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## Energy content of plant organs and population cohorts in *Moringa peregrina*: concepts for species conservation management in arid regions

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Conservation management and sustainable use of *Moringa peregrina* are needed to overcome overexploitation coupled with potential environmental changes. This study demonstrates the energy dynamics of *M. peregrina*, how stored energy influences species persistence amidst environmental challenges, and the importance of energy reserves in the resilience of the species population. Field, greenhouse, and lab experiments were conducted at the levels of population cohorts, plant organs, seeds, and seedlings to demonstrate the relationship between energy content and the persistence of the species. Seedlings and juveniles stored around 12,000 joule/g in roots, while uncoppiced adults stored about 9,000 joule/g in stems, and coppiced adults stored 1,800-4,000 joule/g in lignotubers. In adult trees, the number of sprouting stems is correlated with the energy content in lignotubers. Over the ten years of seed storage, a rapid rate of energy depletion was observed, ranging from 16,821 to 5,059 joule/g, which is associated with decreased germination and viability. The energy content in two-month-old seedlings varied from 240 to 800 joule/seedlings under 200 and 800 mm rainfall, respectively. The unstable population structure could be ascribed to the depletion of stored energy in lignotubers following uncontrolled coppicing and the rapid depletion of seed energy, which hinders the population resilience.

**Keywords:** Population Demography, Coppicing, Lignotuber, Seed Germination, Resource Allocation

### INTRODUCTION

Energy content in different plant cohorts from seedlings to adults, as well as energy content in plant organs, such as roots, lignotubers, and seeds, is an important issue for assessing the energy fixation, transformation and flow efficiency, and utilization by the plant for persistence and reproduction (Long 1934, Golley 1961, Yajing et al. 2007, Núñez-Regueira et al. 2004, Lin and Cao 2008). At different levels of organization, the energy content is a fundamental functional trait and it is as an adaptive strategy at individual, population, community, and ecosystem levels and can be utilized by the up-level consumer organisms to maintain material cycling and energy flow in the ecosystem (Cummins and Wuycheck 1971, Paine 1971, Ren and Peng 1999, El-Khatib and Hegazy 2001, Lin and Cao 2008, Ostermann et al. 2021).

In desert environments, due to the frequent and extended drought periods, unpredictable rainfall and stressful temperatures, plants have often evolved persistence adaptive strategies to ensure continuous reproductive success and complementarity between vegetative and sexual reproduction (Hegazy 1994, Hegazy and Lovett-Doust 2016). Many tree and shrub species in arid ecosystems developed lignotubers, at the base of the stem, which are considered energy, nutrients, and bud storage organs with a “life insurance” function for resprouting and vegetative

growth from disturbances which cause mortality of the aboveground shoot, such as, drought, fire and anthropogenic shoot cutting (Carrodus and Blake 1970, Bamber and Mulette 1978, Sutton and Tinus 1983, Dell et al. 1985, Çolak et al. 2009). Generally, plants which resprout post-disturbance may not be successful over a longer term in creating secondary trunks. As reported by Carrodus and Blake (1970) the presence of an inhibitory substance exerts an incomplete apical dominance in *Eucalyptus obliqua* seedlings that diminished upon decapitation stimulating branching from the lignotubers. Hitherto, literature from desert regions around the world provides little information about the ecology of repeated sprouting from lignotubers under stressful environmental conditions.

As for sexual reproduction, seed germination is a complex and crucial process that determines the subsequent seedling establishment. This process requires enough amounts of stored energy and nutrients, where the germinating seeds and seedlings lack nutrient uptake and photosynthetic systems (He et al. 2019, Nietzel et al. 2020). Seeds contain energy as storage metabolites to support germination and early stages of seedling growth where the mitochondrial energy production is limited, where changes in the energy components of the seed; lipids, proteins and carbohydrates may manifest in changes of seed weight and calorific content of the seed (Tripathi and Khan 1990, Angelovici et al. 2010,

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Sreenivasulu and Wobus 2013, Galili et al. 2014). At the seedling and juvenile stages, frequent dieback of shoot may occur, where sprouting takes place by production of secondary trunks at the point where the root and shoot system meet (Sutton and Tinus 1983, Canadell and Zedler 1994). In disturbed habitats, even when trees escaped trunk cutting, the basal sprouts may die off before being developed into secondary trunks (Personal observation on *Moringa peregrina*).

The species persistence in nature is threatened due to overexploitation and stressful environment. The local dwellers collect the different plant organs for use as fuelwood, folk medicine (leaves and seeds), water purification (seeds), and food additive and fodder (Hobbs 1998, Hegazy et al. 2014). It is characterized by short germination time, high seedling growth rate, and high rate of growth from cuttings (Gomaa and Picó 2011, Salaheldeen et al. 2015). Over collection is considered a conservation threat that needs understanding the energy dynamic of the trees and best practices around cutting back trees to help guide local people in how to best manage the local trees.

As an adaptive evolutionary mechanism to overcome the stressful conditions, *M. peregrina* and many woody plants have evolved reproductive strategy that combines between vegetative sprouting from the coppiced trunk “persistence niche” and seeding strategy “recruitment niche” (*sensu* Harper 1977, Hegazy 1994). Previous studies on *Moringa peregrina* reflected the decline of the populations, lack of recruitment, low Fruit-set and low representation of seeds in the soil seed bank (Hegazy et al. 2008; Hegazy et al. 2009, Dadamouny et al. 2016, Vaknin and Mishal 2017). The present study aims to: (1) screen the energy content of different plant organs in different population cohorts including seedling, juvenile, and uncoppiced and coppiced adults, (2) investigate the relationship between seed energy and germination, and (3) determine the energy allocation to different seedling organs raised under simulated rainfall water treatments to detect the early water requirements for seedling establishment. The authors hypothesize the presence of direct relationship between the energy content of the plant organs and the vegetative sprouting and seed germination. This relationship is an indicator for predicting future population dynamics as based on sprouts from the cut stems and the germination of seeds, as an important asset for species conservation and resilience.

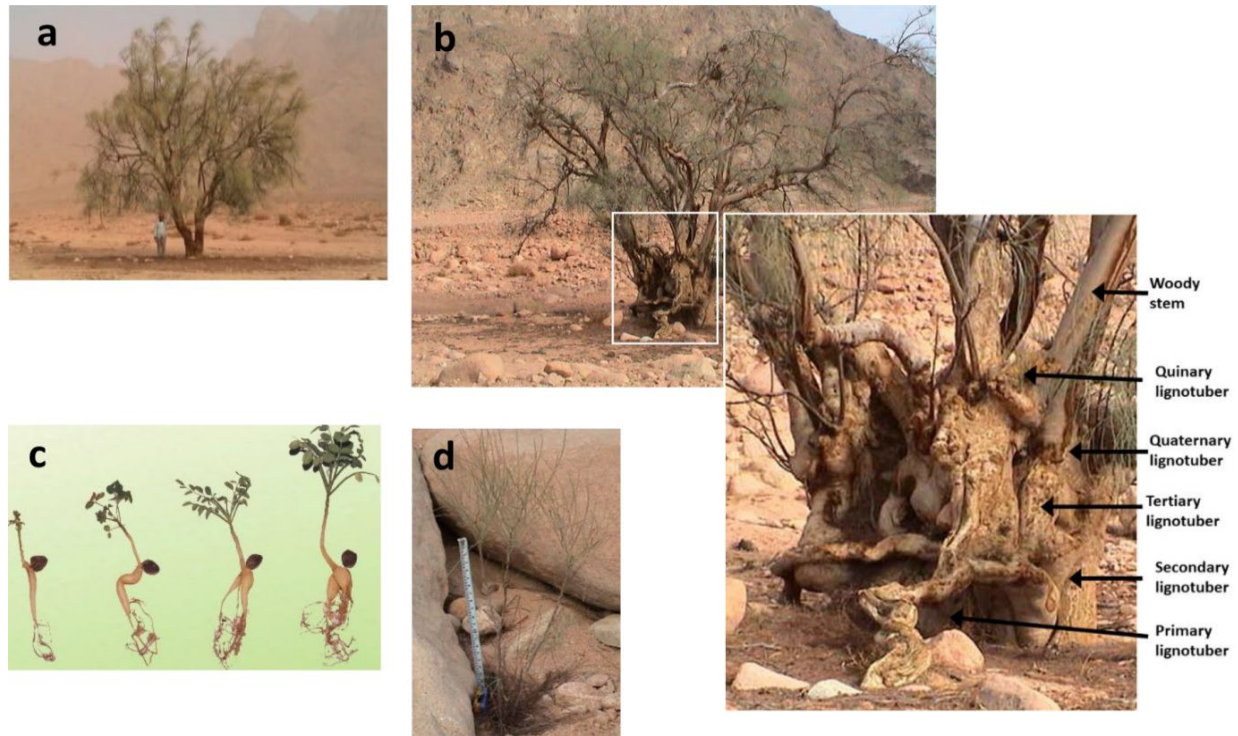
## MATERIALS AND METHODS

### Study species

The distribution of *Moringa peregrina* (Forssk.) Fiori (Family: *Moringaceae*) in Egypt is restricted to the mountainous regions of the Red Sea and South Sinai (Hegazy et al. 2008). It is characterized by short germination time, high seedling growth rate, and high rate of growth from cuttings (Gomaa and Pico 2011, Salaheldeen et al. 2014). The plant populations are established on rocky mountain slopes and in valley bed and sides. The natural plant populations of *M. peregrina* (Figure 1a&b) survive frequent drought periods and are subject to repeated stem cutting or dieback and seed collection by local dwellers. Multiple lignotubers can form per individual adult due to repeated wood cutting of old stems. Individuals in the study population showed up to five orders from primary to Quinary lignotubers overtopping each other or aggregated together (Figure 1b). The seedlings show storage roots from the early stages as shown in Figure 1c.

### Population demography

The natural population of *M. peregrina* growing in the Mount Qattar region, Red Sea coast, the eastern desert, Egypt (27° 07' 55" N, 33° 18' 11" E, 665 m a.s.l) was demographically investigated in July 2015 (Figure 1a). The climate in the region is characterized by an average annual rainfall of 45 mm with incidental torrential rain every 5-6 years. The mean monthly temperature ranges from 15.5°C in January to 23.4°C in August, and the relative humidity from 43.6% in June to 55.8% in October (Hegazy 2016). Individuals of the standing *M. peregrina* population were categorized into eight cohorts: (1) seedling cohort identified as individuals developed from seedlings up to one-year sapling, (2) juveniles are the vegetatively growing individuals before reaching flowering stage having an age range from 2-4 years, (3) uncoppiced adults, and (4)-to-(8) covers the coppiced population cohorts subjected to one to five wood coppicing times as identified from the number of lignotubers per individual tree (Figure 1b) from primary to quinary. The lignotuber in adult individuals is identified as the swollen portion at the base of the trunk noticed following to coppicing. The numbers of woody stems per different lignotuber orders were counted, excluding the young sprouts less than 2 cm in diameter. Five samples for energy estimation were collected from the roots, lignotubers, and woody stems using a cork borer, where leaf samples were collected from the same individual plants. Samples



**Figure 1.** (a) Uncoppiced individual tree of *Moringa peregrina*, (b) Coppiced tree with five orders of lignotubers, (c) Seedlings at early growth stages with storage roots (d) Three-year-old juvenile plant represents the growth of two-years-old coppiced seedling.

were placed in paper bags, transported to the laboratory, oven-dried at 80 °C, and ground into fine powder before measuring the calorific content.

### Greenhouse experiment

Mature seeds were collected in July 2018 from 15 different trees chosen randomly, pooled in one stock in tightly closed dark bottles, and preserved dry in laboratory conditions. The experiment started in March 2019 in the open greenhouse of the Faculty of Science, Cairo University. Seeds were sown at a depth of 2 cm in soil brought from the plant's natural habitat after sieving in 2 mm mesh to remove large stones and gravels larger than 2 mm. For the priming of seeds, a homogeneous size was selected, and seeds were imbibed on a wet paper towel overnight prior to sowing.

The imbibed seeds were sown in 75 pots (22 cm diameter and 25 cm depth) at a rate of 5 seeds per pot. After germination, the seedlings were thinned to two healthy individuals per pot. The pots were separated into five groups representing five water treatments. Plants were regularly watered over the 60-day experiment with quantities determined by the

simulated rainfall water treatments of 100, 200, 400, 600 and 800mm.

These treatments represent the range of habitats where *M. peregrina* populations occur in the study region, from low-income runnel sites to high water income depressions and wadi beds, which collect runoff water that may reach amounts exceeding 600mm per year (c.f. Hegazy et al. 2008, Hegazy and Kabieli 2010, Gomaa and Pico 2011). Each treatment was represented by 15 replications: 10 replicates for determination of energy content (five replicates after 30 days and another five after 60 days) and five replicates for dry weight determination at the end of the experiment. The 100 mm treatment did not survive to the end of the experiment; only values at 30 days were obtained for energy content and dry weight measurements. For the other treatments, energy content was measured after 30 and 60 days, and dry weight was determined at the end of the experiment after 60 days (c.f. Hegazy and Kabieli 2010). At the termination of the experiment, plants were harvested and separated into roots, stems, and leaves. The materials were oven-dried at 80 °C and ground to fine powder to measure plant organs' calorific content under different water treatments.

The dry matter allocation to different plant organs was calculated as a percentage of total plant weight.

### Seed germination and viability

Mature seeds of *M. peregrina* were collected from the study population in July 2010. The seeds were preserved in tightly closed dark bottles under laboratory conditions. Germination and viability tests were carried out. Tests were performed in August every year during 2010-to-2020. The energy content of whole and decorticated seeds was evaluated yearly during the storage period. Germination was performed in covered glass Petri dishes (15x1.5 cm) on Whatman No.1 filter paper and 5 ml distilled water. The tests were performed on 125 seeds distributed in five replications as 25 seeds per Petri dish. The dishes were placed in an incubator adjusted to day-night temperatures of 25:15°C. The light was supplied by white, fluorescent tubes with light intensity of 250  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at the dish surface. The number of germinated seeds was counted daily for two weeks. The seed viability was tested by a 1.0% solution of 2,3,5-triphenyl tetrazolium chloride (TTC) dissolved in distilled water. One hundred seeds were tested for viability in five replications, each 20 seeds per replicate. Because of the large size and hard coat, the seeds were moistened on a moist paper towel for 24 hours to allow complete hydration of all seed tissues and to activate the germination process. The seeds were stained in Petri dishes for 12 hours at room temperature 25°C with sufficient TTC solution to cover the seeds and allow their absorption. A control set of seeds was placed in distilled water for comparison with the stained seeds. After removal from the TTC staining solution, the seeds were rinsed with distilled water, and the seed coat was removed carefully before examination with a stereomicroscope. The viable tissues were stained with bright or faint red colour, while the non-viable tissues appeared off-white in colour, liquid-logged, blurred, and lackluster. The seed embryo was examined to confirm viability, and seeds were considered non-viable when the radicle and plumule tips appeared off-white.

### Energy content of plant material

Plant organs' energy content (calorific value, joule per gram dry weight) was measured by calorimeter model IKA-C200 in the ecology laboratory at King Saud University, Saudi Arabia. Plant root, stem, lignotuber, and leaf materials were oven-dried at 80 °C and then ground into a fine powder. Samples of approximately 250 mg were then used to determine

the caloric content. For seeds, the caloric content was measured on whole and decorticated seeds. Five replications were measured for each sample. The calorific contents are expressed as  $\text{Jg}^{-1}$  dry weight. In the present study, we defined the root as the lower portion of the seedling, below the attachment point of cotyledons to the embryonic axis, and the stem as the upper portion of the seedling, above the attachment point of cotyledons to the embryonic axis. The transition zone between root and stem could be considered the origin of the lignotuber identified in adult trees. The energy content of seeds was measured for whole and decorticated samples.

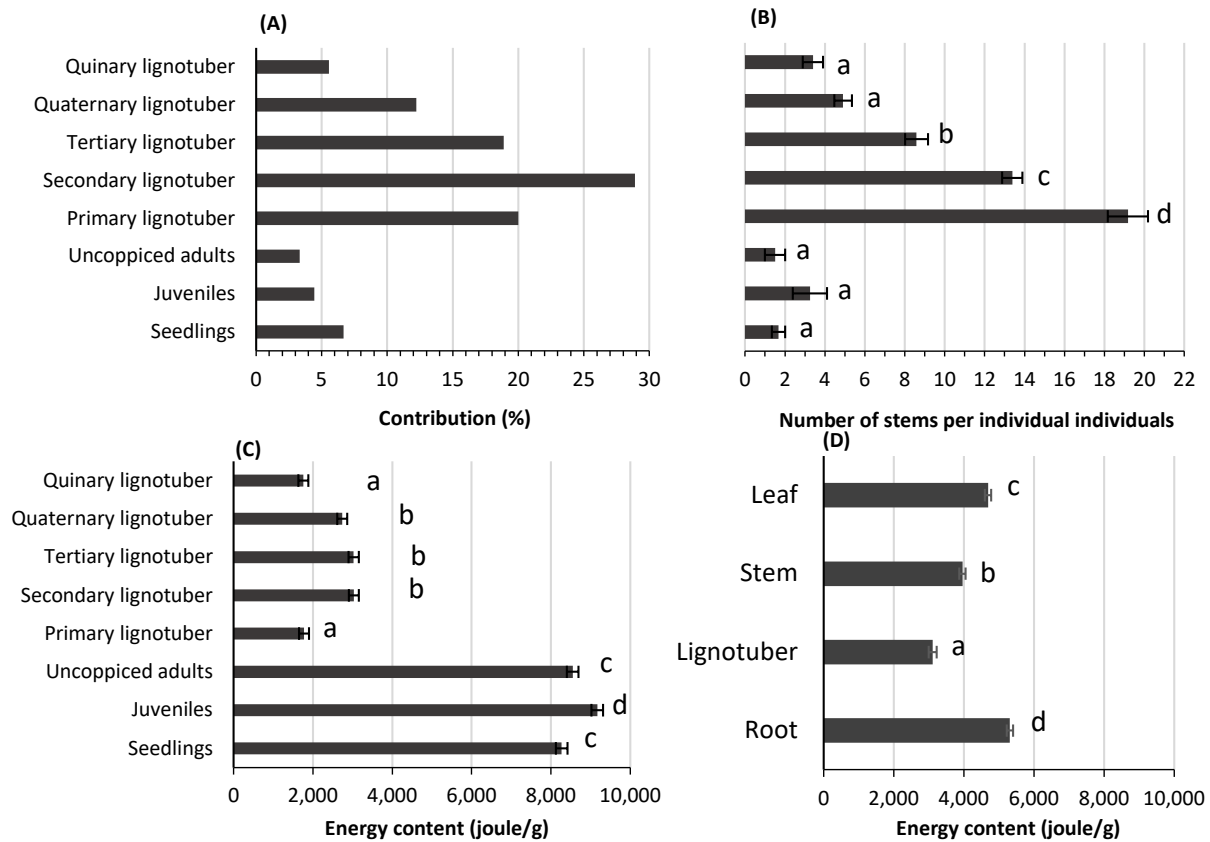
### Statistical analysis

The demography of *M. peregrina* population was calculated as the percentage contribution of different cohorts. The number of stems per individual, energy content, and dry matter allocation in different organs were presented as means  $\pm$  standard errors. Significant differences were considered at 0.05 level. Two-way ANOVA was used to test the significance of the relationship between (1) cohorts and plant organs and their interaction on the energy content, (2) water treatment, plant organ, and their interaction on the energy content and dry weight of seedlings. One-way ANOVA was used to test the least significance of differences (LSDs) between means: (1) among cohorts and plant organs within the same cohort, (2) among storage years of seeds for germination, viability, and energy content of whole and decorticated seeds, and (3) among treatments in the same plant organ and among plant organs for the same treatment. The statistical analyses were performed using SPSS (version 18) software.

## RESULTS

### Population demography

Trees of *Moringa peregrina* with primary, secondary, and tertiary lignotubers dominated the site by 20%, 28.9%, and 18.9%, respectively, while trees with secondary lignotubers showed the highest contribution (Figure 2a). A similar trend was shown for the mean number of stems per individual: 19.2, 13.4, and 8.6 stems per individual for trees with primary, secondary, and tertiary lignotubers, respectively, whereas trees with primary lignotuber showed the highest value (Figure 2b). The population demonstrates an unstable population structure with a low contribution of seedlings (6.7%), juveniles (4.5%), and uncoppiced adults (3.3%) with a maximum number of stems recorded in juveniles: 3.3 stems per individual (Figure 2a and b).



**Figure 2.** Demography and energy content of *Moringa peregrina* population in the study area. (a) population demography, (b) mean number of stems per individual for each population cohort, (c) the overall mean energy content (joule/gram dry weight) in different population cohorts, and (d) mean energy content in different organs; each value represents the mean of energy content in all cohorts for the same organ. Different lower-case letters indicate significant differences among means. Values are means  $\pm$  SE. (1 joule  $\approx$  0.239 calorie).

The two-way ANOVA revealed significant differences in energy content values among the different cohorts and for the plant organs (Figure 2c and d). Seedlings, juveniles, and uncoppiced adults showed the highest values for energy contents: 8,269.9, 9,169.5, and 8,550.9 joule/g, respectively. The trees with lignotubers showed lower energy content ranging from 1,772.7 joule/g in the primary lignotuber to 2,029 joule/g in the secondary lignotuber, respectively (Figure 2c). The overall mean energy content in the root in all cohorts showed the highest value (5,310.3 joule/g) followed by the leaf, stem and lignotuber which showed the lowest value: 3,111.8 joule/g (Figure 2d).

The amount of energy stored in each plant organ belonging to the different cohort (Figure 3) revealed significantly high values in the roots, amounting to 12,256 joule/g in seedlings and 12,040 joule/g in juveniles. The uncoppiced adults showed high value in the stem, reaching 9,098 joule/g. The trees with

primary lignotubers showed a value in the leaf of 2,068 joule/g, while the secondary lignotubers attained a value of 3,911 joule/g in the leaf. The trees with tertiary, quaternary, and quinary lignotubers showed the significantly highest values for energy stored in lignotubers amounting to 4,110, 3,705, and 2,262 joule/g respectively as compared to the other plant organs. Values of energy content in trees with lignotubers showed a bell-shaped pattern with the highest values of 4,110 joule/g in the tertiary lignotuber; then values decreased on both sides to reach minimum values (1,866 and 2,262 joule/g) in trees with primary and quinary lignotubers respectively (Figure 3ii).

In coppiced trees with tertiary, quaternary, and quinary lignotubers, the decreased number of sprouting stems after coppicing (from 8.5 to 3.4 stems per tree) is associated with the decrease in energy content of the lignotubers (from 4,110 to 2,262 joule/g) of the corresponding population cohorts

(Figure 2b and 3ii). The trees with primary and secondary lignotubers showed a balanced distribution of stored energy among organs with higher energy storage in the leaf, lignotuber, and stem as compared to other cohorts (Figure 3), which produced the highest number of sprouting stems after coppicing: 13.2 and 19.1 stems per tree, as compared to 8.5, 4.9, and 3.4 sprouting stems per tree in trees having tertiary, quaternary, and quinary lignotubers respectively (Figure 2b).

### Seed germination and viability

A decreasing trend was observed in the energy content of whole seeds and the germination and viability percentages over the ten years of seed storage period (Figure 4). The effects of seed energy content on germination and viability are not significant as tested by the general linear model. Seed viability is more influenced by the energy content as compared to seed germination. The decorticated seeds showed consistently higher energy content values than whole seeds, with a difference of 3,109 joule/g after harvest (year zero), which increased to 5,706 joule/g in the tenth year (Figure 4). The linear regression revealed a higher energy depletion rate in the seeds over the years.

Values of energy content of whole seeds amounted to 16,821 joule/g after collection, corresponding to germination and viability of 64.6% and 91.4%, respectively, then decreased gradually over storage years to reach 14,569 joule/g in the fifth year, corresponding to germination and viability of 25.2% and 51.2% respectively (Figure 4). The energy content of the whole seeds reached 5,059 joule/g in the tenth year of storage, corresponding to germination and viability of 0.8% and 16%, respectively (Figure 4). The linear regression revealed a close rate of loss of viability and rate of germination detracting over the storage years.

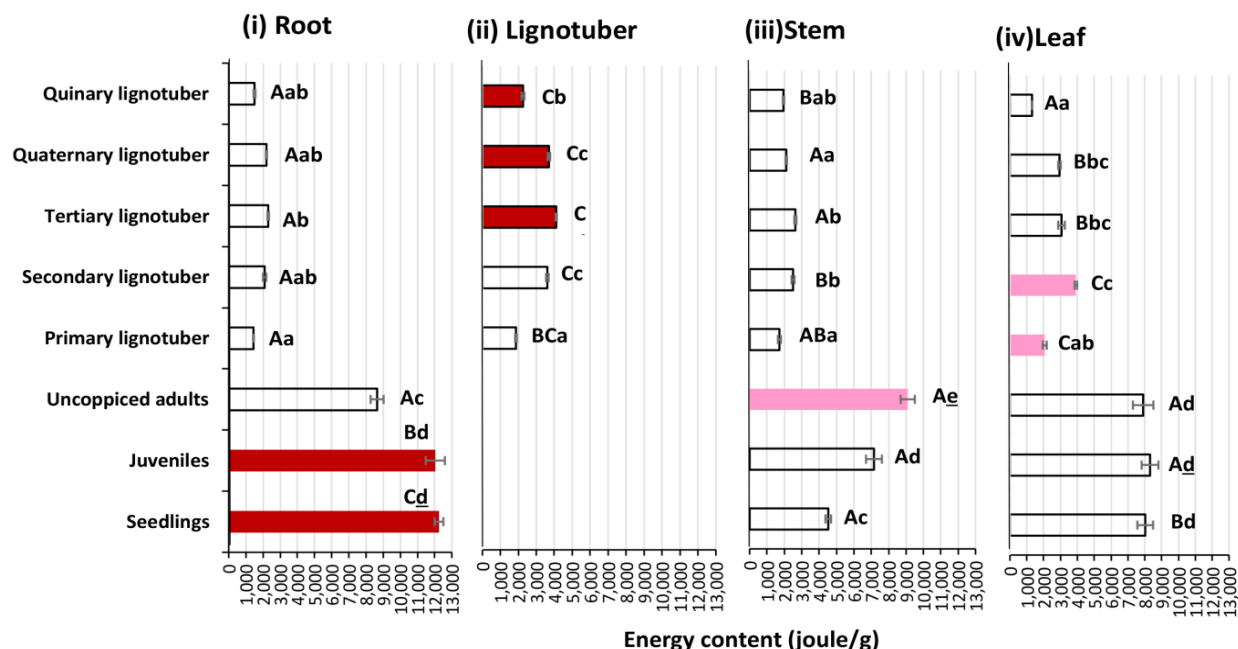
### Water treatments

Under the experimental water treatment equivalent to 100 mm rainfall, *M. peregrina* seedlings survived for only 30 days. The energy content of plant seedlings was lower than 2,000 joule/g in different plant seedling organs, ranging from 929.6 joule/g in the leaves to 1,733.6 joule/g in the roots (Figure 5a). The subsequent higher water treatments showed a gradual increase in the energy content of all plant organs. The energy content increased in roots from 8,621 joule/g under 200 mm treatment to 15,268 joule/g under 800 mm treatment. Similarly, the

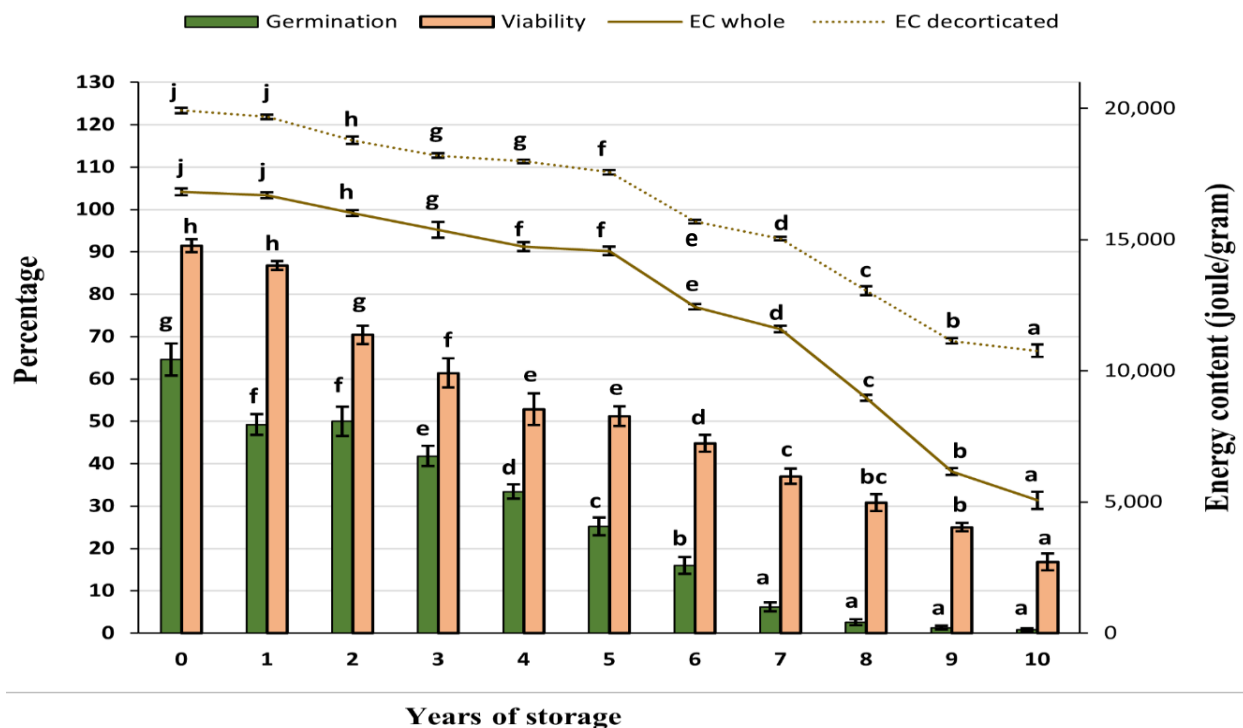
energy content of stems increased from 3,174 joule/g in 200 mm treatment to 6,615 joule/g in 800 mm treatment. In leaves, the energy content increased from 4,027 joule/g in 200 mm treatment to 11,744 joule/g under 800 mm treatment. Alternatively, the energy content of stems attained the lowest values among other organs, followed by leaves and roots, which showed the highest value: 15,268 joule/g under 800 mm treatment (Figure 5a). A similar pattern was obtained for plants at 60 days of the experiment, showing a gradual increase in the energy content in all organs with increased water supply, while lower values were obtained in stems followed by leaves then roots (Figure 5b). The energy content of roots increased from 12,978 joule/g in 200 mm treatment to 17,359 joule/g in 800 mm treatment. The energy content increased in stems from 4,589 joule/g in 200 mm treatment to 9,451 joule/g in 800 mm treatment. As for leaves, the energy content increased from 4,134 joule/g in 200 mm treatment to 13,627 joule/g in 800 mm treatment.

Two-way ANOVA revealed that the energy content was significantly affected by the water treatment, organ, and their interaction. The rate of change in energy content, as affected by water treatments (for values after 30 and 60 days of the experiment), showed varied patterns among different organs (Figure 5c). The root of seedlings showed a decreased rate of change in energy content as the water treatment increased from 200 mm to 800 mm: rate of change = 0.50, 0.25, 0.16, and 0.13, respectively. As for stems, the rate of change in energy content increased from 0.45 to 0.52 and 0.70 in 200, 400, and 600 mm treatment, then decreased to 0.43 in 800 mm treatment. Alternatively, the rate of change in energy content in the leaf showed alternation between increasing and decreasing values, with negative rates under 400 and 600 mm treatments: -0.45 and -0.06, respectively, and a maximum rate of 0.16 under 800 mm treatment (Figure 5c).

The dry matter allocation showed that seedlings raised under 100 mm water treatment attained the lowest values of plant dry weight as compared to the plants raised under higher water treatments, with the highest allocation to the stem amounting to 9.6 grams per individual and the lowest allocation to the leaf: 2.2 gram per individual (Figure 6a). The dry weight of plant seedlings increased with the increased water treatment for the root, stem, and leaf. The highest dry matter allocation was directed to stems, and the lowest allocation was directed to leaves in all water treatments (Figure 6b).

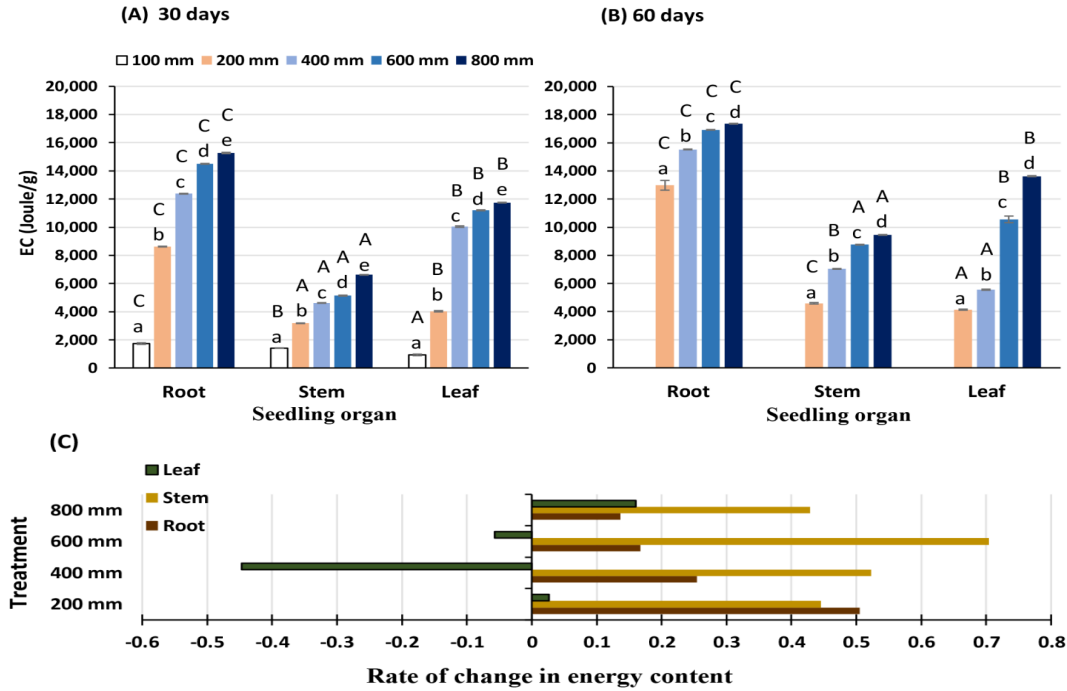


**Figure 3.** Energy content (joule/gram) in different plant organs of *Moringa peregrina* demographic cohorts; (i) Root, (ii) Lignotuber, (iii) Stem, and (iv) Leaf. Within the same plant organ (vertical), different lower-case letters indicate significant differences among means of different cohorts, letters are underlined for significantly highest values. Within the same cohort (horizontal), different capital letters significant differences among means of different organs; bars with significant highest values are shaded in red, and bars with non-significant highest values are shaded in rose. Values means  $\pm$  SE.

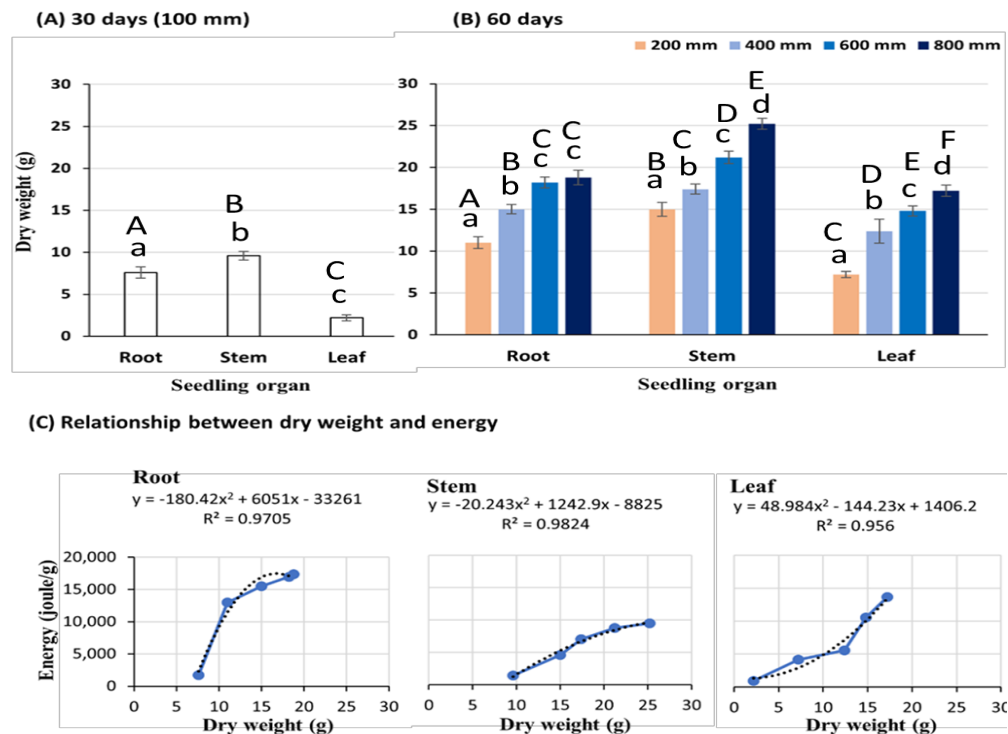


**Figure 4.** Percentages of germination and viability (bar graph) of *Moringa peregrina* over 10 years storage and the corresponding energy content of whole and decorticated seeds (line graph). The linear relationship for the germination throughout the storage years is  $y = -6.7418x + 66.91$ ,  $R^2 = 0.9626$ , and for the viability is  $y = -7.2345x + 95.08$ ,  $R^2 = 0.9783$ . The linear relationship for energy depletion throughout the storage years in the whole seeds is  $y = -1198.9x + 19777$ ,  $R^2 = 0.9046$ , and for the decorticated seeds is  $y = -961.88x + 21940$ ,  $R^2 = 0.9387$ . Different letters indicate significant differences among means of storage years. Values means  $\pm$  SE.





**Figure 5.** Energy content of *Moringa peregrina* plant organs raised under 100, 200, 400, 600 and 800 mm rainfall treatments. Values are measured after (A) 30 days and (B) 60 days of plant growth, and (C) the change in energy content from the 30-to the 60-days experiments in different organs. Within the same plant organ, different lower-case letters indicate significant differences of means among treatments. Among different organs, different upper-case letters indicate significant differences of means in the same treatment. Values are means  $\pm$  SE.



**Figure 6.** Dry matter allocation for different organs of *Moringa peregrina* seedlings raised under different water treatments, after (A) 30 days for 100 mm treatment, and (B) 60 days for 200, 400, 600, and 800 mm treatments. Within the same plant organ, different lower-case letters indicate significant differences of means among treatments. Among different organs, different upper-case letters indicate significant differences of means in the same treatment. Values means  $\pm$  SE. Relationships (polynomial trendline, dotted line) between dry weight and energy in different organs is shown in (C), water treatments are indicated on the curve.

The highest dry matter values were reached in the 800 mm treatment, with 18.8, 25.2, and 17.2 grams per individual allocated to the root, stem, and leaf, respectively. Increasing relationships (polynomial trendline) are shown between dry matter and energy stored in different plant organs (Figure 6c). In the root, a sharp increase in energy storage is associated with the increase in dry matter in the seedlings raised under 100 mm to 200 mm, then a smooth increasing trend is observed for higher water treatments. A slower rate of increase in energy storage as the dry matter increased was observed in the stem. The rate of change in energy storage as the dry matter increased in the leaf showed a high rate of increase in the seedlings raised under 400 to 800 mm.

## DISCUSSION

### Energy for growth and sprouting

**Among plant cohorts:** The average energy content in plant organs was higher than 8000 joule/g in *M. peregrina* seedlings, juveniles and uncoppiced adults, while attained less than 4000 joule/g in coppiced trees. Seedlings and juveniles represent only about 11% of the population reflecting unstable structure, while about 70% of the trees are coppiced with primary, secondary, and tertiary lignotubers. Cohorts may have complementary roles for energy storage according to available resources and plant needs throughout the life span of the trees, where this is considered complementary role of plant functional traits in the ecosystem regarding the calorific value (Yan et al. 2018). The energy depletion in lignotubers associated with decreased sprouting, i.e., there was decreased sprouting from lignotubers with lower energy storage, revealing that coppiced trees need transition recovery periods between successive cutting events for replenishing stored energy (Mesleard and Lepart 1989, Moyo et al. 2015&2016, Spencer et al. 2019).

**Among plant organs:** Allocation of energy to different organs is a plant specific strategy that provides insights about the energy utilization strategy and division of labour adopted by the species (Zeng 2012, Yan et al. 2018). The study of *M. peregrina* population showed the presence of an allocation strategy distributing energy among organs in different cohorts. The seedlings and juveniles stored most of the energy in roots amounted 12000 joule/g, uncoppiced adults showed balanced distribution among root, stem, and leaf. The higher amount of energy stored in roots of seedlings and juveniles is considered a storage strategy linked to possible

higher risk of these cohorts to avoid complete die back (Tredici 2001). Alternatively, coppiced trees showed the highest storage of energy in lignotuber, ranging from about 2000-to-4000 joule/g, except in primary and secondary lignotubers where leaves stored similar amounts of energy content. As an energy storage organ and bud bank organ, the lignotubers were reported to determine the early sprouting capacity, the architectural pattern, and the response of trees to disturbance and environmental stresses (Carrodus and Blake 1970, Molinas and Verdaguer 1993, Tredici 1998, Wildy and Pate 2002).

The comparatively high energy content in leaves, specifically in primary and secondary lignotuber cohorts in the present study, shed light on the importance of leaves in directly providing the energy needed from plant assimilates in these cohorts. In the same context, Gärtner and Farahat (2021) assumed that stem growth in *M. peregrina*, as cambium activity and ring formation, is supported by new assimilates derived from leaves in addition to non-structural carbohydrates stored from the previous year. However, data provided in the present study revealed the correlation between energy stored in lignotubers of *M. peregrina* and the number of stems sprouting after coppicing in tertiary, quaternary, and quinary lignotubers. This ensures that lignotubers are important energy storing and bud bank organs in coppiced plants, an important asset for sprouting, survival and population dynamics.

### Energy for seed germination and seedling establishment

Energy stored in seeds is crucial for viability and germination (Baskin and Baskin 1998, Hegazy 2000 & 2001, Nietzel et al. 2020). The rapid decrease of energy content in seeds from about 17000 to 5000 joule/g, coinciding with similar decrease in viability percentages from 90 to 16 %, and germination percentages from 65 to 1 %, explains the low contribution of seedlings to *M. peregrina* population. As for the seedling growth after two months of germination, the energy content (energy in joule per gram multiplied by the dry weight of the plant organ, then summed for all organs) in the seedlings ranged from about 240,000 and 800,000 joule/seedling at 200- and 800mm rainfall equivalent water treatment respectively. If these values were compared to about 30,000 joule/seedling in 100 mm treatment that supported life of seedlings for one month, one may infer the importance of water in the life of seedlings for storing more energy as a strategy for successful

establishment. This explains the distribution of the highest amount of energy in plant seedling is confined to the root stock. Furthermore, comparatively moderate dry matter allocation was recorded in root which can be explained by the more rapidly increasing relationship between dry matter and energy content of roots and underground stem portion as compared to stems and leaves (Hegazy 2001, Hegazy and El-Khatib 2001). This may be explained by the relationship between dry matter allocation and energy content of plant stems and root stocks.

### Implications for species management and conclusions

Lignotuber formation in *M. peregrina* results from multiple coppicing due to wood collection from old trees by local dwellers as an adaptive behaviour to maintain a persistent vegetative stump. In arid regions, natural coppicing in plants may occur in the seedling and juvenile stages under extended years of drought or years with less than average rainfall (Hegazy 2001, Hegazy and Lovett-Doust 2016), where coppicing is considered a multiple reiteration by resprouting of a persistent stump. In *M. peregrina*, coppiced individuals, due to the repeated cutting or natural dieback of shoots, the basal part of the stump forms an overlapped lignotubers on the upper part of the root that remains alive and resprouting new shoots. With age, the first formed lignotubers are subject to decay and become pithy. The continuous sprout recruitment of branches from lignotubers of the coppiced plants depends largely on the amount of stored energy and number of basal dormant buds and their potential for developing new sprouts. The lignotuber formation ensures a yearly reproductive cycle even during years of severe drought, an important feature for persistence and dynamics of the population.

Calorific value in *M. peregrina* varied among plant organs and population cohorts. For lignotubers, the values decreased with age, while among cohorts the values increased with the tree age. This seems attributed to the specific wood anatomy that yields more lignin and hence the higher calorific value as the trees grow older (Farahat and Gärtner 2019, Sardabi et al, 2021, Sseremba, et al. 2021). The combination of energy storage in lignotubers and persistent seeds produced from the different cohorts of the population supports population persistence with overlapping generations, that provide a safeguard against unpredictable and variable desert environments and ensures the species persistence

around the years of severe drought and to take advantage of the post-drought conditions. As a result, intra-population variations of survival, energy allocation, seed energy content and viability may serve as an advantage for population persistence and dynamics. The intra-population variations and the combination of continued vegetative sprouting from multiple lignotubers and sexual propagation by production of seeds produce diversity of functional traits within the population.

Since the calorific value of a plant organ is the amount of energy per unit mass or volume released on complete combustion, suggesting a species management perspective to restrict *M. peregrina* wood cutting to the old large-size branches. This selective wood cutting improves durability and conserves the species' persistence and sustainable use in arid regions. Appropriate coppicing based on the sprouting behavior of the species is of prime importance for the sustainability of wood harvesting and would buffer the impact of coppicing, taking into consideration the impacts of undergoing climate change (Twine and Holdo 2016, Bradford et al. 2022). As the present study links the energy content in lignotubers of adult plants to the sprouting potentiality, we recommend the use of calorific value as a monitoring tool to predict future sprouts and manage wood cutting by the local dwellers. As a conservation measure, the coppicing of trees should be restricted to the low energy content branches.

The study of *Moringa peregrina* has revealed important insights into the species' energy dynamics and reproductive strategies in response to environmental stress and human exploitation. While seedlings and juveniles have significant energy reserves, their low population numbers raise concerns for long-term survival. The species' coppicing behavior appears to be linked to stored energy in lignotubers, indicating that strategic management could enhance its resilience. However, because the study focused on only one population, and there may be seasonal variations that affect seed viability and population dynamics, broader studies are needed to explore the ecological and physiological implications to fully understand conservation and resilience management of this multipurpose use species under overexploitation and expected climate change.

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## COMPETING INTERESTS

The authors declare no conflict of interest

## AUTHOR'S CONTRIBUTION

Conceptualization: AKH. Methodology- Field, laboratory and greenhouse studies: AKH, MKO, ZSH. Data analysis: all authors. Manuscript drafting: AKH. Review and editing: all authors. Overall guidance: AKH. All authors have read and agreed to the published version of the manuscript.

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