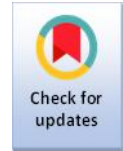


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Transpiration rate is the key trait for selecting species for better water use efficiency: A case study on four agroforestry tree species



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Abstract

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Water stress has been the prime concern for plant survival and productivity. In this context a physiological trait, water use efficiency has been the center of focus over the past decade. Selecting species for better water use efficiency without compromising on productivity have been shown to be effective in coping with water stress without losing productivity. Therefore, a pot experiment was conducted on four agroforestry tree species (*Ziziphus mauritiana*, *Bombax ceiba*, *Moringa oleifera* and *Morus alba*) where growth, biomass production and water use efficiency was measured under controlled and water stress. The results showed that growth traits like plant height, stem diameter, biomass production, leaves, stem and roots decreased in all the species under water stress. However, the highest decrease was evidenced in the species showing high growth rate (*Morus alba* and *Moringa oleifera*), and lowest was recorded in slow growing species (*Ziziphus mauritiana* and *Bombax ceiba*). Water use efficiency was found the highest in slow growing species as compared to fast growing species. A large decrease in transpiration rate and stomatal conductance was evidenced in fast growing tree species (*Morus alba* and *Moringa oleifera*) as compared to slow growing species (*Ziziphus mauritiana* and *Bombax ceiba*). However, CO₂ assimilation rate although varied across the species but remained insignificant across the control and water stress treatment. Therefore, it can be concluded that *Ziziphus mauritiana* is better adapted to water stress and this adaptivity is controlled by transpiration rate rather CO₂ assimilation rate.

1 Introduction

Water scarcity has become one of the most pressing limitations to agricultural productivity, ecological sustainability and landscape resilience across much of the global tropics and subtropics. Increasing climatic variability, erratic rainfall patterns, rising evapotranspiration rates and prolonged droughts have intensified the challenges faced by both natural and man-made ecosystems (Mehta, 2024). Agroforestry systems, which integrate trees with crops and livestock, are considered among the most promising land-use strategies for improving microclimates, increasing biodiversity, enhancing soil fertility, and stabilizing agricultural production under water-limited conditions (Cao et

al., 2022; Sun et al., 2023). However, the success of agroforestry under such conditions relies fundamentally on selecting tree species that possess traits enabling them to tolerate drought, regulate water loss, and maintain physiological performance especially in water scarce conditions. Among these traits, transpiration rate is a direct indicator of stomatal behavior and water loss per unit leaf area has emerged as a crucial parameter for evaluating deficiency of water in species and their adaptability and overall water use efficiency (Usama et al., 2025; Lamani et al., 2022). Transpiration, which accounts for over 95% of total water loss in plants, represents a central physiological process linking photosynthesis, water transport, and thermal regulation (Wu et al., 2022). The rate of transpiration is regulated primarily by stomatal aperture, leaf anatomy, vapor pressure deficit, and root water uptake capacity, and therefore reflects the balance between carbon gain and water loss. Species that maintain low transpiration rates under drought generally conserve soil moisture more effectively and exhibit higher intrinsic water-use efficiency, enabling them to survive and function during extended dry periods (Mehta, 2024). Conversely, species with high transpiration rates tend to deplete soil moisture more rapidly, experience faster declines in leaf water potential, and become vulnerable to hydraulic failure, especially under severe or persistent drought (Islam et al., 2023). Because stomatal behavior under water stress is strongly species-specific and often genetically controlled, transpiration rate provides a reliable physiological metric for identifying drought-tolerant tree species suitable for agroforestry in water-limited landscapes (Stratopoulos et al., 2019). the concept of water-use efficiency commonly defined as the ratio of carbon gained (via CO₂ assimilation) to water lost (via transpiration) is closely tied to the regulation of transpiration. High-WUE species typically employ conservative water-use strategies, characterized by rapid stomatal closure during drought, high leaf turgor maintenance, and investment in root growth or stem biomass to sustain hydraulic safety margins (Zafar et al., 2023; Mehta, 2024). In agroforestry settings, the inclusion of high-WUE and low-transpiration species is particularly beneficial because such species reduce competition with crops for soil moisture, enhance overall system productivity, and improve microclimatic moderation (Sharma and Kumar, 2023). By contrast, species with high transpiration rates may intensify water competition, exacerbate drought stress on both them and associated crops, and ultimately reduce the stability and sustainability of the system. Hence, effective agroforestry design in water-scarce regions must be guided by a clear understanding of species-specific transpiration behavior and its relationship to water-use efficiency.

Several studies have highlighted the importance of transpiration rate as a trait for screening drought-tolerant species suitable for reforestation, silvopastoral systems, and agroforestry. For instance, Duursma et al., (2019) demonstrated that species with inherently low stomatal conductance exhibit better survival and growth under chronic water limitation. Similarly, Alneyadi, (2024) found that xerophytic species such as *Ziziphus* and *Prosopis* maintain reduced transpiration through tight stomatal regulation and osmotic adjustment, enabling them to thrive under arid conditions. These findings suggest that transpiration rate functions not only as an indicator of short-term physiological response but also as a predictor of long-term ecological fitness in dryland environments. Despite this, many agroforestry projects continue to rely on traditional species selection criteria such as growth rate, economic value, timber quality, or nitrogen-fixing ability without adequately considering physiological traits that determine drought survival and ecosystem water balance. As a result, there is an urgent need for research that identifies physiological markers, such as transpiration rate, which can reliably predict species performance and suitability for agroforestry in

water-limited landscapes. The present study is grounded in this context and aims to establish transpiration rate as a key functional trait for selecting tree species with superior water-use efficiency. The underlying premise is that species with inherently low transpiration rates, especially under water-deficit conditions, conserve water more effectively and display greater drought tolerance, making them ideal candidates for agroforestry in drought-prone regions. This idea is supported by several theoretical frameworks in plant physiology and ecology. One such framework is the drought avoidance vs. drought tolerance model (Lamani et al., 2022), which posits that plants survive drought either by minimizing water loss (avoidance) or by maintaining physiological function at low water potentials (tolerance). Another framework is the hydraulic limitation hypothesis, which states that species capable of reducing transpiration maintain higher hydraulic safety margins, decreasing the risk of xylem cavitation and wilting. These frameworks collectively highlight the central role of transpiration in mediating plant water status, hydraulic function, and drought resilience.

Given increasing global water scarcity, the identification of low transpiration rate, high water use efficient species is essential for the long-term sustainability of agroforestry systems. Such species reduce water competition with crops, enhance system sustainability and improve resilience to climate change. The current study therefore seeks to build on existing eco-physiological knowledge by evaluating species commonly used in agroforestry (*Ziziphus mauritiana*, *Bombax ceiba*, *Moeringa oleifera* and *Morus alba*) through the lens of transpiration rate and water use efficiency. Study aims to identify species that balance growth with conservative water use, thus offering the best prospects for agroforestry under drought stress.

2 Materials and Methods

2.1 Field survey and collection of genotypes:

Genetic material was collected through field surveys in the following zones of Punjab in the months of April to July 2022.

- Rainfed (Rawalpindi)
- Rice-wheat (Mandi bahauddin)
- Mixed crop (Faisalabad)
- Cotton-wheat (Bahawalpur)

Each zone was visited and genetic material was collected for each species.

- 1) For *Ziziphus mauritiana* (Berl), open-pollinated, mature, and healthy (disease free) mother trees were selected on visual basis, and 100-200 seeds were collected per tree in April-May 2022. Since the seed were enclosed in the fruit, mechanical scarification was done to remove the fruit carp before sowing.
- 2) For *Bombax cieba* (Simbal), seeds and suckers were collected in the months of April-May 2022. Since the Simbal seeds are lint wrapped, therefore seed cotton was removed before sowing. Stumps were also collected from different sources like i) from local nurseries and ii) roadside young trees.
- 3) For *Moringa oleifera* (Moringa), pods were collected in the month of May-June 2022 from mature and healthy trees. Seed were collected from the pods manually before sowing. Along with seed, stumps of Moringa were also collected from local nurseries.

- 4) For *Morus alba* (Mulberry), shoot cuttings were taken from various sources i) from the field, ii) along the road, and iii) from the private nurseries.

The planting material of all four tree species was tagged properly corresponding to their location of collection (zone). All the planting material was brought back to forestry nursery where dedicated nursery beds 4'x15' were prepared. 15x7" plastic bags were filled with peat and sand mixture 1:1 ratio and seeds, suckers and shoot cuttings of respected tree species were planted in months April to June 2022. One bed was allocated for each collection site (zone) therefore, 4 beds per species were prepared with each bed having almost 624 plants per species (Figure I).



Figure I: Nursery beds of *Ziziphus mauritiana* (Ber), *Bombax cieba* (Simbal), *Moringa oleifera* (Moringa) and *Morus alba* (Mulberry). Each species has 4 beds corresponding to 4 collection zones. Each bed has 6 rows of 26 plants/row, thus aprox. 624 plants per species.

2.2 Experimental stepup and stress application:

Ziziphus mauritiana (Ber), *Bombax cieba* (Simbal), *Moringa oleifera* (Moringa) and *Morus alba* (Mulberry) were tested for phenotypic plasticity for productivity traits and transpiration efficiency. A comparative trail was set at Forestry nursery, University of Agriculture Faisalabad under natural daylight. Individuals of each species were planted in pots and were randomly assigned to either of the two treatments i) under the well-watered treatment (WW; field capacity) and ii) under the water stress treatment (WS, 60% of the field capacity). Microclimate including temperature (T°C) and relative humidity (RH%) was measured all along the experiment using Logtag (Haxo-8, Log Tag Recorders, Auckland, New Zealand).

2.3 Measurement of growth and physiological traits

Growth parameters were recorded twice a week during the experiment. Chlorophyll contents were measured on fully mature leaf of each individual using SPAD meter. Water use efficiency was measured using portable photosynthesis system (C3050, China) at the end of the experiment (after two months of stress application). Fully mature and well-lit leaf was selected from each species and leaf gas exchange was measured under ambient light, temperature, and CO₂ concentration. Net assimilation of CO₂ (A) and stomatal conductance (gs) and transpiration rate (E) were estimated on each individual. Plants were excised into four components; stems, branches, leaves,

and roots and were stored in paper bags. Plant samples were dried at 60°C to constant weight in a heat oven. Total biomass production and allocation to each plant compartment were calculated.

2.4 Statistical analysis

Data was subjected to two-way ANOVA for species, treatment and interaction effect. Mean are presented with their standard error. All the data in the experiment was analyzed using STATISTICA, Version 12.1, France.

3. Results

3.1 Meteorological conditions of research area

Air temperature varied between 36°C to 38°C during the experiment. Relative humidity varied between 63 to 76% during the experiment. Concentration of CO₂ in the atmosphere remained between 288 to 345 umol/ mol. The increase in CO₂ during the experiment was because of the air exhaled by the PI and daily paid labor during the measurement. Light intensity was also measured during the experiment that remained between 780 to 1280 umol/m²/s.

3.2 Interspecific differences in plant growth and biomass production

Species and treatment effect was found significant (Table 1). Water stress had a negative effect on plant height that was reduced significantly ($p < 0.001$). Decrease in plant height under water stress was found maximum in *Morus alba* followed by *Bombax cieba*, *Moringa oleifera* and recorded minimum in *Ziziphus mauritiana* (Figure 5). The findings confirm that *Ziziphus mauritiana* is more tolerant to water stress and *Morus alba* is least tolerant to water stress. Only species effect was found significant (Table 1). Water stress had not any negative effect on stem diameter which remained nonsignificant for all the species especially under water stress ($P = 0.671$). However, the highest diameter was recorded in *Ziziphus mauritiana* followed by *Bombax cieba*, *Moringa oleifera* and *Morus alba* (Figure 6). These results reveal that *Ziziphus mauritiana* invests more biomass in stem section compared to other tree species under the given water stress treatments.

Table 1: Means of morphological and physiological traits measured during the experiment. Data was analyzed using two-way ANOVA for species, treatment and interaction effect.

Species	Treatment	Plant height (cm)	Stem diameter (mm)	Stem BM (g)	Leaves BM (g)	Root BM (g)	SPAD
<i>Morus alba</i>	Control	85.1 (0.12)	7.49	31.6	16.7	28.7	49.8
	WS	70.4 (0.15)	7.72	14	9.77	12.8	43.7
<i>Moringa oleifera</i>	Control	70.7 (0.17)	8.23	20.2	6.13	24.9	48.6
	WS	59.1 (1.12)	8.82	11.5	5.45	14.2	40.9
<i>Bombax cieba</i>	Control	80.4 (1.06)	8.7	12.2	10.5	12.2	51.9
	WS	66	9.1	9.73	11.5	10.6	47.4
<i>Ziziphus mauritiana</i>	Control	64.7	8.9	15.1	8.01	17.3	34
	WS	58.1	9.14	15.3	9.09	15.5	31.2
	S- effect	0.001	0.001	0.001	0.001	0.001	0.001
	T-effect	0.001	0.129	0.001	0.007	0.001	0.001
	SxT- effect	0.192	0.939	0.001	0.001	0.001	0.067

Leaf, stem and root dry weight decreased significantly between the species under water stress ($p < 0.001$). Decrease in stem leaf and root dry weight was found maximum in *Morus alba*, followed by *Moringa oleifera*, *Bombax cieba*, and *Ziziphus mauritiana* (Figure 7). In contrast, leaf dry weight remained nonsignificant for all the species. Results revealed that *Ziziphus mauritiana* is more tolerant and *Morus alba* is least tolerant to water stress. Total dry weight also decreased significantly in all the species. Decrease in total dry weight under water stress was maximum in *Morus alba* followed by *Moringa oleifera*, *Bombax cieba*, and *Ziziphus mauritiana* (Figure 10).

3.3 Interspecific differences in physiological parameters.

Various physiological parameters were recorded and found significant among all the species ($p < 0.001$). SPAD (chlorophyll values) decreased significantly under water deficit conditions. Maximum decline in SPAD values was found in *Moringa oleifera*. Other species like *Morus alba*, *Bombax cieba*, and *Ziziphus mauritiana* exhibited nonsignificant decrease in SPAD values (Figure 11).

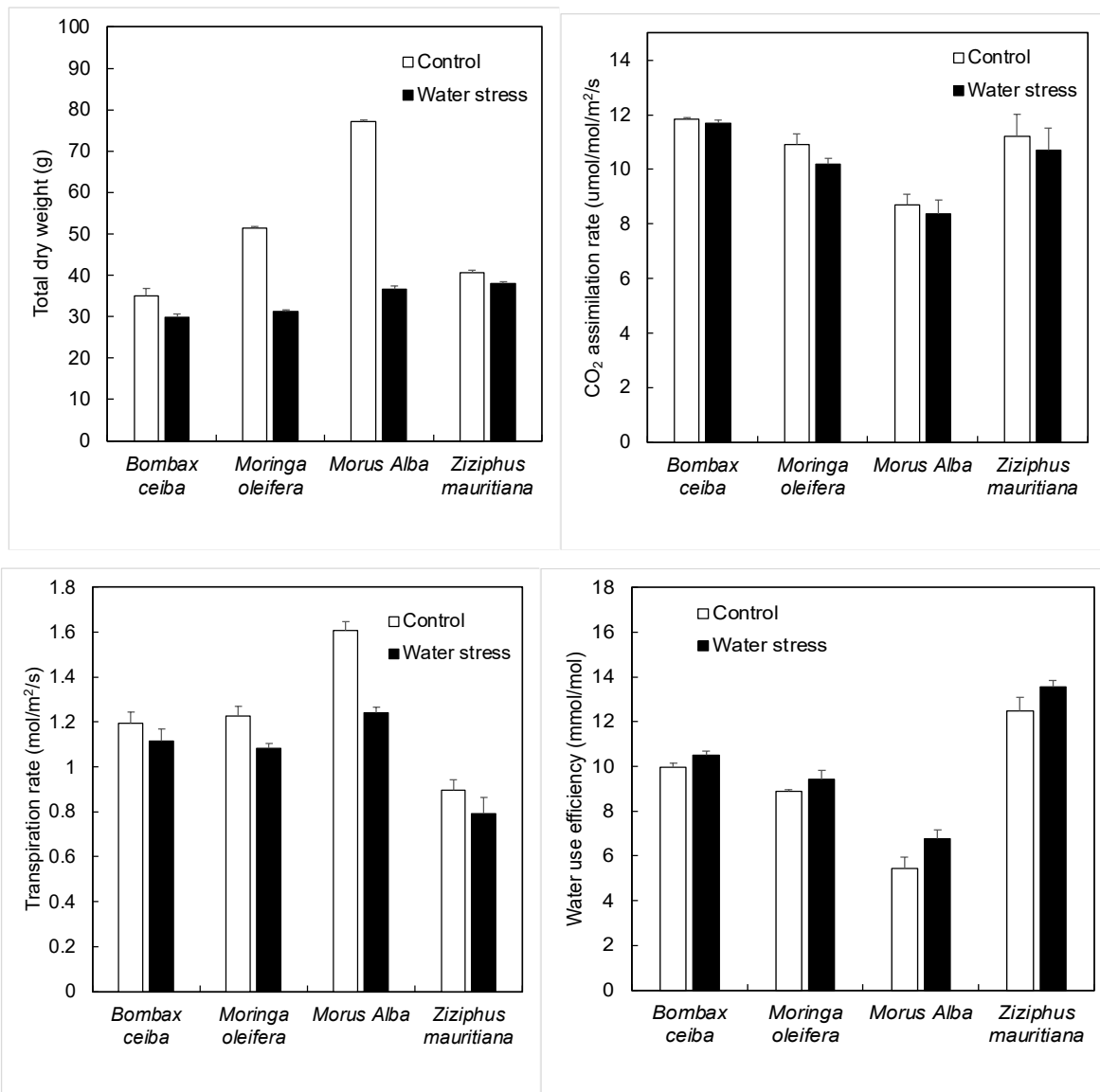


Figure 1.2.3.4. Physiological parameters of all the four species measured during the experiment.

Other physiological parameters including CO₂ assimilation rate, transpiration rate and water use efficiency were measured and results revealed that CO₂ assimilation rate differed nonsignificant across the four species (Figure 12) while transpiration rate and water use efficiency differed significantly among species under water stress. It was found that transpiration rate of *Ziziphus mauritiana* was lowest and it used water efficiently in comparison to the *Morus alba*, *Bombax cieba* and *Moringa oleifera* (Figure 13, 14). In contrast, study

found *Morus alba* with lowest water use efficiency and highest transpiration rate. *Bombax cieba*, and *Moringa oleifera* demonstrated moderate results.

4 Discussion

The present study evaluated four species, *Ziziphus mauritiana*, *Morus alba*, *Bombax cieba* and *Moringa oleifera*. Results exhibited markedly different morphological and physiological responses to the water stress. In this experiment, *Ziziphus mauritiana* consistently showed the highest drought tolerance, as evidenced by the smallest reduction in plant height and the least decline in total biomass, minimal decrease in chlorophyll values, the lowest transpiration rate and highest water use efficiency. These patterns align closely with contemporary studies reporting that *Ziziphus mauritiana* and other *Ziziphus* species are among the most drought resilient agroforestry trees in arid and semi-arid regions. (Sivalingam et al., 2021) demonstrated that *Ziziphus mauritiana* maintains comparatively stable leaf water potential, exhibits effective osmotic adjustment, and shows conservative stomatal behavior during water deficit conditions, allowing it to sustain physiological activity when many mesic species undergo severe decline. Similarly, Usman et al., (2021) and Traore et al., (2024) documented that *Ziziphus mauritiana* maintains growth under substantial soil moisture deficits due to its deep rooting structure, high carbohydrate reserve and ability to regulate transpiration more than many other co-occurring species. These findings mirror the results obtained in the present study, where *Ziziphus mauritiana* displayed low transpiration and high-water use efficiency, suggesting efficient water management and regulation of stomatal aperture. In contrast, *Morus alba* revealed the greatest reductions in height and diameter, leaf, stem and root dry weights, alongside the lowest water use efficiency and highest transpiration rate under the water deficit conditions, signaling that it is the least drought-tolerant among the tested species. This observation is strongly supported by previous work: Zafar et al., (2023) reported significant declines in SPAD values, photosynthetic efficiency and above ground growth in *Morus alba* under water scarcity; Sun et al., (2023) found that *Morus alba* leaves exhibit substantial pigment degradation and oxidative stress when subjected to water scarce conditions, leading to reduced biomass accumulation; and Mohammadi et al., (2022) noted that *Morus alba* tends to maintain partially open stomata during early drought exposure, causing excessive water constraints align directly with the results of current study, particularly the high transpiration and significant biomass reduction observed under water stress. The intermediate responses of *Moringa oleifera* and *Bombax cieba* also align with earlier findings that classify these species as moderately drought tolerant. For instance, Rahim et al., (2024) found that *Bombax cieba* seedlings show measurable, but not extreme, declines in biomass, root elongation, and chlorophyll under water deficit, suggesting that the species uses a mixture of avoidance and tolerance strategies depending on stress severity. Similarly, Luo et al., (2021) reported that *Bombax cieba* maintains moderate levels of gas exchange under drought but undergoes significant decline under prolonged or intense moisture limitation consistent with the moderate position of *Bombax cieba* relative to the other species in the present study. On the other hand, *Moringa oleifera* is widely recognized for its relative resilience in semi-arid environments; however, several controlled-environment experiments have reported significant reductions in chlorophyll content, leaf water potential, and stomatal conductance under moderate-to-severe drought. Islam et al., (2023) observed that *Moringa oleifera* leaves undergo rapid pigment degradation and membrane destabilization during drought, which corresponds with the substantial decline in SPAD values recorded for *Moringa oleifera* in the present experiment. At the same time, its biomass reduction was not as severe as that of *Morus alba*, matching the intermediate drought classification reported by Bekka et al., (2022), who found that *Moringa oleifera* maintains root activity and moderate photosynthesis under deficit irrigation. The pattern of biomass allocation observed in the present study-specifically, the relatively higher investment in stem diameter and biomass by *Ziziphus mauritiana* also agrees with widely accepted models of drought tolerance. Many drought-tolerant tree species redistribute carbon from height elongation to supportive tissues such as stems and coarse roots during water deficit, thereby improving hydraulic safety margins. This mechanism is well documented in the work of Oliveira et al., (2021) and Kahmen et al., (2022), who explained that maintaining stem integrity and hydraulic conductivity allows tolerant species to continue water uptake and transport under declining soil moisture.

Similarly, the negligible effect of drought on stem diameter observed in the current study is consistent with studies showing that secondary growth is generally less sensitive to short-term drought than primary shoot growth (Lv et al., 2024). SPAD values responses recorded in this study also match the literature, with *Moringa oleifera* showing strong decline and *Ziziphus mauritiana* exhibiting only mild reductions. Chlorophyll stability is regarded as a hallmark of drought tolerance, as outlined by Singh et al., (2021) and Lamani et al., (2022), and the strong maintenance of SPAD values in *Ziziphus mauritiana* reflects the higher oxidative stress tolerance capacity of species. Similarly, differences in transpiration rate and water use efficiency observed among species correspond directly with earlier findings comparing xerophytic versus mesophyte trees, where drought-adapted species demonstrate lower stomatal conductance and higher water use efficiency (Zhu et al., 2021). Collectively, these correspondences between the current results and previous research support the conclusion that *Ziziphus mauritiana* possesses a suite of morphological and physiological traits that confer high drought tolerance, while *Morus alba* lacks these adaptive mechanisms and is therefore more vulnerable. The alignment of these findings with established literature reinforces the robustness of the present results and strengthens confidence in the inferred drought-tolerance hierarchy.

Conclusion

Large interspecific differences were found for productivity and water use efficiency in all the four tree species. Although lowest growth rate was found in *Ziziphus mauritiana* however, water stress tolerance was found the highest in *Ziziphus mauritiana* as compared to other three species. This water stress tolerance was not controlled by the CO₂ assimilation rate as it remained non-significant under water stress as compared to control condition but was controlled by the transpiration rate that was found more sensitive to water stress and decreased significantly under water stress. Resultantly, water use efficiency was also found the highest in *Ziziphus mauritiana* followed by *Bombax cieba*, *Moringa oleifera* and *Morus alba*.

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