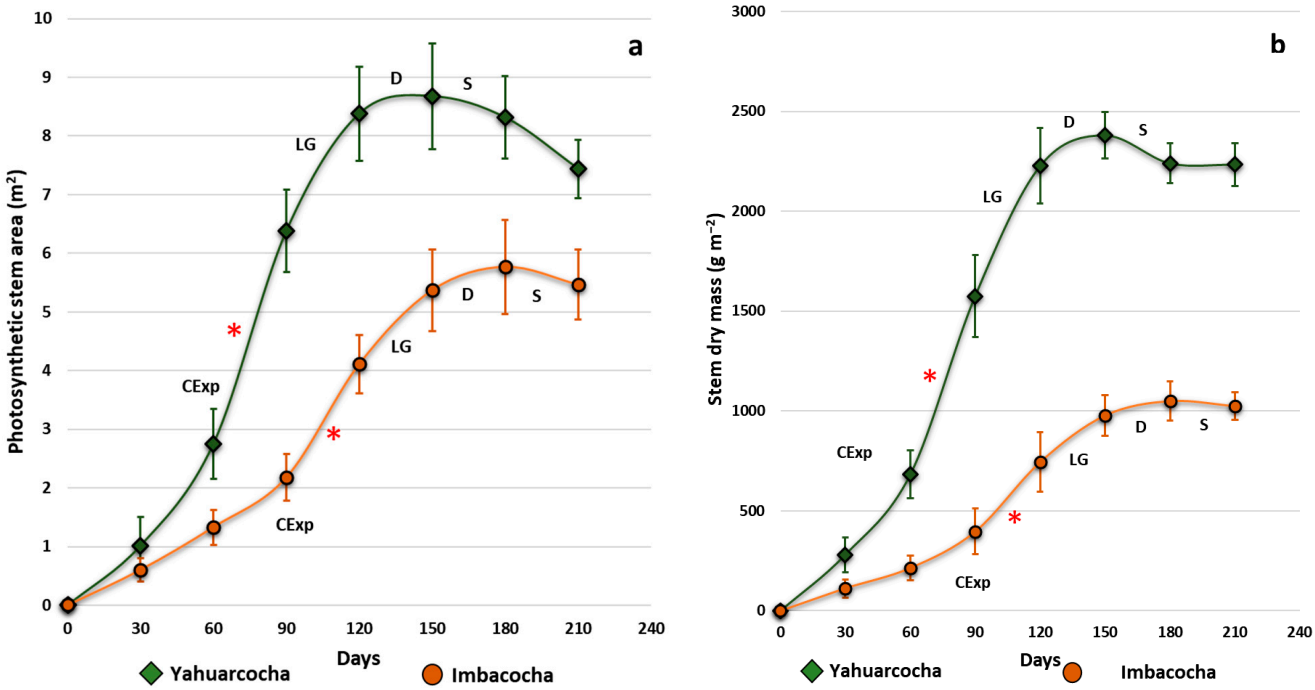


Figure 5. Vegetative growth curves of Totora (*Schoenoplectus californicus*) over a 210-day period: (**a**) photosynthetic stem area; (**b**) stem dry mass. Vertical bars represent standard deviations (n = 4). CExp = exponential growth; LG = linear growth; D = deceleration; S = senescence. * indicates interval of greatest growth. Temporal changes in stem dry biomass and photosynthetic area of *S. californicus* in Yahuarcocha and Imbacocha over 210 days. Four phenological phases were identified: exponential growth, linear growth, deceleration, and senescence. In Yahuarcocha, favorable nutrient conditions accelerated the initial phases, leading to maximum biomass earlier than in Imbacocha, indicating an optimal harvest point around day 150.

A similar pattern was observed in the analysis of stem dry mass (Figure 5b). As with the photosynthetic area, plants grown in Imbacocha exhibited a 30-day growth delay compared to those from Yahuarcocha. The highest dry mass for Yahuarcocha plants (2380 g m^{-2}) occurred at 150 days, while the Imbacocha plants reached their maximum dry mass (1050 g m^{-2}) at 180 days.

Relative Growth Rate (RGR) and Absolute Growth Rate (AGR) exhibited distinct patterns between lakes (Figure 6). RGR peaked for Yahuarcocha plants between 60 and 90 days (0.029 g g^{-1} day^{-1}) and for Imbacocha between 60 and 120 days (0.021–0.023 g g^{-1} day^{-1}). AGR reached its maximum in Yahuarcocha at 120 days (35.2 g day^{-1}), whereas Imbacocha plants peaked at 150 days (13.6 g day^{-1}). Error bars in Figure 6a,b reflect data variability across four spatial replicates.

Regarding the dynamics of the Absolute Growth Rate (AGR), as shown in Figure 6b, distinct values were observed between the two lakes throughout plant development. The highest AGR was recorded in the Yahuarcocha cultivation at 120 days (35.2 g day^{-1}), whereas the Imbacocha plants reached their peak AGR at 150 days (13.6 g day^{-1}), a value less than half that observed in Yahuarcocha.

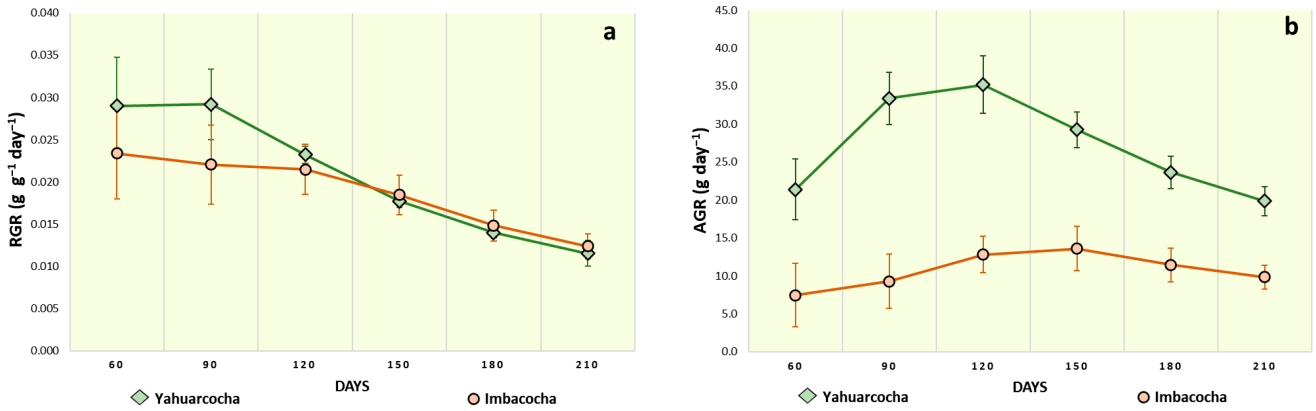


Figure 6. (**a**) Relative Growth Rate (RGR) of *Totora* (*Schoenoplectus californicus*) cultivated in the lakes of Yahuarcocha and Imbacocha, measured at regular 30-day intervals. (**b**) Absolute Growth Rate (AGR) under the same conditions. Vertical bars represent standard deviation (n = 4). Data were collected from March to September 2018. Absolute Growth Rate (AGR) and Relative Growth Rate (RGR) during the growth cycle. Peaks and declines correspond to phenological transitions. In Yahuarcocha, AGR and RGR increased rapidly and then dropped during deceleration and senescence; in Imbacocha, nutrient limitation delayed these transitions. The decline in AGR marks the most efficient harvest window.

Through the calculation of various indices associated with the vegetative growth analysis of Totora, several relationships were established that are relevant for understanding the physiological performance of this species in the high Andean lakes of northern Ecuador. The Relative Growth Rate (RGR), for instance, is influenced by two main factors: (1) the physiological component of the photosynthetic organ, known as the Net Assimilation Rate (NAR), and (2) the morphological component, referred to as the Leaf Area Ratio (LAR).

Therefore, identifying the contribution and degree of correlation between these indices (NAR and LAR) is essential for interpreting the species-specific growth dynamics under these environmental conditions. The correlation analysis (Figure 7a) between NAR and RGR for Yahuarcocha plants revealed a strong positive linear relationship (R^2 = 0.9875). Similarly, the relationship between LAR and RGR (Figure 7b) exhibited a positive linear correlation (R^2 = 0.8469). These results indicate that, in Yahuarcocha, both morphological (LAR) and physiological (NAR) aspects of the photosynthetic apparatus contribute to the relative growth rate of *Schoenoplectus californicus*.

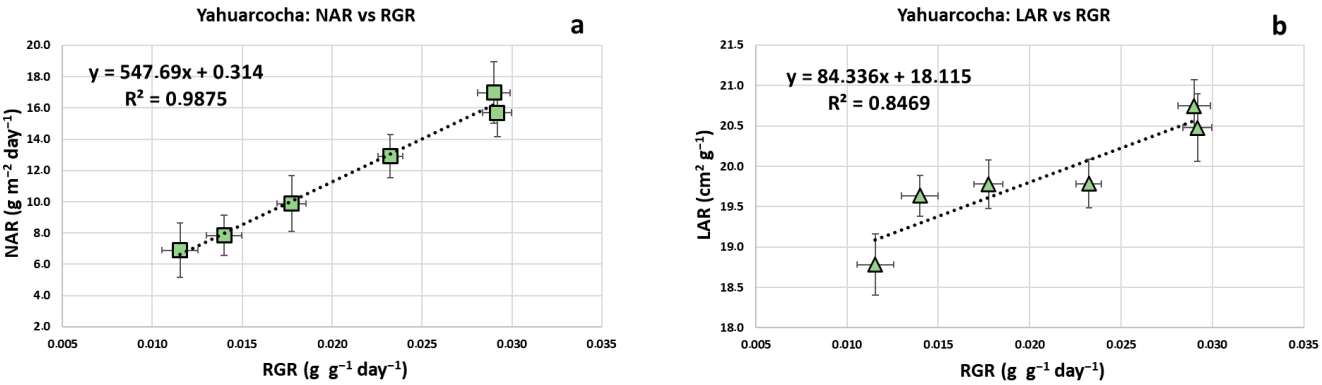


Figure 7. Degree of correlation between growth variables for *Totora* (*Schoenoplectus californicus*) cultivated in Lake Yahuarcocha. (**a**) Net Assimilation Rate (NAR) versus Relative Growth Rate (RGR). (**b**) Leaf Area Ratio (LAR) versus Relative Growth Rate (RGR). The linear regression equations (y) are shown alongside the corresponding coefficients of determination (R^2).

For the Totora plants (*Schoenoplectus californicus*) from Imbacocha, the results revealed a highly positive linear correlation between Net Assimilation Rate (NAR) and Relative Growth Rate (RGR), with a coefficient of determination of $R^2 = 0.9841$. In contrast, the relationship between Leaf Area Ratio (LAR) and RGR was very weak ($R^2 = 0.1038$), as shown in Figure 8. Alternative regression models—such as exponential, logarithmic, polynomial, and power functions—also yielded low correlations, all with determination coefficients below 10%.

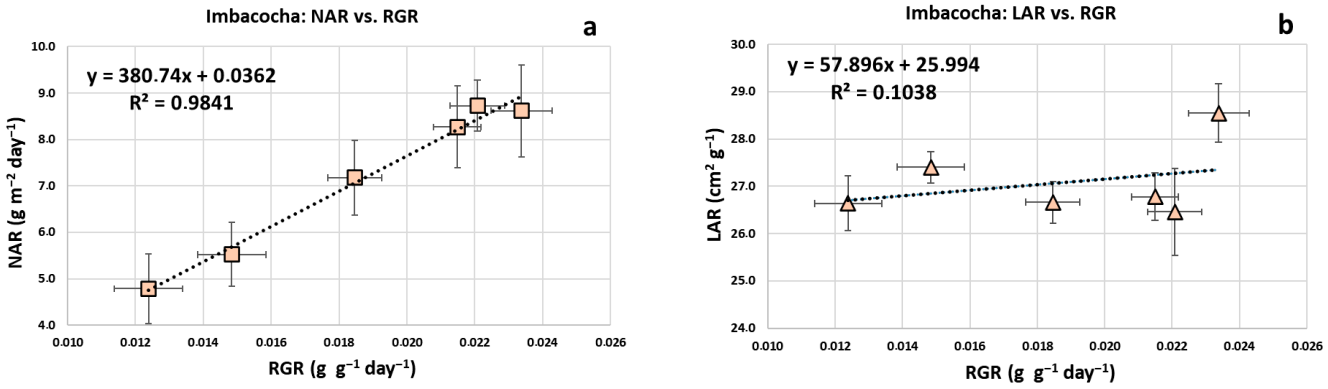


Figure 8. Degree of correlation between growth variables for *Totora* (*Schoenoplectus californicus*) cultivated in Lake Imbacocha. (**a**) Net Assimilation Rate (NAR) versus Relative Growth Rate (RGR). (**b**) Leaf Area Ratio (LAR) versus Relative Growth Rate (RGR). The linear regression equations (y) are shown along with the corresponding coefficients of determination (R^2).

Correlation analyses between growth indices revealed distinct contributions of physiological and morphological components to the vegetative growth of Totora (*Schoenoplectus californicus*) in Lakes Yahuarcocha and Imbacocha. In Yahuarcocha, the Net Assimilation Rate (NAR) showed a strong positive linear correlation with the Relative Growth Rate (RGR) ($R^2 = 0.9875$; Figure 7a), and the Leaf Area Ratio (LAR) also exhibited a positive correlation with RGR ($R^2 = 0.8469$; Figure 7b). These strong correlations suggest that both photosynthetic efficiency (NAR) and morphological adaptation of the photosynthetic surface (LAR) drive relative growth in Yahuarcocha. In contrast, for Imbacocha, NAR correlated strongly with RGR ($R^2 = 0.9841$; Figure 8a), whereas LAR had a minimal contribution to RGR ($R^2 = 0.1038$; Figure 8b). The weak LAR-RGR correlation in Imbacocha indicates that growth is primarily driven by photosynthetic efficiency rather than morphological changes in the photosynthetic apparatus. Alternative regression models—such as exponential, logarithmic, polynomial, and power functions—also yielded low correlations for LAR-RGR in Imbacocha, all with determination coefficients below 10%. These findings highlight that, in Imbacocha, the physiological efficiency of the photosynthetic apparatus (NAR) is the dominant factor influencing growth, while morphological adaptations (LAR) play a limited role.

These findings suggest that the growth dynamics of Totora in Lake Imbacocha are primarily driven by the physiological efficiency of the photosynthetic apparatus (i.e., NAR), rather than by morphological adaptations of the photosynthetic organ (i.e., LAR).

As previously mentioned, the Relative Growth Rate (RGR) is determined by the dynamic behavior of both the Net Assimilation Rate (NAR) and the Leaf Area Ratio (LAR), as RGR is mathematically defined as the product of these two indices. Therefore, in addition to examining their correlation with RGR, it was pertinent to analyze the absolute values of NAR and LAR throughout the cultivation cycle. As shown in Figure 9a, both NAR and LAR values for *Totora* (*Schoenoplectus californicus*) plants grown in Yahuarcocha exhibited a proportional decline over the course of the experiment.

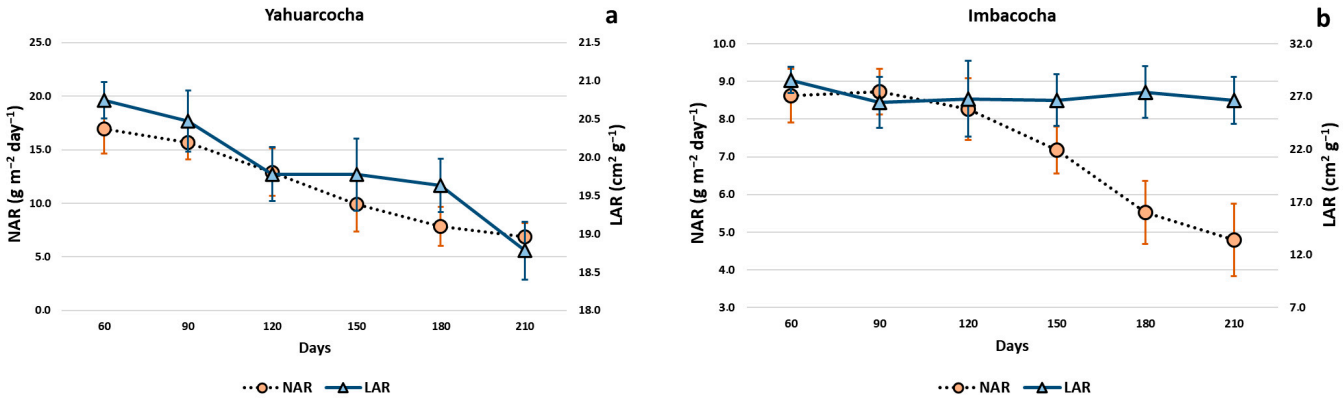


Figure 9. Comparative values of Net Assimilation Rate (NAR) and Leaf Area Ratio (LAR) over a 210-day cultivation period for *Totora* (*Schoenoplectus californicus*) populations from two lakes: (**a**) Yahuarcocha; (**b**) Imbacocha. Temporal dynamics of Net Assimilation Rate (NAR) and Leaf Area Ratio (LAR). Both parameters decreased toward the end of the cycle, reflecting the shift to reproduction and senescence. Higher initial values in Yahuarcocha indicate vigorous photosynthesis, whereas in Imbacocha, growth relied more on NAR under nutrient-limited conditions.

However, in the case of Totora (*Schoenoplectus californicus*) plants grown in Imbacocha, the behavior of NAR and LAR differed. As shown in Figure 9b, the Net Assimilation Rate (NAR) reached its peak at 90 days (8.7 g g^{-1} day^{-1}), after which its values declined steadily through day 210. In contrast, the Leaf Area Ratio (LAR) remained nearly constant throughout the duration of the experiment. As previously discussed, this variable showed limited contribution to the overall growth performance of Totora in Lake Imbacocha.

Regarding the Harvest Index (HI)—defined as the average proportion between the yield of the harvested organ (aerial stems) and the total plant biomass [25]—the two cultivation environments exhibited very similar absolute values. HI ranged from 52.7% to 54.4% in Yahuarcocha, and from 47.6% to 51.0% in Imbacocha. In both cases, the proportion of harvested biomass (stems) relative to total plant biomass was similar (Figure 10).

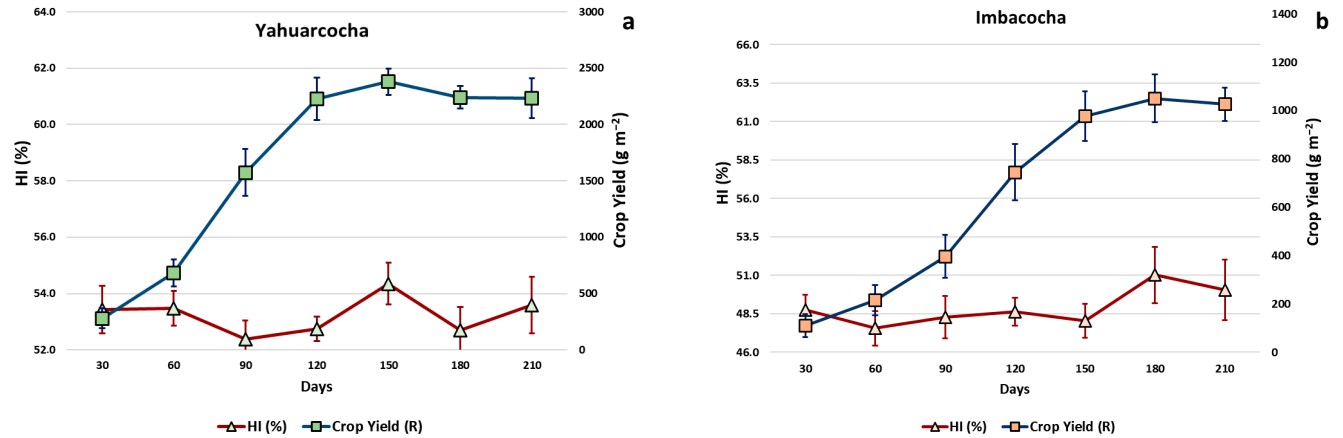


Figure 10. Variation in Harvest Index (HI) and Crop Yield (R) for *Totora* (*Schoenoplectus californicus*) plants cultivated in: (**a**) Lake Yahuarcocha; (**b**) Lake Imbacocha.

Finally, the Crop Yield (R)—calculated as the product of Total Biomass and Harvest Index (HI)—fit the expected sigmoid growth curve in both environments. This pattern was consistent for Totora cultivated in Yahuarcocha and Imbacocha (Figure 10). However, in quantitative terms, the plants from Yahuarcocha displayed higher peak crop yield values (2380 g m^{-2} at 150 days), compared to the maximum yield registered in Imbacocha (1050 g m^{-2} at 180 days).

4. Discussion

The results of total nitrogen and phosphorus concentrations reveal clear differences between Yahuarcocha and Imbacocha lakes, which may directly influence the growth of totora (*Schoenoplectus californicus*). Likewise, nitrogen and phosphorus are key factors that directly regulate photosynthesis. These elements are also fundamental in defining the trophic status of lacustrine systems. The N:P ratio is critical for determining which nutrient limits growth, as studies on *Schoenoplectus* spp. have shown that in environments where phosphorus falls below critical thresholds, growth is constrained by this element even when nitrogen is abundant [62]. This suggests that nutrient monitoring in the studied lakes should primarily focus on phosphorus, provided that nitrogen concentrations are known to be high.

As shown in Table 2, Yahuarcocha Lake records the highest concentrations of total phosphorus (TP = 272 μg L^{-1}) and total nitrogen (TN = 4125 μg L^{-1}), suggesting an environment highly favorable for primary productivity; these conditions support vigorous growth of totora, with greater density and biomass. In the case of Imbacocha, phosphorus levels are high, but reach only about 80% of those measured in Yahuarcocha, while nitrogen is lower, reaching just 50% of the nitrogen recorded in Yahuarcocha [63]. This indicates a nutrient supply that is sufficient, but not optimal, likely resulting in moderate development of totora, with lower density and coverage compared to Yahuarcocha. Additionally, the elevated TP and TN levels in Yahuarcocha indicate greater nutrient availability, enhancing both phytoplankton productivity (Chl *a* = 71.1 μg L^{-1}) and the direct and indirect nutrient supply for emergent macrophytes such as totora.

Regarding the analysis of vegetative growth in totora (*Schoenoplectus californicus*), the study revealed marked differences between populations from Yahuarcocha and Imbacocha lakes, with plants from Yahuarcocha exhibiting superior growth metrics, including a 51% greater stem dry mass and a 28% larger photosynthetic area at the end of the 210-day evaluation period (Figure 5). These findings support the hypothesis that nutrient availability, driven by the hypertrophic status of Yahuarcocha compared to the eutrophic conditions of Imbacocha, enhances growth performance [39]. Mechanistically, nutrient enrichment in Yahuarcocha—particularly the high levels of nitrogen and phosphorus—likely increases photosynthetic efficiency by enhancing RuBisCO activity and CO_2 fixation capacity, thereby directly boosting the net assimilation rate (NAR) [38]. This elevated NAR, together with strong correlations between the relative growth rate (RGR) (R^2 = 0.9875; Figure 7a) and the leaf area ratio (LAR) (R^2 = 0.8469; Figure 7b), suggests that growth in Yahuarcocha is supported by both physiological components (high photosynthetic rates) and morphological traits (expanded photosynthetic area relative to biomass) [47]. In addition, evidence indicates a strong correlation between total phosphorus and chlorophyll *a* in shallow lakes, such as Yahuarcocha with a maximum depth of 7 m [63], where increases in TP rapidly translate into higher algal biomass (Chl *a*), with the consequent intensification of internal nutrient recycling (release from phytoplankton and sediments). This reinforces a high and sustained trophic state. Such dynamics foster a "feedback loop" that maintains elevated P and N availability in the water column, benefiting plant production in zones where macrophytes can access these resources (through the rhizosphere and even foliar uptake) [64]. As a result, totora plants have developed physiological and morphological adaptations that enable them to capitalize on these significant nutritional advantages provided by their immediate habitat.

In Yahuarcocha, the combination of high nutrient availability and strong physiological responses (high NAR and RGR) promotes rapid biomass accumulation and sustained photosynthetic activity, which in turn accelerates internal nutrient cycling through feedbacks between phytoplankton, sediments, and macrophytes. The decomposition of senescent

Totora tissues likely contributes to nutrient regeneration in the rhizosphere, enhancing the retention and transformation of nitrogen and phosphorus within the wetland matrix. This process reinforces the role of *Schoenoplectus californicus* as a key species in nutrient sequestration and recycling, consistent with patterns observed in other nutrient-rich shallow lakes [63,64]. Moreover, the rapid growth and morphological expansion (high LAR) observed in Yahuarcocha enable Totora to dominate littoral zones, displacing other macrophytes and shaping the structure of plant communities. Such competitive traits are typical of early- to mid-successional stages in eutrophic wetlands, where fast-growing emergent species drive vegetation dynamics and ecosystem functioning [47]. In contrast, the physiological patterns observed in Imbacocha—characterized by nutrient limitation, reduced LAR contribution, and strong dependence on NAR—suggest a more conservative growth strategy, which may slow successional trajectories and maintain more heterogeneous vegetative mosaics under chronic harvesting pressure. Collectively, these findings highlight how nutrient enrichment and physiological performance interact to regulate both nutrient cycling and plant community succession in Andean lacustrine wetlands.

In contrast, Imbacocha Lake, with a maximum depth of 30 m [63], considerably greater than Yahuarcocha, may face limitations in sustaining a nutrient feedback cycle, resulting in low P and N availability in the water column. This, combined with chronic harvesting pressure, is reflected in a weak LAR–RGR association (R^2 = 0.1038; Figure 8) and a predominant reliance on NAR (R^2 = 0.9841) for growth, due to reduced biomass allocation to photosynthetic tissues [39]. Specifically, chronic harvesting pressure in Imbacocha likely alters allocation patterns, diverting resources away from stem photosynthetic production and increasing sensitivity in LAR, thereby reducing the proportion of photosynthetically active tissue relative to total biomass. This differential response highlights how nutrient enrichment enhances NAR through physiological mechanisms, whereas harvesting pressure restricts morphological adaptations, limiting the contribution of LAR to growth. Similar patterns have been documented in other emergent aquatic plants, such as *Typha angustifolia* and *Phragmites australis*, which exhibit greater biomass accumulation under nutrient-rich conditions [22,65]. Taken together, these results underscore the combined influence of nutrient status, physiological allocation, and anthropogenic pressure on the growth dynamics of totora.

At the conclusion of the 210-day evaluation, totora (*Schoenoplectus californicus*) plants from Yahuarcocha exhibited a 51% greater stem dry biomass and a 28% larger photosynthetic surface area compared to those from Imbacocha (Figure 5a,b). In Yahuarcocha, growth dynamics were driven by strong correlations among relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR), with NAR showing a robust relationship with RGR (R^2 = 0.9875; Figure 7a) and LAR also contributing importantly (R^2 = 0.8469; Figure 7b). This advantage, reflecting greater nutrient availability—particularly nitrogen and phosphorus—may enhance RuBisCO activity and CO_2 fixation capacity, thereby improving photosynthetic efficiency [38]. In contrast, plants from Imbacocha exhibited weak LAR–RGR associations (R^2 = 0.1038; Figure 8), while NAR correlated strongly with RGR (R^2 = 0.9841), indicating that growth is constrained primarily by nutrient limitation and further exacerbated by chronic harvesting pressure [16,66–68]. The anatomical similarity of photosynthetic stems in both populations suggests that physiological factors, rather than morphological traits, account for the observed differences [69,70].

For an accurate interpretation, it is also necessary to consider the contribution of heterotrophic nitrogen fixation in roots and rhizomes (13.8–32.5% of total nitrogen content) [71], together with the role of phytoplankton communities in recycling and releasing nutrients from sediments in shallow lakes such as Yahuarcocha. This likely translates into improved physiological efficiency in such environments and further reinforces the ecological and

management implications of these findings. Nevertheless, the relationship between phytoplankton (Chl *a*) and macrophytes is complex and depends on the balance between nutrient supply and physical limitations (light/penetration). In Yahuarcocha, the high Chl *a* values (71.1 μg L^{-1}) indicate an intense phytoplankton bloom that increases turbidity and reduces water column transparency, which for submerged macrophytes usually results in direct light limitation. However, for emergent macrophytes (totora), this light limitation does not constrain growth, since their photosynthetic apparatus (aerial stems) is located above the water surface. The adaptive success of totora, despite high phytoplankton concentrations that may compete for dissolved nutrients at the water–plant interface, may be explained by its capacity for phosphorus storage and uptake from sediments [72]. Moreover, totora can exploit sediment-bound phosphorus through the rhizosphere, although its efficiency is modulated by dissolved TP concentrations [73].

The phenotypic differences observed between totora (*Schoenoplectus californicus*) populations in Imbacocha and Yahuarcocha, particularly the reduced biomass yield in Imbacocha (Figure 5), support the hypothesis that growth in Imbacocha relies more heavily on net assimilation rate (NAR) due to chronic harvesting pressure. Centuries of continuous extraction in Imbacocha have imposed persistent disturbances that alter biomass allocation, reduce the production of new photosynthetic stems, and increase the sensitivity of the leaf area ratio (LAR) [16,68]. These observations are consistent with patterns documented in other harvested wetland species, where frequent cutting reduces tillering and photosynthetic capacity, ultimately lowering biomass yield [66–68,74,75]. In contrast, the mid-20th-century introduction of totora cultivation in Yahuarcocha, together with lower harvesting intensity, supports strong correlations among relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR), enabling plants to sustain vigorous growth under favorable nutrient conditions. These findings underscore the crucial role of long-term anthropogenic pressures in shaping totora growth dynamics and confirm that reduced harvesting pressure in Yahuarcocha enhances both physiological and morphological contributions to growth.

Totora (*Schoenoplectus californicus*) in Imbacocha and Yahuarcocha lakes exhibited sigmoidal growth curves with distinct phases of exponential growth, linear increase, deceleration, and senescence (Figure 5) [76]. Plants from Imbacocha showed an approximate 30-day delay in all growth phases compared to those from Yahuarcocha, both in photosynthetic area and stem dry mass, likely reflecting lower nutrient availability [77], consistent with observations in other species such as *Capsicum annuum*, where greater nutrient supply enhances leaf area [78,79]. The exponential phase, driven by the activation of lateral buds and tillering, improved photosynthetic capacity and concluded with flowering at 90 and 120 days for Yahuarcocha and Imbacocha, respectively [66,80]. Notably, the conical arrangement of totora photosynthetic stems—a morphological adaptation that minimizes self-shading—appears to maintain efficient light capture and competitive dominance along the shores of both lakes. These findings indicate that while local environmental conditions modulate growth rates, intrinsic structural traits enable robust growth, highlighting the interplay between environmental constraints and adaptive strategies in the growth dynamics of totora.

Flowering involves the redistribution of substances produced during photosynthesis toward these newly formed structures, thereby reducing the availability of photosynthates for biomass accumulation. In *Oryza sativa*, for example, the pre-flowering and post-flowering stages are critical for total dry matter production and are key determinants of seed yield [81,82]. Furthermore, plants growing in open environments often experience a reduction in their photosynthetically active area as leaves overlap, leading to decreased light interception due to self-shading [48,83], which ultimately lowers overall photosynthetic

activity. However, the conical arrangement of the photosynthetic apparatus represents an evolutionary adaptation that minimizes self-shading [84], particularly in comparison with broad-leaved species. Consequently, the dominance of totora populations over associated shoreline vegetation in the studied lakes can be attributed to this specific form of structural adaptation.

In totora cultivation in Yahuarcocha and Imbacocha lakes, stems are harvested every six months. However, data from the present study indicate that maximum biomass accumulation in Yahuarcocha's totora stands is reached at five months (Figure 5) [85]. Thus, by the sixth month, the crop has entered a senescent phase, resulting in reduced biomass levels and a loss of harvestable material due to this temporal mismatch. This pattern is not observed in Imbacocha's totora cultivation, where the cropping cycle coincides with the peak of biomass accumulation (six months). Such synchrony highlights the long ancestral relationship between cultivators and totora in Imbacocha and also suggests the potential to transfer this knowledge to farmers in Yahuarcocha, encouraging them to adjust their practices and increase harvested yields [86]. The hypothesis that selecting a specific timing or period is more efficient for harvesting *Schoenoplectus californicus* (totora) in Lake Yahuarcocha can only be assessed and confirmed through longitudinal studies encompassing several years of observation, in order to account for interannual variability in the species' growth dynamics.

Describing the growth of a plant or crop requires objective indicators that can be validated. In this regard, the Relative Growth Rate (RGR) is a key parameter for such analyses. The RGR pattern indicates that totora plants in Yahuarcocha exhibit higher values, at least during the first 90 days of cultivation (Figure 6a). A rapid growth rate can confer ecological and competitive advantages by enabling plants to reach larger sizes in shorter periods, thereby improving their capacity to capture resources such as light, water, and nutrients [42,87]. These advantages depend on accelerated production of photosynthetic tissues and allow, plants to escape early vulnerable stages, where small size increases susceptibility to herbivory. This phenomenon is part of the trade-off between resource allocation for growth and defense [88,89]. Totora plants in Yahuarcocha may have developed mechanisms promoting rapid growth during early and more sensitive developmental stages, where competition is a critical factor for survival [90,91].

After the initial stages critical for totora survival, RGR values in both populations converge, with well-adapted stands forming dense, monospecific herbaceous layers. The gradual decline in RGR observed after 90 days (Figure 6a) can be attributed to biomass redistribution toward newly formed organs, such as reproductive structures. In rice plants, for example, up to 90% of the total dry matter accumulated in the grains originates from post-flowering redistribution processes, while the remaining 10% comes from remobilization of dry matter previously stored in leaves and stems before flowering [81,92].

The Absolute Growth Rate (AGR), which represents the amount of dry mass accumulated by plants per unit of time, revealed that totora plants in Yahuarcocha Lake are more efficient in dry matter accumulation—approximately 150% higher—than those in Imbacocha Lake. Several factors may explain this difference: (a) extrinsic or environmental factors that constrain growth, particularly nutrient availability, which differs between the two lakes [39,93]; (b) intrinsic factors, including morphological and physiological traits that interact to varying degrees and influence vegetative growth [94]; and (c) synergistic effects, in which totora plants exhibit high growth rates due to competitive advantages over coexisting species within the same ecological niche, especially under the favorable nutrient conditions observed in Yahuarcocha [39,94].

The relationship between competitive strategies and vegetative growth among species has been well documented [94,95]. Under conditions similar to those observed in Yahuar-

cocha (YAH 1), totora can exhibit greater growth (higher density, higher annual productivity) due to increased availability of N and P and higher primary production, which sustains a continuous flow of recycled organic matter and nutrients. In Imbacocha, intermediate TN and TP values and lower Chl *a* (23.4 μg L^{-1}) indicate reduced primary production and diminished internal recycling, resulting in relative nutrient limitation for totora that decreases its biomass and coverage [39]. Therefore, the observed pattern—more vigorous totora in Yahuarcocha and less developed stands in Imbacocha—is consistent with the combination of high TP/TN and high Chl *a* in Yahuarcocha versus intermediate nutrient values and lower Chl *a* in Imbacocha.

The onset of the growth deceleration phase (Figure 5), which occurs at 120 days in totora plants in Yahuarcocha and at 150 days in Imbacocha, appears to be driven by a reduction in AGR values (Figure 6). This decline is likely due to the increase in non-photosynthetic tissue and mutual shading among photosynthetic stems.

The differences observed in RGR and AGR values between the two totora cultivation sites initially suggest variation in physiological activity. For example, the faster-growing plants in Yahuarcocha may exhibit higher photosynthetic rates, lower respiration rates, or a combination of both. An alternative explanation could lie in morphological differences, such as a greater proportion of biomass allocated to stems or a higher specific photosynthetic area in faster-growing plants. To evaluate these hypotheses, Relative Growth Rate (RGR) was partitioned into two components: the physiological component, Net Assimilation Rate (NAR), and the morphological component, Leaf Area Ratio (LAR). It is important to note that RGR is the product of LAR and NAR [96]. Furthermore, variation in RGR among herbaceous species is predominantly explained by LAR, while NAR plays a secondary role or interacts depending on irradiance and species traits [47,48]. Meta-analyses consistently show that specific leaf area (SLA) and leaf mass ratio (LMR) strongly contribute to LAR and, consequently, to RGR differences [97].

The strong positive relationships between the physiological growth component, NAR, and RGR (R^2 = 0.9875), as well as between the morphological component, LAR, and RGR (R^2 = 0.8469), indicate that both components contribute substantially and comparably to totora growth in Yahuarcocha Lake (Figure 7). In other words, these plants are characterized by high photosynthetic rates (NAR) and a relatively large photosynthetic area in proportion to total plant biomass (LAR).

The strong positive relationships between the physiological growth component, NAR, and RGR (R^2 = 0.9875), as well as between the morphological component, LAR, and RGR (R^2 = 0.8469), indicate that both components contribute substantially and similarly to totora growth in Yahuarcocha Lake (Figure 7). In other words, these are plants characterized by high photosynthetic rates (NAR) and a relatively large photosynthetic area in proportion to total plant biomass (LAR) [47]. Previous studies have shown that such traits are common in fast-growing species, where growth is driven by high net assimilation and an expansive deployment of leaf area [97,98]. This strategy is especially advantageous in nutrient-rich environments such as Yahuarcocha, where competitive dominance among aquatic macrophytes is linked to efficient resource acquisition [99].

In the case of totora cultivation in Imbacocha Lake, the relationship between NAR and RGR is strongly positive (R^2 = 0.9841), whereas the linear relationship between LAR and RGR is very weak (R^2 = 0.1038). This suggests that totora growth in Imbacocha is explained almost entirely by the physiological component (NAR). In other words, the RGR of plants in this lake is primarily determined by the performance of the photosynthetic apparatus, regardless of their structure or biomass, over a given period (Figure 8).

High contributions of NAR to species growth also imply a differential distribution of biomass among plant organs, as well as chemically distinct processes involved in leaf area

development [34]. For example, a high foliar nitrogen content is likely to increase RuBisCO concentration, thereby enhancing the contribution of NAR [38,100]. Similar findings in forest trees indicate that variation in NAR is the main determinant of RGR in light-rich environments and is strongly associated with foliar nitrogen content and photosynthetic rate [58].

In Yahuarcocha cultivation, NAR and LAR values gradually decreased from the start of the experiment to the final evaluation at 210 days (Figure 9a). The decline in NAR values is likely associated with the redistribution of resources toward other metabolic activities related to flowering and fruiting, and, to a lesser extent, with shading effects. On the other hand, the decrease in LAR (Figure 9b) can be attributed to a gradual reduction in the ratio between photosynthetic area and total plant biomass, resulting in a corresponding decrease in photosynthetic activity [44,101].

In totora plants from Imbacocha Lake, as in the previous case, NAR values gradually decrease as a result of the redistribution of resources toward other metabolic activities. However, LAR remains relatively constant (Figure 9b). A possible explanation for this phenomenon is a compensatory strategy, in which the mass of photosynthetically active organs is reduced relative to the plant's active photosynthetic area. This could be achieved through increased production of aerenchymatous parenchyma tissue in the stems, a process mediated by ethylene [102–104].

Totora crops in Yahuarcocha and Imbacocha lakes exhibit very similar Harvest Index (HI) values, which could be attributed to the fact that both populations belong to the same species. Furthermore, it can be speculated that the Harvest Index is a crop characteristic that did not respond to the differing nutrient conditions of the lakes (trophic state) or to other environmental factors, suggesting that it may be considered a highly stable attribute [105–107].

Finally, Yield (Y) exhibits the typical sigmoidal curve of vegetative growth, as expected, for totora crops in Yahuarcocha and Imbacocha lakes. However, in absolute terms, yield in Yahuarcocha was 227% higher than that of the Imbacocha crop. This difference is largely explained by the greater nutrient availability in Yahuarcocha, a lake classified as hypereutrophic, compared to the eutrophic conditions of Imbacocha [108,109]. Moreover, totora plants from these two lakes have undergone adaptation processes to the specific biological, ecological, and cultural conditions of their environments, reflecting distinct physiological growth mechanisms and dynamics [110,111].

The physiological patterns observed in *Schoenoplectus californicus* across contrasting Andean wetlands provide valuable insights for the sustainable harvesting of macrophytes. In Imbacocha, where nutrient limitation and conservative growth strategies prevail, moderate harvesting may be tolerated without severely affecting plant community structure or nutrient regeneration. In contrast, in wetlands such as Yahuarcocha, rapid growth rates and high morphological plasticity suggest that intensive harvesting could substantially alter vegetation dynamics and internal nutrient cycling. These findings are consistent with previous studies emphasizing the need to adjust harvest intensity and frequency according to the regenerative capacity of the species and the fertility of the local ecosystem [112–114]. For instance, research in constructed wetlands in China has shown that annual harvesting of *Phragmites australis*—a species with a similar ecological role—enhances nutrient removal by preventing sediment accumulation, although seasonal management is required to avoid adverse effects on plant growth during winter, highlighting parallels with nutrient-poor Andean systems [115]. Similarly, in eutrophic European wetlands, harvesting emergent macrophytes such as *Typha* spp. and *Schoenoplectus* spp. has demonstrated a balance between reducing methane emissions and nutrient extraction. Autumn harvests have been recommended to maximize phosphorus and nitrogen removal without compromising

regeneration, a strategy that could be adapted to Yahuarcocha to mitigate risks in highly productive ecosystems [112,116]. Furthermore, studies on floating treatment wetlands designed for urban runoff management indicate that seasonal harvesting of emergent macrophytes optimizes the removal of dissolved contaminants [22], providing a useful parallel for Andean wetland management, where physiological performance must be integrated with local hydrological dynamics. Together, these comparative findings underscore the need for adaptive management strategies that combine adaptive governance, nutrient control, and buffer zone restoration to address socio-ecological risks in lacustrine ecosystem services [22,114]. Integrating plant physiological performance with nutrient status and community succession provides a mechanistic foundation for developing sustainable harvesting strategies in Andean lacustrine wetlands.

Although the results obtained allow for the inference of physiological mechanisms and growth dynamics of totora throughout its cultivation cycle in Imbacocha and Yahuarcocha lakes, based on differential nutrient availability and contrasting trophic conditions, some aspects require further validation to consolidate the conclusions and enhance the applicability of the findings at local and regional scales. In this context, the following limitations are highlighted:

This study was conducted during a single growing season; therefore, periodic monitoring of totora (*Schoenoplectus californicus*) growth dynamics is recommended to detect potential interannual variations. Additionally, this research focused on two lakes of particular importance due to their proximity to populated areas. Future studies should include natural totora populations from other lacustrine systems to capture a broader range of trophic states and pressures affecting populations in diverse ecological settings.

To further explore these findings, research should investigate lakes at different altitudes and latitudes, including those with diverse trophic characteristics. Experimental manipulations under controlled (laboratory) conditions could provide mechanistic insights into the interactions between environmental factors, potentially contributing to the optimization of cultivation practices. For example, it would be valuable to assess whether reducing anthropogenic pressure and harvest intensity in Imbacocha enhances biomass production. Additionally, comparative studies with other emergent aquatic plants, such as *Typha* or *Phragmites*, could clarify whether the observed growth patterns are species-specific or broadly applicable to other Andean wetland macrophytes.

It would also be appropriate to complement these findings with analyses of nitrogen and phosphorus in their assimilable forms, both in the water column and in *Schoenoplectus californicus* (totora) tissues, which would allow for the determination of whether nutrient limitation is primarily due to phosphorus, nitrogen, or both. Furthermore, the role of microbial nitrogen fixation under different nutrient regimes could further elucidate physiological adaptations, providing practical implications for the sustainable management of *Schoenoplectus californicus* and wetland conservation.

Finally, in the present study, it was not possible to calculate the statistical significance of the observed correlations due to inherent limitations in the design and the specific conditions of fieldwork, which restrict the applicability of certain formal analyses in natural settings. Nevertheless, this situation is a common feature of field research and does not invalidate the descriptive patterns identified. It is recommended that future studies, ideally with larger and longer data series, incorporate hypothesis testing or confidence intervals to complement and strengthen the interpretation of the observed relationships.

5. Conclusions

Differences in nitrogen and phosphorus concentrations between Yahuarcocha and Imbacocha generate clear contrasts in primary productivity and Totora development. The high nutrient availability in Yahuarcocha supports greater biomass, macrophyte density, and internal nutrient recycling, whereas intermediate nutrient levels in Imbacocha constrain growth. Chlorophyll *a* serves as a key trophic indicator, reflecting phytoplankton biomass and nutrient availability in the water column, thereby indirectly contributing to Totora's vegetative performance.

The superior growth of Totora in Yahuarcocha—showing 51% higher dry biomass and 28% greater photosynthetic area compared to Imbacocha—is explained by the synergy of physiological and morphological factors. Elevated nitrogen and phosphorus availability enhances photosynthetic efficiency through increased RuBisCO activity and CO_2 fixation, while expansion of the relative leaf area (LAR) maximizes light capture, resulting in sustained growth in a favorable hypertrophic environment.

In Imbacocha, Totora growth relies almost exclusively on net assimilation rate (NAR) due to lower nutrient availability, greater lake depth, and harvesting pressure. The contribution of LAR is minimal, indicating a compensatory strategy in which plants maintain photosynthetic activity through resource redistribution and the adjustment of photosynthetically active tissues. This pattern contrasts with Yahuarcocha, where the combined action of NAR and LAR maximizes vegetative yield.

The growth dynamics of Totora reflect the integration of trophic factors, environmental conditions, and anthropogenic pressures. In Yahuarcocha, high water fertility and reduced human intervention sustain robust growth, while in Imbacocha, nutritional constraints and intensive management limit biomass accumulation. Nevertheless, morphological adaptations of the species—such as the conical arrangement of stems—maintain efficient light interception, showing that final performance depends both on resource availability and on the plant's physiological and structural strategies.

The findings of this study highlight the importance of understanding how nutrient availability, environmental conditions, and anthropogenic pressures interact to regulate the growth and productivity of Totora in Andean lake systems. Moreover, the results carry significant economic and cultural implications, supporting sustainable harvesting practices, biodiversity conservation, and the maintenance of ecosystem services such as nutrient regulation and aquatic habitat protection.

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