


Ecophysiological Effects of Groundwater Drawdown on Phreatophytes: Research Trends during the Last Three Decades

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Abstract: A systematic synthesis of phreatophytes' responses to groundwater drawdown would provide a more complete picture of groundwater-related research aimed at the sustainable management of groundwater-dependent ecosystems amid climate change. Following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines, the ecophysiological effects of groundwater drawdown on phreatophytes and methodological approaches were synthesized from peer-reviewed articles published from 1988 to 2022. The highest relative count of studies was found in arid and semi-arid high-income countries, such as Australia and North America (18–24%), while the lowest relative count to no data was found in hyper-arid countries, such as north African countries (0–3.65%). The groundwater depth effects on phreatophyte ecophysiology had the highest relative count (53.65%), followed by large-scale tree plantation effects on the groundwater characteristics (44.37%) and groundwater depth and biological invasion relationship (1.99%). The results revealed that as the groundwater depth increased, the phreatophytic vegetation growth, productivity, and community structure decreased across the ecosystem types. A groundwater withdrawal also had a significant impact on the physiology of the phreatophytes, specifically on the transpiration rate, xylem water potential, hydraulic conductance, and photosynthetic rate. Many of the reviewed studies concluded that large-scale tree plantations can deplete groundwater resources due to an increased evapotranspiration rate. Further, species' diversity, evenness, dominance, composition, and distribution, as well as the Normalized Difference Vegetation Index (NDVI), are commonly measured parameters in the reviewed studies through vegetation and groundwater monitoring. Amid applied and contemporary problems, this synthesis may provide researchers with cues to conduct studies relevant to the integrated and sustainable conservation and management of groundwater-dependent ecosystems, particularly in data-poor, hyper-arid countries.

Keywords: arid; biological invasion; evapotranspiration; groundwater depth; groundwater extraction; hyper-arid countries; tree plantation; PRISMA



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1. Introduction

Groundwater serves as the world's most critical freshwater source influencing various processes, including plant physiology, community dynamics, and vegetation distribution and composition [1,2]. As the global population grows, however, the demand for water from natural sources increased dramatically, which could lead to an overexploitation, pollution, and the depletion of groundwater resources through a groundwater extraction. When an unsustainable extraction exceeds the aquifer recharge, the groundwater may be depleted, and streams may dry up over time [3]; this may negatively impact the growth, productivity, and ecophysiology of groundwater-reliant plants. Global climate changes have also shown serious impacts on the subsurface hydrology and surface-groundwater interactions, resulting in a serious seasonal groundwater drawdown [4].

Globalization, climate change, and other anthropogenic causes may aggravate groundwater depth fluctuations and the subsequent effects on plants. Specifically, ecosystems that depend on groundwater are predicted to be under more stress from both the direct and

indirect consequences of climate change [5]. Hence, the sustainable management of groundwater systems has recently received much attention and thus being considered as a policy instrument in many parts of the world, including Australia, the USA, the Netherlands, and South Africa [6]. However, the implementation of groundwater-related studies is difficult due to many factors (e.g., the groundwater characteristics, climate, location, geology, vegetation types, and aquifer types, among others) interacting in a complex manner. Such a difficulty may have a profound influence on the availability of the information necessary for the sustainable management of groundwater-reliant ecosystems. Research patterns across the globe may vary depending on these interacting factors. Thus, an understanding of the research trends and a synthesis of the ecophysiological responses of phreatophytes, to the altered groundwater availability would derive a clearer picture about groundwater-related research towards the sustainable management of groundwater-dependent ecosystems amid climate change. A synthesis on the existing data on the effects of fluctuations in the groundwater level on the ecophysiology of phreatophytes have not yet been made to date.

In hyper-arid ecosystems, obligate phreatophytes that are well adapted to water-deficit environments habitually depend on groundwater as a moisture source, especially when there is little to no recharge from the rainfall. Phreatophytic vegetation also uses groundwater as a source of their nutrients from the phreatic surface [7]. The presence of phreatophytes is indicative of altered hydrological regimes caused by a groundwater drawdown because some species only occur at a particular depth of the groundwater [8]. Generally, plant species that can adjust water foraging strategies by rapid vertical root growth toward deep underground water sources can survive long periods of water scarcity. A groundwater drawdown can influence the growth, morpho-anatomical structures, water-sources use, and ecophysiology of the phreatophyte community, and these influences are well-documented in the literature. Morpho-anatomically, for instance, the leaf area tended to be larger for trees under shallow groundwater than for trees in deep groundwater [9]. Groundwater-altered trees also had a smaller vessel-lumen area than the control ones [10]. Physiologically, an altered groundwater availability resulted in a decreased xylem water potential (ψ), maximum photosynthetic rate, and carboxylation efficiency of *Populus euphratica* Olivier and *Tamarix ramosissima* Ledeb seedlings [11]. Although these effects are well-documented, the magnitude of the effects of groundwater drawdown on plants may vary depending on species, phreatic characteristics, life history traits, ecosystem types, environmental conditions, and their interactions. For example, contrasting plant water-use responses to the groundwater depth was observed across plant developmental stages (seedlings to mature trees) of *Haloxylon ammodendron* (C.A.Mey.)Bunge in China [12]. The groundwater responses of some phreatophytes also vary depending on the distance from the river [13]. Further, a phylogenetic study revealed that root groundwater uptake (RWU) strategies are similar among closely related trees based on the rooting depth, water table depth, and rooting depth ratio, and the isotopic composition of the groundwater uptake [14]. A body of knowledge reported also that RWU strategies depend on the species' identity, for example, gymnosperms and angiosperms have contrasting water sources [15,16].

Consequently, the ecological and physiological effects of a groundwater drawdown on phreatophytes were systematically synthesized. Specifically, the present systematic review assessed the knowledge gaps, research trends, and methodological approaches from peer-reviewed articles published during the last three decades (1988–2022) by conducting a rigorous article screening and assessment procedures. The selection of the publication date range was based primarily on the availability of relevant published articles and the degree of comprehension that is appropriate for the research questions. The systematic review was guided by the following questions: (1) what is the geographical distribution of the studies across the globe?; (2) what is the trend in research topics, parameters, and methodological approaches during the last three decades?; and (3) what is the frequently tested hypothesis about groundwater–vegetation research? The present work will improve our understanding of the phreatophyte responses to groundwater fluctuations amid the

impacts of climate change, land use changes, and other human-induced causes of groundwater drawdown. The result of the systematic review may also offer cues to researchers to conduct studies relevant to integrated and sustainable conservation and the management of groundwater-dependent ecosystems amid climate change.

2. Materials and Methods

2.1. Data Collection

From June to September 2022, a systematic literature review (SLR) was conducted to find relevant evidence on the current understanding of the topic and answer the formulated research questions from peer-reviewed articles published between 1988 and 2022. The SLR yielded an initial total of 9544 articles from ScienceDirect, PubMed, and Google Scholar search databases, following the literature search method commonly used for biological science research [17]. These databases are among the most popular search engines for peer-reviewed original articles [18,19], and they are frequently cited in published SLR articles across disciplines, e.g., [20,21]. Some articles were obtained by conducting a direct search from the list of references/bibliography of the downloaded articles and searching them on Google.

A search test was performed first to refine the search terms. Following that, the final search terms were developed, taking into account the most important keywords in each set of search terms, namely the groundwater level, groundwater depth, and phreatophytes (Table 1). To exclude, broaden, or define the search results, Boolean search strings (i.e., “AND” and “OR”) were inserted in all uppercase letters in the search tab of each database. The AND Boolean operator was used to include both important keywords (e.g., “groundwater” AND “phreatophytes”). The OR operator was used to look for records in each database containing any of the terms separated by the operator (e.g., “groundwater level” OR “groundwater depth”). To find the exact phrase or word, each keyword was surrounded by quotation marks (“”). Each database’s advanced search feature was used by specifying the keywords, publication year range, and article type. To avoid bias in the search terms, we did not include more specific terms (e.g., the specific name of a country or region or species names of phreatophytes).

Table 1. The search terms used and their corresponding initial results in ScienceDirect, PubMed, and Google Scholar databases, and direct search.

Search Terms	No. of Articles				
	Science Direct	PubMed	Google Scholar	Direct Search	Total
“groundwater level” OR “groundwater depth” AND “effects”	740	828	208	33	1269
“groundwater” AND “phreatophytes”	377	16	4170	16	4579
“water table” AND “phreatophytes”	310	6	3630	30	3696

2.2. Screening and Selection of Articles

Following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines for appraising articles, the articles were screened to identify studies for inclusion in the review. Figure 1 presents the screening process, including the inclusion and exclusion criteria. To ensure consistency and minimize selection errors and biases, the screening was conducted by only one reviewer. The SLR included all quantitative, qualitative, and a combination of the two methods that used either experimental or observational designs to ensure a comprehensive representation of the literature. We initially screened the titles, abstracts, and keywords to exclude obviously irrelevant material. The search terms that did not appear in the paper’s title, abstract, or keywords were removed in this step. The SLR also excluded grey literature and articles that were not peer reviewed and were not published within the publication date range. The papers were further screened by excluding articles that were not written in English, irrelevant, or duplicated. Articles with the same publication year, title, and author were excluded at this stage using the Mendeley

Reference Manager (version 2.72.0) and, in some cases, a pivot table in a Microsoft Excel Spreadsheet. All articles that met the first set of the inclusion criteria were chosen for a further investigation and content evaluation based on an abstract skim reading. The SLR did not include articles that were not open access or had no free full texts. The databases provide links to PDF copies of the papers, and if none were found, they were searched in other research websites (e.g., ResearchGate). All the abstracts were skim-read, and those with unclear findings were excluded. Articles were validated by skimming the main text and focusing solely on the paper's results and methodology sections. Here, all papers that had ambiguous results and did not provide a detailed explanation of the methods used were excluded. The following assessment questions to ensure the quality of the SLR were considered: (1) are the articles peer reviewed?; (2) are the methods, measurements, and research designs appropriate and well-described?; and (3) are the results presented in a clear manner?

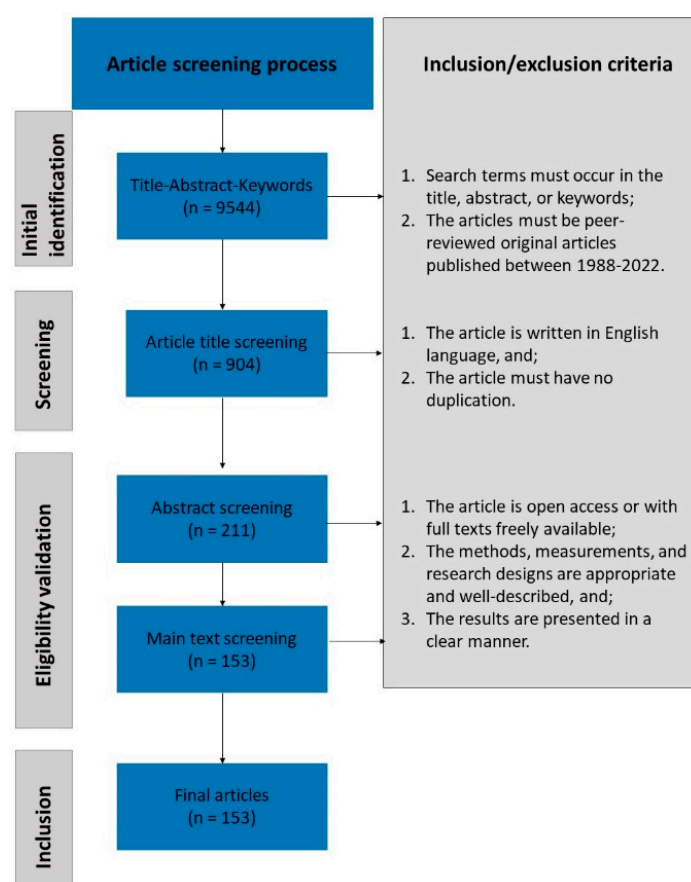


Figure 1. Flow chart of inclusion and exclusion of peer-reviewed articles for the systematic review.

2.3. Data Extraction, Management, and Analysis

Data were extracted from each article and encoded in Google Sheets using the extraction criteria listed in Table 2. The year of publication was determined from the article's page, and the country of study was determined from the "Study site description" of each article. All articles that did not provide any details about the study site were removed, and the country was searched using Google for articles that only mentioned specific names of places (e.g., basin) with coordinates. Data on the mean annual precipitation (mm) of each study site was extracted from each article to relate the geographical distribution of the studies with aridity condition across the globe. The research topic was derived primarily from the keywords in the article title and was further subdivided into three groups based on the hypothesis under consideration (only for hypothesis-driven studies). The list of dominant phreatophytes mentioned in the articles was made to better explain how they

grow, survive, and adapt in a phreatophytic environment. The article's study site description provided the majority of the information on the dominant species. The majority of the information on the variables/parameters measured and the methods used to measure them was derived from the paper's experimental design and/or data analysis sections. Finally, we classified the articles as either ground-based, laboratory-based, or greenhouse-based studies, or modelling/simulation studies.

Table 2. The criteria used for the extraction of information from the selected peer-reviewed original and review articles.

Extraction Criteria	Information Considered and Justification
1. Publication year	Between 1988 and 2022; to get enough number of studies.
2. Country of study site	Worldwide; to map the geographical distribution of studies and the trends of publications.
3. Precipitation	Mentioned mean annual precipitation in the article; to map the amount of precipitation received by the study sites during a specific study period and relate it to aridity conditions.
4. Topic	Keywords in the title; to determine research trends during the last three decades.
5. Dominant phreatophytes	The plant species mentioned as dominant in the study site; to determine which among the identified phreatophytes are well-studied and determine how they respond to groundwater fluctuations.
6. Variables/parameters measured	All variables measured in order to achieve the objectives of the study; to determine which variables are frequently used across the world.
7. Methodological approaches	All methods employed for measuring the variables/parameters; to determine which methods are frequently used.
8. Type of study	Field-based, laboratory-based, greenhouse-based, simulation/modelling or combinations; to determine the extent of research investments/efforts for each country.

2.4. Scope and Limitations

The current systematic review included only peer-reviewed, freely available articles written in English and published between 1988 and 2022. All of the articles are at least indexed in Scopus, and materials published as brochures or technical manuals were not considered. The data on the precipitation were based only on the mentioned values in the reviewed studies. However, the number of databases used, the period/duration of review (34 years), and the search strategies were all based on systematic review protocols. Additionally, strict eligibility criteria were followed for the inclusion and exclusion of articles. Thus, the data and the approach we used can already help us summarize the results and identify knowledge gaps and research trends in groundwater–vegetation research.

3. Results

The current systematic review revealed that the majority of studies on the topic originated in Australia and North America, followed by China and Sweden (Figure 2a). Contrarily, a low number of studies to no data were mostly found in low-income countries (LICs), especially those in the arid and semi-arid zones of in South America (e.g., Chile), Central Asia (e.g., Kazakhstan), Western Asia (e.g., Saudi Arabia), the Middle East (e.g., Jordan), and Africa (e.g., Namibia).

The most frequently cited reason for conducting the research is that groundwater-dependent organisms are among the least studied but most vulnerable components of global biodiversity in the face of climate change. The majority of the reviewed studies were conducted in one of these countries' ecologically and economically important basins (e.g., Central Perth Basin and Swan Coastal Plain in Western Australia; Tarim River basin in China; and Everglades National Park in the United States).

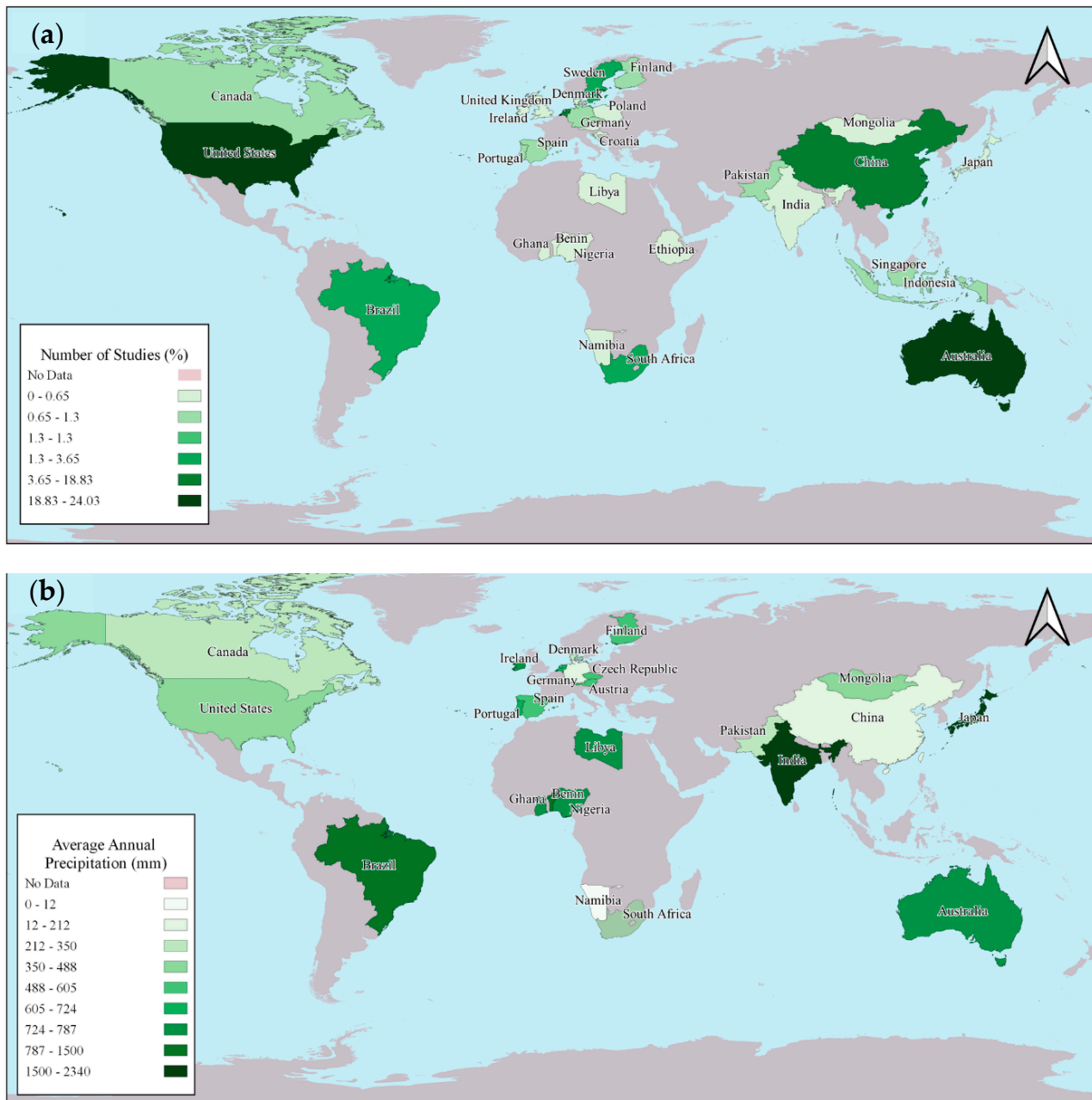


Figure 2. (a) Groundwater–vegetation studies by country and (b) mean annual precipitation mentioned in the reviewed literature.

Here, we showed that most of the groundwater–vegetation studies across the globe are ground-based, followed by simulation, and its combination, such as in Australia and the USA (Figure 3). Some countries, particularly those with a low number of studies, rely heavily on simulation studies (e.g., Benin, Croatia, England, India, and Singapore). Contrarily, the types of studies conducted in some countries are purely ground-based, for example those conducted in Spain, Indonesia, Ghana, and Ethiopia. Greenhouse studies were found only in the United States, accounting for less than 5% of all the studies conducted in the country.

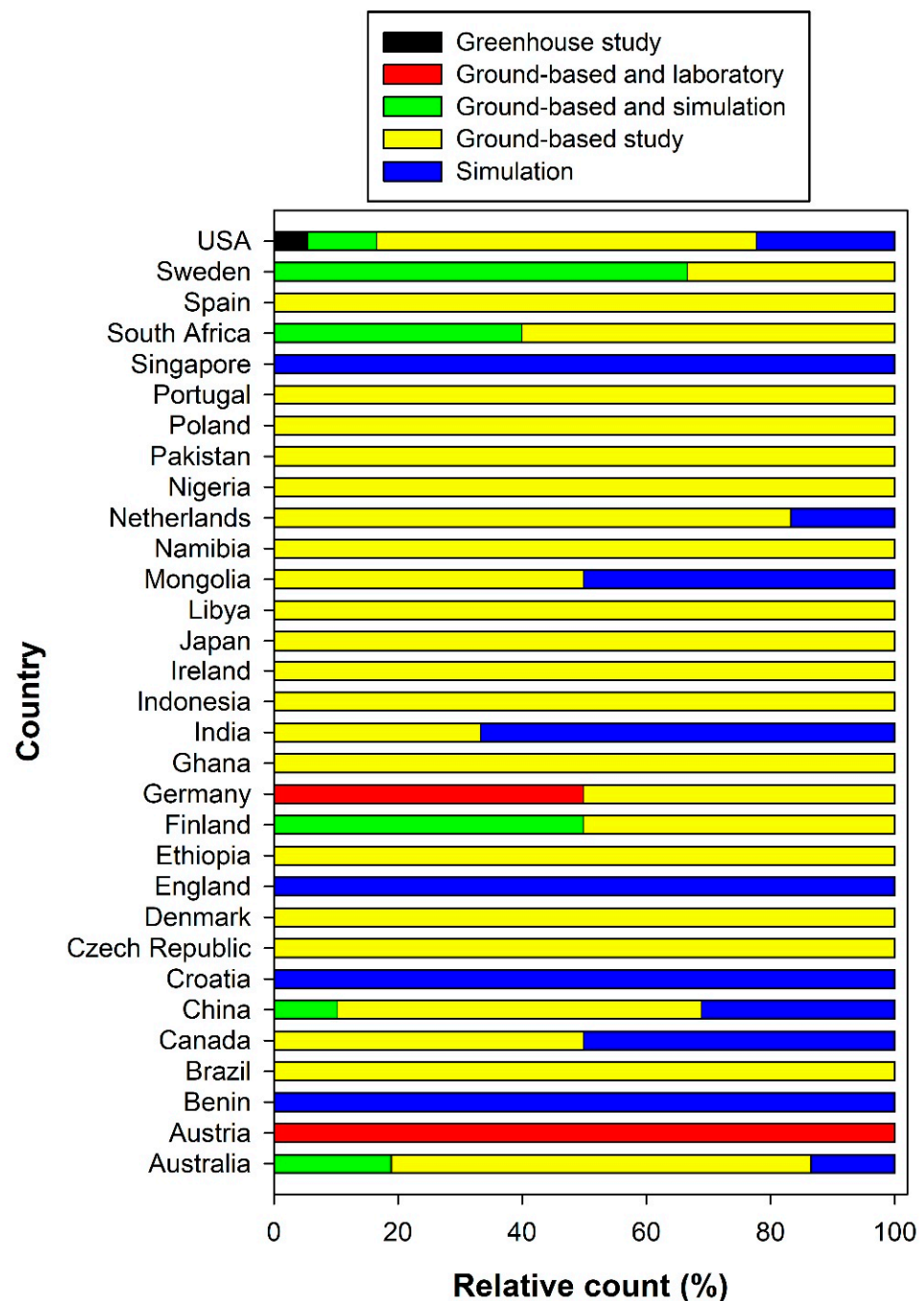


Figure 3. Type of groundwater–vegetation research conducted across the globe.

The groundwater–vegetation research topics were divided into three categories based on the three most commonly tested hypotheses. The effects of the groundwater depth on plant growth, physiology, species diversity, and the community structure were found to be the most frequently studied topics, accounting for 53.65% of all studies (Table 3). The most common methodological approach in this first group of topics is to monitor changes in vegetation and the groundwater depth over time using commonly measured parameters such as the species diversity, evenness, dominance, composition, and distribution, as well as the Normalized difference vegetation index (NDVI). The groundwater physicochemical characteristics (water quality, groundwater flux/use/recharge/storage) were also common in the reviewed studies, as was the groundwater depth monitoring. The analysis of the changes in the xylem vessel characteristics of the phreatophytes across

varying groundwater depths using dendrochronological/cross-dating techniques were also common. Many studies also used hydrological modeling, stable isotope techniques, and thermocouple psychrometry to correlate plant traits (such as growth and physiology) with soil physicochemical properties, environmental conditions, and groundwater depth.

Table 3. Research topics, parameters, and methods based on the frequently tested hypotheses about groundwater–vegetation relationship.

Tested Hypotheses	Relative Count (%)	Frequently Measured Parameters	Frequently Used Methods
Plant growth, physiology, species diversity, and community structure are related to groundwater depth.	53.64	Species evenness/diversity/dominance/distribution/composition, plant communities/growth/mortality/distribution/type, Normalized difference vegetation index (NDVI), xylem vessel characteristics, groundwater flux/use/depth/recharge/storage, soil physical and chemical properties, environmental conditions	Dendrochronological technique/cross-dating, stable isotope techniques, groundwater monitoring, vegetation monitoring, thermocouple psychrometry, remote sensing (Landsat), hydrologic modeling
Tree/farm plantations deplete groundwater due to increased evapotranspiration.	44.37	Evapotranspiration, root uptake/density/depth/length, stem sap flow/xylem water, leaf water potential, and environmental conditions	Zero-flux plane (ZFP) method, Eddy-covariance method, stable isotope techniques, groundwater monitoring, vegetation monitoring, heat field deformation method, heat pulse method, remote sensing (Landsat)
Declines in groundwater depth may promote biological invasion.	1.99	Leaf water potential, groundwater flux/use/depth/recharge/storage, plant cover, species richness	Stable isotope techniques, groundwater monitoring, vegetation monitoring, thermocouple psychrometry

The hypothesis that tree/farm plantations deplete groundwater due to an increased evapotranspiration ranked second (44.37%). The most frequently measured parameters in the second group of topics were changes in the evapotranspiration, root characteristics, stem sap flow/xylem water, leaf water potential, and environmental conditions (air temperature, precipitation, wind speed, relative humidity, and solar radiation). Studies that tested such a hypothesis usually used the zero-flux plane (ZFP), heat field deformation (HFD), and Eddy-covariance methods to measure and estimate the evapotranspiration, sap flux density, and hydrological processes. Groundwater monitoring, vegetation monitoring, and/or remote sensing with Landsat satellite imagery are commonly used to obtain the measurements. Stable isotope techniques were also commonly used to determine the water use efficiency, gas exchanges, plant water's absorption, uptake, and usage, and soil water movement.

Only 1.99% of the research was focused on the relationship between a biological invasion and groundwater depth (Table 3). The commonly used parameters to test whether declines in the groundwater depth may promote a biological invasion were changes in the leaf water potential, groundwater characteristics, plant cover, and species richness. Stable isotope techniques, groundwater monitoring, vegetation monitoring, and thermocouple psychrometry were also used in the studies in this topic group.

In this systematic review, the dominant phreatophytes mentioned in the articles were determined (Figure 4). The *Eucalyptus camaldulensis* Dehnh. (River Red Gum) was the most frequently studied species among the mentioned dominant phreatophytes. This is followed by *P. euphratica* (Euphrates poplar, desert poplar), *T. ramosissima* (Salt cedar), *Banksia attenuate* R.Br. (Candlestick banksia), and *Quercus robur* L. (European oak). The

other dominant species mentioned in the reviewed studies had less than a 3% relative frequency (Figure 4).

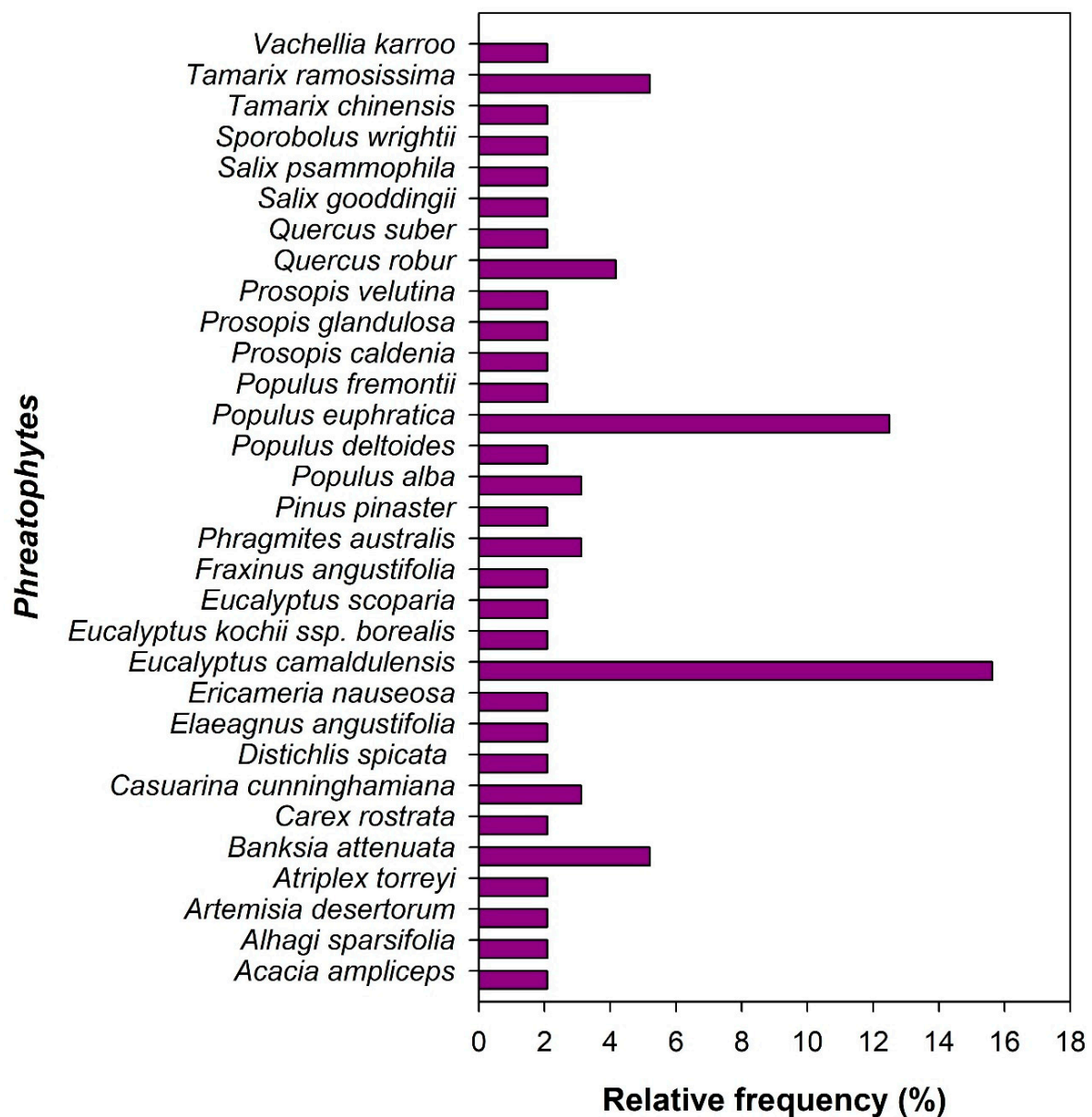


Figure 4. Dominant phreatophytes mentioned in the reviewed articles published between 1988 to 2022.

Lastly, the current systematic review provided a summary of the interactions between modifications to groundwater parameters and phreatophytic vegetation (Figure 5). The changes in the groundwater characteristics that arise from significant changes in the climatic patterns, land uses, and evapotranspiration rates in a specific aquifer typically led to the ecophysiological impacts. For instance, variations in the groundwater depth eventually had a significant impact on the plant root growth, morpho-anatomical features and functions, and physiological processes, all of which had an indirect impact on the growth, diversity, and distribution patterns of the phreatophytes. Serious changes in the groundwater characteristics can also suppress the native phreatophytes and promote the growth of invasive plant species.

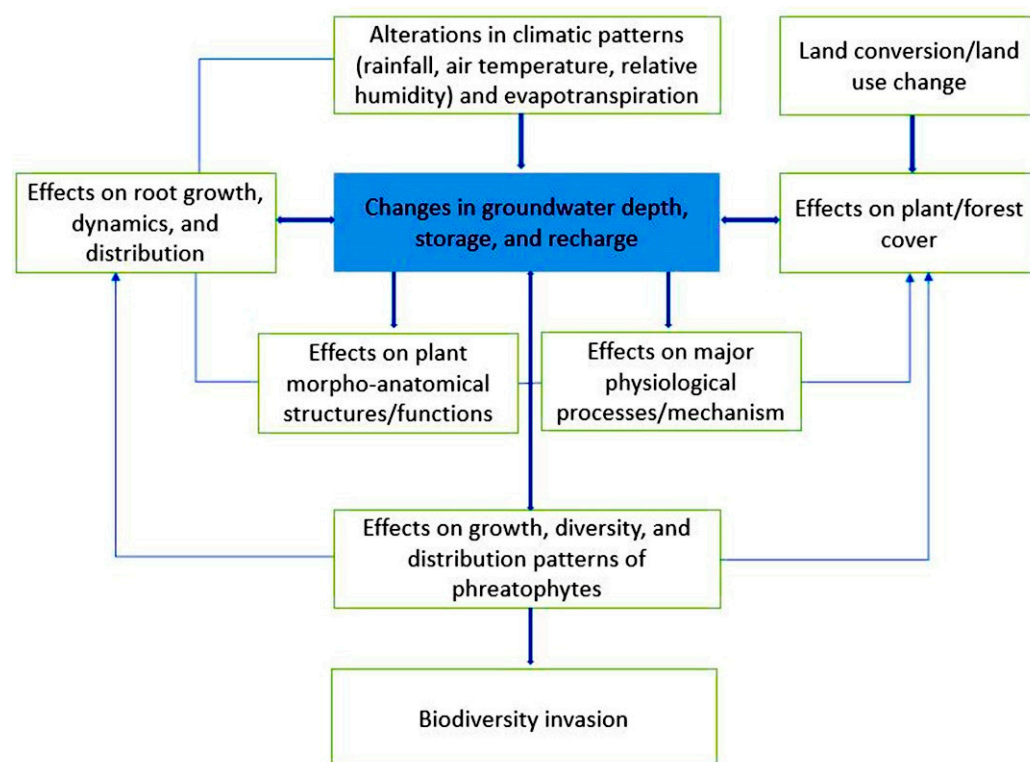


Figure 5. Synergistic effects of changes in groundwater characteristics on phreatophytic vegetation.

4. Discussion

4.1. Trends in Groundwater–Vegetation Research during the Last Three Decades

Here, a high number of studies about the topic was evident in high-income countries (HICs) with arid or semi-arid climates, particularly in ecologically and economically important basins, which serve as important habitat and groundwater resources for biodiversity [22,23]. A rich biodiversity is associated with groundwater discharge zones in Western Australia, where groundwater-dependent vegetation requires groundwater to maintain the function, composition, and structure [24]. Because the Tarim River basin in China has an extremely hot and dry climate, for instance, phreatophytes rely heavily on the groundwater availability [22]. These groundwater-dependent ecosystems, on the other hand, have been identified as the most vulnerable to a groundwater abstraction and utilization, as well as large-scale land use changes. Further, most of the regions with arid and semi-arid climates, regardless of their economic conditions, face enormous groundwater spatio-temporal distribution challenges which have been caused by climate change [25]. As the demand for groundwater is rapidly increasing with climate-induced hydrological changes and human population growth, a high number of studies in Western Australia, North America, and northern China could also be in response to the need to sustain the global economy and provide societal needs (e.g., food and water). This is due to the fact that more than one-third of the water used for sustaining life on Earth and the economy is sourced underground [26–28].

Despite a widespread recognition of the significance of groundwater–vegetation studies, a low number of studies to obtaining no data in low-income countries (LICs) can be attributed to financial and technical constraints in conducting labor-intensive research, such as groundwater monitoring studies. A study shows that while North America, western Europe, and East Asia had the highest share (i.e., >40%) of global research, countries in central Asia and northern Africa had less than a 1% share despite positive perspective of LICs on research [20,29]. Ground-based studies, which are mostly done through long-term groundwater and vegetation monitoring, were the dominant type of research in this review, particularly in HICs. This may be difficult for LICs because groundwater-related studies

are typically based on discrete measurements (borehole scale) [30]. In the reviewed articles, simulation studies using remotely sensed data ranked second as the most common type of study, particularly in HICs. Because the reviewed studies were mostly conducted on the ground, technological advances in the in situ monitoring designs and remote sensing techniques may be lacking. Furthermore, when compared to other types of studies, the costs of analytical techniques for measuring the most common parameters used to monitor the responses of groundwater-dependent vegetation to groundwater changes are relatively high. Among the techniques covered in this review were dendrochronological techniques (tree-ring dating), stable isotope techniques, Eddy covariance, and elemental analyzers, which all require intensive financial inputs. Overall, both groundwater–vegetation research and simulation studies necessitate significant inputs of resources (e.g., labor, capital, and technology), leaving resource-limited LICs far behind in groundwater–vegetation research.

4.2. Are Plant Growth, Physiology, and Species Diversity Related to Groundwater Depth?

Phreatophytes are highly plastic to water-deficient environments through dynamically adjusting the root growth and distribution for the effective foraging and uptake of water [31,32]. A modeling study, however, revealed the effects of root dynamics on the plasticity of phreatophytes to water-deficient environments may depend on the rate of the root growth, particularly when the groundwater decline exceeded 0.8 cm day^{-1} [31]. The increase in the root depth of pines [33] and oaks [34] under a decreasing groundwater level exemplify such a high root plasticity. The present review found that several oak species are the dominant phreatophytes, which could be explained by their deep rooting characteristic as a physiological strategy to cope with water scarcity [35]. Plants with the ability to send roots to great depths and access the groundwater table can generally withstand drought while maintaining a leaf water potential [36]. Moreover, some *Eucalyptus* species are normally found in phreatophytic communities as they can also thrive even in areas where the groundwater depth exceed the plant rooting depth [37]. This could explain the reported high dominance of *E. camaldulensis* and *P. euphratica* in the study sites of the reviewed articles. *E. camaldulensis* possesses deep sinker roots which grow deep towards areas of a higher water supply [38], including groundwater, and have high rates of a hydraulic conductivity [39].

Some species of phreatophytes invest in developing a dense network of dimorphic roots (with two distinct root forms) that are linked to other penetrating roots (e.g., sinker and taproots) to efficiently access the groundwater [34]. Other deep-rooted phreatophytes exhibited a water adaptation phenomenon called a hydraulic lift (HL) when they experienced extreme drought conditions as the groundwater depth increased. An HL is defined as the translocation or release of soil moisture through root systems in response to soil water potential gradients [40]. Trees use topsoil water during normal conditions and groundwater with a hydraulic lift during seasonal drought [34]. An example of phreatophytic tree species that exhibit a hydraulic lift mechanism is *P. euphratica* [41]. This species has the ability to lift water from deeper to shallow soil layers [42].

Groundwater is a major source of water for plant transpiration, influencing other phreatophyte physiological processes. As a result, interactions between soil, groundwater, and plant roots may affect the photosynthetic responses and plant–water relationships as the groundwater depth increases. In an arid environment, for example, the net photosynthetic rate of *P. euphratica* was strongly related to the groundwater depths, and the species relied on a stomatal limitation and osmotic adjustment when exposed to a limited water supply [43]. Without groundwater access, Myrtaceae shrub species showed significant reductions in the xylem water potential and stomatal conductance, particularly during seasonal drought [44]. The effects of fluctuations in the groundwater on the xylem water potential may also control carbon partitioning via changes in the phloem pressure gradients [45]. This is because the xylem water potential is affected by the sapwood–heartwood ratio, root and stem pressure, and hydraulic conductance. Furthermore, the sapwood-related sap flow influences a plant transpiration as the groundwater depth increases. A

study found low sap flow values in deep (30 m) groundwater zones or areas where the groundwater depth had increased significantly [46]. Moreover, a reduction in the xylem hydraulic capacity of oak trees growing in sites with a groundwater extraction was also reported in groundwater-fed forest stands in south-western Germany [47].

Phreatophytes are thought to respond to an extreme groundwater limitation by adjusting their anatomical structures. The vascular features (vessel size and density) of hydrologically altered stems of *Populus x euramericana* were strongly governed by the water supply in the study site in the reviewed studies [10]. The authors also discovered that the vessel's size and density were related to the circumferential stem growth. The vessel-related variables (e.g., the mean vessel area) of oak species in groundwater-extracted forest stands correlated strongly with soil moisture anomalies [47]. A significant influence of a groundwater level alteration on the tree-ring width and earlywood vessel lumen area was also observed in *Q. robur* [48]. A similar pattern was observed in the case of *Alnus glutinosa* Gaertn. when exposed to groundwater level fluctuations [49]. Overall, these changes in the vessel's anatomical structures may have effects on the hydraulic conductivity and radial growth of phreatophytes.

The effects of a groundwater depth fluctuation on a plant's anatomy and physiology may have a significant impact on the dynamics of plant growth and productivity, nutrient cycling, and, ultimately, species diversity. Old and large diameter *P. euphratica* trees (>80 years old) dominated the Tarim River in northern China, indicating that the groundwater depth had a significant effect on the species' growth and productivity [50]. Dendrochronological techniques revealed that the growth of *Prosopis caldenia* Burkart trees was enhanced at optimal depths (i.e., 2–8 m), whereas decreasing the depth (i.e., 2 m) resulted in the death of the trees in Argentina's semiarid woodlands [51]. A different pattern was observed in northern humid forests using tree cores from the *Pinus resinosa* trees, namely a decreasing effect of groundwater as the groundwater depth increased (1–5 m below land surface) [52]. A simulation study using 500-year data showed a wide range of groundwater depths which had a positive impact on the development of biomass and a species' composition [53]. In Amazonia, a similar pattern was observed, with long-term inventory plots in a shallow water table (5 m) having a lower aboveground productivity and biomass production than those in the deep-water table [22,54]. Furthermore, several studies have found a significant interacting effect of the water table depth and climatic factors on the growth and productivity [54,55].

Here, topics answering the research question on whether groundwater dynamics drive significant impacts on the forest dynamics, particularly species diversity and the plant community structure, were also dominant. The river-groundwater interaction controlled the zonation of the species composition and diversity in an arid riparian ecosystem [56]. When the groundwater depth exceeds 4 m, the Shannon–Wiener index, Simpson index, and Pielou index all decrease significantly, resulting in a low overall vegetation coverage in China's Desert Riparian Zone [57]. A similar pattern was observed in an arid grassland ecosystem, i.e., the plant species diversity decreased with an increasing groundwater depth, and it was not related with a depth greater than 3.5 m [58]. This is most likely due to the short root length of the grassland herbaceous plants [59]. Seasonal variations in the groundwater depth along topographic gradients had a greater impact on the tree density and diversity in savannas than the soil and groundwater nutrient variations [60]. Tree abundance and diversity were found to be lower in shallow groundwater (0.18–1.31 m) than in deep sites. This is due to savanna trees' inability to tolerate excessive soil water during the wet season and insufficient soil water during the dry season at low elevations where larger groundwater level fluctuations were observed. Restricted aerobic zones (anoxic condition) may significantly restrict the root growth of savanna trees during waterlogged and water-deficit conditions during wet and dry seasons, respectively, controlling the vegetation structure [60,61]. The relationship between the depth-to-groundwater and plant community ecological properties is visible not only in arid and semi-arid ecosystems, but also in mesic ecosystems. For example, the decline of some oak species in Croatia's

Drava valley has been linked to an increase in the absolute mean groundwater level [62]. Furthermore, in mesic *Eucalyptus* woodlands in Australia, the plant species composition varied significantly across the groundwater depths (2.4 m–43.7 m) and was independent of the effects of other environmental factors [63]. The same study, however, discovered no direct relationship between the groundwater depth and total plant abundance. The authors attributed the findings to the species' varying abilities to tolerate waterlogged and dry conditions at shallow and deep groundwater sites.

4.3. Can Tree Plantations Deplete Groundwater Resource?

The most well-studied research topics were those that supported the “infiltration–evapotranspiration trade-off hypothesis.” According to several studies, large-scale tree planting for reforestation and afforestation programs may endanger groundwater resources, particularly in arid and semi-arid regions [64–66]. Previous research found a strong link between an increased forest biomass production and a decreased stream flow due to an increased evapotranspiration [65,67]. This is because plantation evapotranspiration may exceed precipitation, exacerbating water shortages from groundwater sources. If not exceeding precipitation, some obligate phreatophytes (e.g., *Quercus douglasii* Hook. & Arn.) tend to have a high evapotranspiration (i.e., 80%) which comes primarily from the groundwater [68]. *Eucalyptus grandis* W. Hill ex Maiden and *E. camaldulensis* Dehnh. Plantations derived approximately 15% of their transpiration requirements from groundwater at sites with a relatively low rainfall [69]. Some of the fast-growing phreatophytes (e.g., *Populus* spp.) also have a greater transpiration rate than the precipitation the site usually received, resulting in a further decline in the groundwater table [70]. A study conducted in Australia, for example, discovered that the mean annual evapotranspiration ($1090 \text{ mm year}^{-1}$) in *Pinus radiata* D. Don and *E. globulus* Labill. plantations was greater than the site's mean annual precipitation (630 mm year^{-1}) [71]. The analysis also revealed a declining trend in groundwater resources in the Inner Mongolian Plateau, which corresponded to the NDVI trend, with the decline attributed primarily to the negative effects of evapotranspiration and a low precipitation [72]. Furthermore, the groundwater salinization in the afforested plots in the Argentine Pampas was attributed to the groundwater consumption by planted trees, as well as the evapotranspiration [73].

The reviewed studies also suggested that, while afforestation can boost primary production, it can also degrade the water resource quality due to the tree water use, climate, and soil texture. Field experiments, for example, revealed that afforestation reduces the surface runoff by up to 20% due to the forest canopy interception [74]. They also discovered that afforestation can significantly reduce the groundwater recharge (the downward movement of surface water to groundwater) due to the tree soil uptake and increased water holding capacity of the forest soils. A similar study found that among land uses, forests had lower groundwater recharge rates, and restoring bare land further reduced the recharge rates in semi-arid tropical/subtropical regions [75]. This pattern corresponds to the opposite effect of clearcutting, that is, an increased groundwater recharge [76]. A similar study demonstrated that when forests are converted to a different land use with less canopy cover, the groundwater recharge increased by about 8% [75]. Overall, evidence suggests that tree plantations can deplete groundwater resources.

4.4. Can a Decline in Groundwater Depth Promote Biological Invasion?

Invasive tree species have been shown in studies to have a significant impact on groundwater depths or catchment water budgets [76,77]. Specifically, groundwater use by *Prosopis* sp., which is one of the phreatophytic invasive alien plant species (IAPS) worldwide, affected the surface runoff, groundwater recharge, and evaporation [78]. Invasive phreatophytic species have also been shown to reduce the precipitation available for the groundwater recharge [79]. In Africa, it was reported that a species of *Prosopis* had a high estimated water use ($3.1\text{--}3.3 \text{ billion m}^3 \text{ yr}^{-1}$), resulting in serious impacts on the availability of water [77]. In an attempt to investigate the effects of clearing on the groundwater use by an

invasive *Prosopis* tree plantation, experiments showed that up to $70 \text{ m}^{-3} \text{ month}^{-1}$ of water can be saved for each hectare of the plantation cleared [76]. This suggests that deep-rooted invasive species can excessively use a groundwater resource and distract hydrological and ecological processes, especially in an arid environment. These groundwater effects were attributed to the invasive species' deep-rooting characteristic, highly water-consuming ability, active water uptake, and evergreen leaf habit, which could further increase the groundwater abstraction throughout the year [77]. As a result, invasive tree species with such characteristics may compete for the groundwater resources which are necessary for the growth and survival of other indigenous species, particularly in water-stressed areas. As hydrological regime fluctuations result in a species replacement, declining groundwater may increase the competition among species and expand the invasive ones [80]. According to one study, an invasive species stands consumed more groundwater and had a higher evapotranspiration than indigenous species stands [81], posing a threat not only to the water resource but also to the native plant diversity. Overall, a significant drop in the groundwater levels can suppress indigenous plant communities and encourage a biological invasion.

5. Conclusions and Way Forward

Finally, the present systematic review was the first to synthesize the trends in groundwater-vegetation research topics and methodology. It was discovered that the majority of the studies (mostly ground-based) came from arid or semi-arid high-income countries, whereas the majority of low-income countries, particularly those in the arid and semi-arid zones between latitudes of 15° and 30° in both the northern and southern hemispheres, had a low number of studies. In terms of research topics, studies on the effects of the groundwater depth on plant growth, physiology, and species diversity yielded the highest percentage, followed by studies on the effects of tree plantations on groundwater resources and the relationship between a decline in the groundwater depth and a biological invasion. The commonly measured parameters in the first group of topics include the species' diversity, evenness, dominance, composition, and distribution, as well as the Normalized difference vegetation index (NDVI) via a vegetation monitoring or plant surveys, and groundwater monitoring. Changes in the evapotranspiration, root uptake/density/depth/length, stem sap flow/xylem water, leaf water potential, and environmental conditions were the most frequently used parameters in the second group of topics. Lastly, changes in the leaf water potential, groundwater depth, plant cover, and species richness were frequently used parameters to determine whether a decrease in the groundwater depth promotes a biological invasion.

We discovered that changes in the groundwater had a significant impact on the plant's growth, physiology, and plant community structure via changes in the morpho-anatomical traits (e.g., the root length, root density, xylem vessel diameter, and vessel density), physiological traits, and plant community structure (e.g., transpiration, xylem water potential, and carbon assimilation). The general pattern observed is that as the groundwater depth increased, the phreatophytic vegetation growth, productivity, diversity, and composition decreased across the ecosystem types. The current review also discovered that the majority of studies reported a decrease in the groundwater resource as a negative impact of large-scale tree plantations due to increased evapotranspiration rates, particularly in hyper-arid zones. Finally, a significant drop in groundwater levels can suppress indigenous phreatophytes and favor invasive ones, which are more generalist and better adapted to changing environmental conditions. Overall, groundwater fluctuations may have ecological and physiological effects on phreatophytes, although the magnitude may vary depending on the variable interactions (e.g., species characteristics, location, and environmental factors). The review also noted that a combination of chronic groundwater extraction and abiotic stress (e.g., drought) may exacerbate the effects which have been identified.

As a result, there is significant space for progress in undertaking studies relevant to the integrated and sustainable conservation and management of groundwater-dependent

ecosystems in the context of practical and contemporary concerns (e.g., climate change). More research is needed on the balanced negative and positive effects of a groundwater extraction, massive land-use changes, such as large-scale tree planting programs (e.g., reforestation), on the groundwater supplies and groundwater-dependent ecosystems, particularly in resource-poor countries or hyper-arid regions. Sophisticated approaches for field-based, modeling, and greenhouse investigations are required, especially in data-poor, hyper-arid areas. Multidisciplinary studies to uncover the complexity of a groundwater and vegetation interaction, as driven by climate change, may potentially be included in future work.

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