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Authors: Yoseph N. Araya, David J. Gowing, Nancy Dise

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ACCEPTED MANUSCRIPT

	1	A controlled water-table depth system to study the influence of fine-scale
1 2	2	differences in water regime for plant growth
3 4	3	
5 6	4	Yoseph N. Araya ^{1*} , David J. Gowing ¹ and Nancy Dise ²
7	5	
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22	13	
23 24	14	Abstract
25 26	15	
27 28	16	A method was developed to maintain water-table depths at a constant level in outdoor
29 30	17	mesocosms. The system included a water treatment reservoir, where tap water was
31	18	microbially deoxygenated and denitrified; an adjustable-level control chamber that set
32 33	19	desired water table-depths and plant growing mesocosms.
34 35	20	
36 37	21	The soil water status was evaluated by constant monitoring using tensiometers,
38 39	22	pressure transducers and dipwells. The robustness of the system was tested by
40 41	23	inducing sudden incidents of flooding and drainage. The system was able to revert to
42	24	the original set water-table depths within 5 and 10 minutes respectively. It also
43 44	25	reliably sustained consistent water-table depths throughout the growing season
45 46	26	without the need for maintenance.
47 48	27	
49 50	28	As an example, the method was used to grow plants at five set water-table depths: 50,
51 52	29	150, 250, 350, and 450 mm below ground surface. Two wet grassland species Festuca
53	30	pratensis (meadow fescue), and Carex nigra (common sedge) were grown and dry
54 55	31	biomass production recorded. Results showed differences in growth response between
56 57	32	the two species to subjected water-table depths. In monoculture, F. pratensis
58 59	33	production followed the order $50 = 150 = 350 > 250 = 450$ mm (p <0.001), while for
60 61	34	C. nigra it was $150 = 250 > 50 = 350 = 450$ mm (p<0.001). In mixture, F. pratensis
62		

did not show a significant trend (p < 0.06), whereas *C. nigra* showed 50 = 150 > 250> 350 = 450 mm (p < 0.001).

The ease of the system to establish constant and or dynamic water-table depths and its reliability outdoors renders it useful for a wide variety of studies involving plant growth.

42 Key words: water-table depth • plant production • soil moisture • niche
43 separation

1. Introduction

Simplified artificial communities and mesocosm experiments are suitable for competition studies, not only by reducing complexity of nature but also due to the high degree of experimental control possible, repeatability and amenability to rigorous statistical design (Fraser and Keddy, 1997; Gibson et al., 1999). Such studies also allow the study of the mechanisms of interaction, such as effect and response (sensu Goldberg, 1990) and determination of relative efficiency (Connolly et al., 1990). It follows then, for any such study to be successful mesocosms need to be designed appropriately.

Soil water status is an important environmental factor affecting several soil and plant processes, particularly in wetland ecosystems. Subtle variations in soil water levels are known to produce significant effects on plant physiological response and soil nutrient availability, thereby influencing experimental work (e.g. Davies and Gowing, 1999; Paul et al., 2003). Therefore, the ability to maintain a constant soil moisture tension over an extended period of time, with actively growing plants and under controlled experimental conditions is essential for environmental and ecological research.

A number of systems to maintain constant water tension have been developed for growth cabinet and greenhouse applications, most in the past 20 years or so. Examples used within growth cabinet were: irrigation with porous steel tubes (Cao and Tibbitts, 1996; Steinberg and Henninger, 1997); and continuous circulating water under negative pressure (Lipiec et al., 1988; Iwama et al., 1991). Snow and Tingey (1985) and Wookey et al., (1991) worked on simpler systems whereby plant pots were suspended above a water column of known depth. Similarly, a capillary mat irrigation system was used under greenhouse conditions by Hoffman et al., (1996). Also, Mueller-Dumbois and Sims (1966) used a container resting inclined over a source of water, thus creating numerous water-table depths over the whole length of the incline plane. At mesocosm scale, turf was grown on a fine sand column with drainage holes fitted at the required depths (Berendse and Aerts, 1984) and water supplied via a piezometer on a daily basis (Van Oorschot et al., 2000).

Often the circulating water and irrigation growth cabinet systems are expensive to construct and maintain. Similarly the "turf on sand" column systems require daily water supply and do not guarantee a constant water-table depth throughout the day. Moreover, some irrigation methods require uniform aggregate ceramic substrate instead of soil, while the circulating water systems have difficulties in maintaining water tension for extended periods of time without siphon failure. Furthermore, the growth cabinet and greenhouse methods in the above examples do not lend themselves easily to outside use. We have developed a novel system to overcome these problems by maintaining constant water-tables outside over a complete growing season. It was also designed to be low cost, and easy to construct, while at the same time easy to maintain and manipulate. The system followed the principles of Snow and Tingey (1985), with certain modifications for use outdoors, including accounting for incoming precipitation and providing a supply of water approximating groundwater.

In this paper the controlled water system is used to study the influence of fine-scale differences in water regime on plant biomass production between two species as an example.

2. Materials and Methods

2.1 Controlled water-table depth system

The controlled water-table system was established at the Open University field site in spring 2003 and still functions to date. The controlled water-table system is composed of three subsystems (Fig.1): a reservoir tank, a control float chamber, and mesocosms themselves. The system operates with a simple ball-valve principle in which the water depth in the plant growing pots and the control chambers equilibrate due to gravity.

The water to the reservoir tank (capacity *ca.* 1200 L) was supplied from a local mains tap. This water was treated by submerging dried molassed sugar beet shreds (Trident

<< Figure 1 >>

110 Feeds (a), Peterborough) at 5 kg month⁻¹ m⁻³ of water, renewed monthly. This was 111 done to stimulate microbial activity, thereby deoxygenating and denitrifying the 112 mains water, thus preventing a source of supplementary nitrogen. Analysis of water 113 samples showed a 90% reduction in dissolved oxygen (from 0.24 mM at inlet to 0.02 114 mM at the outlet); the concentration of nitrate ions decreased from 1.0 μ M in the 115 mains water to 0.07 μ M in the water supplied to mesocosms.

The control float chamber was composed of an 18 L container fitted with a ball-valve apparatus. The valve regulated the flow of water from the reservoir tank into the chamber and subsequently into the mesocosms. The depth of the water level in the control chamber and its height above-ground was adjusted to give desired level in the mesocosms. The chambers were then automatically refilled by water from the reservoir tank to compensate for evapotranspiration losses. Overflow drainage holes were made at the desired water level in the float chamber to allow water entering the chamber as a result of precipitation falling on the mesocosms, to drain out of the system.

Five control float chambers were established to create water-table depths of 50, 150, 250, 350 and 450 mm below the soil surface in the mesocosms. The control chambers were connected by branching hose pipes (diameter 12.5 mm) to the individual mesocosms. The heights of the water level in the control chambers and the soil surface of the plant pots were set using total station surveying equipment (T705, Leica Geosystems[®], Switzerland).

Cylindrical containers made of durable polyvinyl chloride (height 550 mm, diameter 360 mm) were used with a connection to the control float chamber via a pipe fitting at their base. The pots were filled with layers of gravel, sand and loam. The bottom 50 mm of the pot was filled with gravel to ensure a porous, permeable zone for incoming water to disperse uniformly across the mesocosm. Woven polyester fabric was placed on top of this gravel to exclude contamination by the 300 mm deep fine sand layer above it. This sand had a uniform particle size of 225 µm (WBB Minerals[®] RH65) and provided a conductive medium for water under tensions up to 5 kPa. The top 150 mm depth of the profile was filled with a uniform loam mixture (at a density of 1.3)

Mg m⁻³) prepared by mixing 1:1:2 proportions of peat moss, loamy topsoil (Frilford soil series, Bedfordshire, UK) and coarse sand. Furthermore, each pot was inoculated with 100 g of soil from a botanically diverse floodplain meadow, Cricklade North Meadow National Nature Reserve (UK National grid reference SU096958), to transfer existing microbial population. The loam mix had pH of 8, 2.1% C and 0.11% N, 65 mg kg⁻¹ extractable K, 65 mg kg⁻¹ extractable P and 22 mg kg⁻¹ potential mineralizable N. Table 1 gives its moisture release characteristic.

<< Table 1>>

Experimental plants were placed into this loam mix, with roots prevented from entering the fine sand by using a 52 µm nylon mesh (Plastok®) (Fig. 1). Having tested a range of meshes between 30 and 175 µm, a mesh size of 52 µm was selected as it effectively stopped plant root growth, while remaining sufficiently porous to the passage of water. This mesh size compares with similar material used by other investigators for the same purpose (Bethlenfalvay et al., 1991; Kothari et al., 1991). The mesh completely surrounded the loam mix (root zone) to prevent the roots penetrating around its edges.

For the study, three genets each of Festuca pratensis (meadow fescue) and Carex nigra (common sedge) were collected from Cricklade North Meadow. These two species were chosen as they have been observed to coexist in the field, albeit with differing water regime requirements (Gowing et al., 2002). They were asexually propagated in the greenhouse by splitting and kept to mature for one year before the start of the experiment. One clone of each genet from each species (six plants in total) were planted in three combinations: two monocultures and one mixture. The use of clonal materials aimed to standardize genetic diversity (e.g. Antonovics, 1987; Wijesinghe and Hutchings, 1997). The plants were then grown in four replicates at the five water-table depths of 50, 150, 250, 350 and 450 mm below the surface for four months before harvest. Basal nutrients were supplied bimonthly with modified Long Ashton solution (Hewitt, 1952) at full strength dose of 1 L mesocosm⁻¹.

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2.2 Data collection and analysis

The mesocosm system was assessed for reliability by examining soil water tensions. The outcome of plant growth was studied by examining production.

Soil moisture was monitored using both dipwells and tensiometers (type SWT3, Delta-T® Devices Ltd, Cambridge, UK). Daily water level fluctuations were monitored using pressure transducers (Eijkelkamp[®] Divers. The Netherlands), which were also used to assess the stability of water levels especially in response to periods of high evaporative demand and high rainfall.

Above-ground plant production was assessed by harvesting at 20 mm height above the soil surface. The harvested plant matter was then dried at 55 °C for 72 h before weighing. Plant roots were sampled by taking a core of 50 mm diameter and 100 mm depth (volume 1.96 x 10^{-4} m³). Two cores were taken from each monoculture treatment and three cores from each mixture mesocosm.

Collected data were analysed using the analysis of variance on Statistica® 7.0 platform.

3. Results

The treatment growth period lasted four months from April – July 2004. During this period the mean temperature was 14 °C (range 0 - 26 °C) and precipitation 260 mm.

3.1 Comparison between expected and observed water-table depths and maintenance of water level

The water-table depth across the range of treatments was shown to control the soil matric potential (ψ_m) in the top 50 mm of each mesocosm (p < 0.001) (Fig.2).

<< Figure 2>>

	207	
1 2	208	Pressure transducer readings made at five minute intervals over the full growing
3 4	209	period showed that the water levels varied by less than \pm 15 mm, even during periods
5	210	of high evapotranspiration (Fig. 3). Most of this variation was direct response to
2 7 2	211	diurnal temperature fluctuations. Regular manual dipwell readings also correlated
9	212	with the pressure transducers readings ($r^2 = 0.99$, p <0.01).
) 1	213	
2 3	214	<< Figure 3>>
4 5	215	
5 7	216	The response of the system to perturbations was also tested by artificially-induced
, 3	217	drainage and flooding. Flooding was achieved by supplying external water using a
)	218	hose and drainage by disconnecting the water inlet pipe at mesocosm level. Pressure
1 2	219	transducer readings showed it was possible to restore the target water-table elevation
3 4	220	within 5 and 10 minutes respectively, following the perturbation (Fig. 4).
5	221	
- 7 2	222	<< Figure 4>>
9	223	
1	224	3.2 Plant response along a gradient of water-table depth
2 3	225	
4 5	226	The analysis of variance demonstrated a significant effect of water-table depth on
5 7	227	species production (Table 2). The response of individual species is illustrated by
3	228	Figure 5a and 5b, for monoculture and mixture combinations respectively.
)	229	
2	230	<< Table 2>>
3 4	231	<< Figure 5 >>
5	232	
7 3	233	The yield in monoculture for both species showed higher production mostly in the
9	234	wetter end of the water-regime (50 mm for F. pratensis and 150 mm for C. nigra).
1	235	The yield in mixture showed a pronounced difference in the response between the two
3	236	species. Yield of F. pratensis was largely sustained across the range whilst C. nigra's
1 5	237	yield showed a significant decline with increasing water-table depth, particularly at
5 7	238	and beyond 250 mm.
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4. Discussion

Fine-scale differences in water-table depth are known to structure plant communities the field (Silvertown et al., 1999). Conducting experimental work on such populations in the laboratory requires ability to simulate field conditions as closely as possible without losing experimental control. The method described here for controlling watertable depth in outdoor mesocosms is one such solution.

In this method, it was shown that desired water-table depths and soil matric potentials could simply, yet precisely be manipulated by raising or lowering the heights of the control chambers. This is an important advantage in that, if desired, the system could be used to simulate a dynamic water-table as can be experienced in the field. This also overcomes the challenges faced by several earlier stationary systems (e.g. Berendse and Aerts, 1984; Van Oorschot et al., 2000) where water level was mainly controlled by drainage holes. Moreover, our system has the capability to ensure continuous maintenance of subjected water levels, by constantly refilling water lost due to evaporation.

Unlike most controlled systems which require specialist growth matrix and irrigation media (e.g. Cao and Tibbits, 1996; Steinberg and Henninger, 1997) the materials required for our system are comparatively inexpensive and easily available. In addition, our system uses simple gravity principles for water movement, thereby avoiding the need for pressurised circulation systems (Lipiec et al., 1988; Iwama et al., 1991). This is important not only to minimize cost of running the system but also to remove the risk of the siphons breaking down, as happens over extended time duration. Once established the system we built can sustain water-table depths over years, as tested in practice.

In addition to providing full control of water-table depth as in experimental systems, the set-up can be safely left to weather elements outdoors. For example, the system has proved to be robust in maintaining set water-table depth, even when subjected to sudden changes in precipitation and periods of high evapotranspiration demand. Such exposure of the system, to existing meteorological conditions (e.g. sunlight hours,

evapotranspiration, wind) during experimental work means it essentially matches field
conditions. As such, it enables realistic field-level upscaling of experimental findings.

The example experiment conducted on five water-table depths was completed successfully and was able to tease out subtle differences in plant response. Both species in monoculture showed significant response to differences in water-table depth, with their production optima coinciding, e.g. reduction in production occurring at matric potentials > 350 mm. However in mixture their optima were displaced and the shapes of response differed from that observed under monoculture. As such, the optimum for C. nigra shifted toward the higher water-table elevation and F. pratensis to the lower when mixed. These results also corresponded to phytosociological observations made on the two species in the field (Gowing et al., 2002).

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382 FIGURE CAPTIONS

Figure 1 Controlled water-table depth system. Schematic diagram is shown on top.
Photos show (i) control chambers, (ii) a single mesocosm, and (iii) details of a single
control chamber.

Figure 2 Relationship between water-table depths and soil matric potential (ψ_m) in the top 50 mm of each mesocosm. Bars indicate standard deviation (r²=0.99, p<0.001).

Figure 3 Pressure transducer readings of water-table elevations during a sample week
of 10 August – 16 August, 2003

Figure 4 Response of the system to sudden perturbations of drainage (top) andflooding (bottom). Arrows indicate onset of perturbation.

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Figure 5 Biomass production of *F. pratensis* and *C. nigra* in response to water-table depth in monocultures (a) and in mixture (b). Post-hoc Tukey ranking at p = 0.05, is indicated by a, b, c for *F. pratensis* and x, y, z for *C. nigra*. Bars show standard error.

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Table 1.

Soil water content and soil air-filled pore space at selected water tensions

Soil Water Tension	Soil water content	Air-Filled Por
(mm)	(% volume)	Space (%)
0	44	0
50	39	5
100	40	7
200	37	15
300	28	16
400	26	18
500	20	24

Table 2.

Analysis of variance on the effect of water-table depth treatments (50, 150, 250, 350 and 450 mm) on *Festuca pratensis* and *Carex nigra* biomass

Species	d.f.		Pr	oduction	
		Monoculture			Mixture
		F	р	F	р
F. pratensis	4	11.51	< 0.001	0.75	0.571
C. nigra	4	8.42	< 0.001	40.01	< 0.001
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