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Assessing Flood Tolerance Potential of Papaya Germplasm at the Juvenile Stage

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Authors' contributions

This work was carried out in collaboration between all authors. Authors IOB, BMD, KBO and MKO designed the study, performed experiments and wrote the first draft of the manuscript. Authors KA, SOE and JNB managed the literature searches and analyses of the study. All authors read and approved the final manuscript.

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ABSTRACT

Aims: To assess flood tolerance potential of papaya germplasm and determine physiological basis of observed tolerance.
Study Design: Both Experiment 1 and 2 were in RCBD with 2 and 3 treatments respectively.
Place and Duration of Study: Experiments were conducted in a screen-house at the Kwadaso Station of Crops Research Institute, Ghana between February and September 2014.
Methodology: Six weeks old seedlings of 30 papaya accessions were subjected to 90% partial flooding (F90) by standing planting bags with seedlings in 15 L bucket filled with water up to 90% of height of soil level in bags. Control (non-stressed: NS) plants were watered regularly for 1 week. Post flooding recovery of seedlings was monitored for 1 week. In Experiment 2, seedlings of 6 papaya accessions were subjected to 100% flooding (F100) or 50% partial flooding (F50) for 5 weeks, and a post flood recovery period of 6 weeks. Plant height, girth and biomass were measured together with leaf SPAD chlorophyll content, chlorophyll fluorescence, RWC and senescence.

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Results: None of the 30 papaya accessions had high flood tolerance potential, with 60% of accessions studied having low flood tolerance. F90 plants had reduced height and girth relative to control ($p<.001$). Leaf senescence was high in F90 plants ($p<.001$). All six accessions used in Experiment 2 could not withstand 100% flooding longer than 3 days. F50 treatment increased lateral root biomass ($p<.001$), although controls had higher tap root ($p<.001$), total root ($p=.02$) and total plant biomass ($p=.002$) than F50 plants. Leaf RWC ($p=.89$), SPAD chlorophyll content ($p=.05$) and chlorophyll fluorescence ($p=.24$) were not negatively affected by F50 treatment.

Conclusion: None of the papaya accessions studied was able to withstand complete flooding. However, most could tolerate partial flooding of roots for 5 weeks and resume normal growth after release from flood stress.

Keywords: Papaya; Carica papaya; flood tolerance; soil flooding; SPAD chlorophyll content; Chlorophyll fluorescence.

1. INTRODUCTION

The need for irrigation and sometimes the scarcity of arable land drive people to cite agricultural activities near water bodies such as rivers and lakes. Some of these areas may be prone to periodic short term or long term flooding due to poor soil drainage combined with weather events such as storms. Even a defective irrigation system coupled with inadequate soil drainage can lead to temporary flooding.

Further, the effect of climate variability is already being felt around the world with erratic weather patterns inevitably leading to drought and flooding. Areas which may be further away from water bodies are not spared in such drastic events. Although these events are uncommon in certain areas, they occur rather frequently in other areas.

When the soil is waterlogged, excess water displaces air from the air pockets within the soil, whilst the scarce available oxygen is rapidly consumed by plant roots and soil microorganisms [1]. Under such conditions, soil oxygen levels decline to concentrations that restrict aerobic respiration by plant roots [2]. This phenomenon of root hypoxia has negative effects on plant growth and development through altered gene expression, energy consumption and cellular metabolism [3] as well as physiological changes in leaves such as closure of stomata and reductions in leaf water potential and net photosynthesis [4,5].

The decrease in photosynthetic activity observed under flooded conditions results from reduced stomatal aperture [6-9] and decreased leaf chlorophyll content [10,11]. Moreover, reduction in photosynthesis has also been linked to damage to photosystem II [12], resulting from deficiencies in N, P, K, Mg and Ca [11]. Chlorophyll fluorescence measurements have been used to assess damage to photosystem II and consequently photosynthetic efficiency [13,14].

Papaya is a tropical herbaceous fruit tree which is cultivated for its delicious fruits and other plant products such as papain. Papaya cultivation has been boosted in Ghana due to efforts by the government to diversify and increase export of non-traditional crops [15]. However, although papaya has been described as being moderately drought tolerant [16], the crop requires a good amount of water (rainfall or irrigation) for higher yields [17]. This leads many to cite papaya farms in areas with a source of water for irrigation, despite the fact that the area may be prone to waterlogging/ flooding. Papaya is very sensitive to flooding: waterlogging leads to death in a matter of days following closure of stomata and abscission of expanded leaves [16,18,19]. This means that in the event of flooding, there could be complete loss or reduction in income of papaya farmers. Consequently, there is the need to assess the flood tolerance potential of available papaya germplasm in order to advice papaya improvement programmes. Identification of flood tolerant varieties/ accessions will benefit the farmer as well as breeders interested in papaya breeding. Torres-Netto [20] demonstrated genetic variability in papaya cultivar response to water deficit, and we hope that a similar genetic variability in response to hypoxia stress will enable delineation of papaya germplasm into tolerant and intolerant accessions.

The present study was designed to assess the flood tolerance potential of 30 papaya accessions from Ghana and to determine the physiological basis for observed flood tolerance or intolerance.

2. MATERIALS AND METHODS

2.1 Site of Experiment

The experiments were conducted in a screen house located at the Kwadaso Station of the Council for Scientific and Industrial Research – Crops Research Institute (CSIR-CRI) from February to September 2014. The screen house was made of galvanized steel pillars with ash painted iron pipe trusses. The roof was made of transparent (clear) polyvinyl (PV) sheets, whereas the sides were covered with fiberglass mesh to prevent insect intrusion. The screen house of dimensions 11.5 x 7.5 x 3.1 m (Length x Width x Height) had no benches and thus the potted seedlings were set on the floor.

2.2 Plant Materials

Thirty papaya accessions collected from five regions of Ghana namely Ashanti, Central, Eastern, Greater Accra and Volta Region, representing the regions with the highest papaya production, were used in this study. The fruits were harvested at the mature green (with yellow/orange streak) to the yellow/orange ripe stage from home gardens and farms in the five regions and brought to the Kwadaso Station of CSIR-CRI for seed extraction. Seeds were extracted with an abrasive (sand), air dried for three days, placed in air-tight plastic bags and kept in the refrigerator until they were ready for use.

2.3 Planting Bags and Soil

Laminated polypropylene (PP) woven bags of dimension 15 cm x 47 cm (5 kg rice bag) which was folded to obtain a dimension of 15 cm x 30 cm were used. Bags were filled with soil to a height of 30 cm (approx. 9.7 kg of air dried soil) which later reduced to 25 cm after it was saturated with water and allowed to drain overnight. (The interlocking PP strands used for making the bag allowed water to drain slowly without necessarily having to make holes at the bottom of the bag). The soil used was top soil obtained from the top 15 cm soil layer of a previous dump site and a land fallowed for three years. The soil was pooled and thoroughly mixed together to obtain a uniform mixture. The resultant soil was determined to be sandy loam following the 'simple manipulative test' [21].

Seeds were sown at four seeds per bag and later thinned to one seedling per bag a week before imposition of treatments. Bags containing the seedlings were arranged randomly in single rows to achieve a planting distance of 60 cm x 30 cm between and within rows respectively. Seedlings were watered every other day with an equal volume of water (500 ml after sowing and increased to 1000 ml five weeks after germination) until six weeks after germination (WAG).

2.4 Experimental Design and Treatments

The study was carried out as two separate experiments.

2.4.1 Experiment 1: Rapid screening of 30 accessions for tolerance to flooding

This experiment involved the rapid screening of the 30 papaya accessions for their tolerance to flood at the juvenile stage. The experiment was laid out in a randomized complete block design with the 30 accessions as blocks, two treatments (90% partial flooding – F90 and non-stressed – NS) and six replicates. Partial flooding was simulated by setting each bag containing the seedlings in a 15 L volume bucket and filling with water to reach 90% of the height of the soil level in the bag (i.e. 22.5 cm). The water level was checked and maintained daily. The soil moisture for the control was maintained at field capacity (25 - 27% VWC) whereas that of the 90% flooding at a depth of 20 cm was in the range (45-51% VWC) as determined with a Time domain reflectometry (TDR) sensor (Field Scout TDR 100 soil moisture meter, Spectrum Technologies, USA). After 7 days of flooding, the bags were removed from the water and allowed to drain (through tiny holes in the bag) for another 7 days to determine recovery of the seedlings after the flooding. The control plants received 1000 ml water every other day till the end of the experiment.

2.4.1.1 Data collection

Data was collected on plant height, stem diameter, percent leaf senescence and relative growth rate. Plant height was measured with a tape measure from the base (soil surface) to the apex (growing tip) of the plant. Stem diameter was measured with digital Vernier calipers just above the soil surface. Soil moisture content was monitored with a TDR 100 (Spectrum Technologies, USA).

Relative growth rate was calculated using the formula:

$$RGR = \frac{\ln(X_2)-\ln(X_1)}{T_2-T_1}$$

Where, X_1 and X_2 are the values of the parameter such as plant height and stem diameter at time T_1 and time T_2 respectively.

2.4.1.2 Determination of Flood Tolerance Potential (FTP)

The FTP of the accessions was determined using a flood tolerance score (FTS) generated with data from growth parameters (height, stem diameter) and leaf senescence measured during the flood stress and post flood stress period. The seven-point index was based on pairwise comparison of the percent leaf senescence and relative growth rate for height and stem diameter measured under flood-stress conditions and post release from flood-stress. For height and stem diameter, a score of one (1) was given to any accession which recorded higher or no significant difference (p = .05) between flood-stressed and non-stressed plants whereas a score of zero (0) was accorded to any accession in which the values for flood-stressed seedlings were significantly lower than the control. For percent senescence, a score of one (1) was given to any accession with significantly lower values or with no significant difference between flood-stressed and non-stressed seedlings whereas accessions with significantly higher values obtained a score of zero. The severity of flood symptoms observed was also quantified and included in the total FTS. Accessions with > 60% of seedlings either dead or showing severe symptoms of flood stress were given a score of zero (0) whereas those with severe symptoms of flood stress observed in < 30% of plants were accorded a score of one (1). The flood tolerance potential was determined from the total flood tolerance score obtained by the accessions.

2.4.2 Experiment 2: Physiological basis of flooding tolerance

This experiment was carried out to determine the physiological basis of observed flood tolerance or intolerance. The setup and design of Experiment 2 were as described in Experiment 1 above with minor modifications. Six accessions belonging to the medium or low potential flood tolerance groups (selected based on Experiment 1) were used. The number of plants per accession was also increased to eighteen (18).

The Flooding experiment had three treatments (50% (partial) flooding – F50, 100% flooding – F100 and non-stressed – NS). For the F50 treatment, the buckets were filled with water to half the height of the planting bags (12.5 cm) whereas for F100, the water was filled to cover the entire surface of the soil and 1 cm of the stem. The control plants were maintained at field capacity (25-29% VWC) whereas the soil moisture for the F50 and F100 were in the range 49-53 and 60-65% respectively at a depth of 20 cm. The flood stress lasted for five weeks (35 d) whereas the post stress period lasted for six weeks (42 d).

Data was collected on plant height, stem diameter, number of leaves, leaf relative water content (RWC), SPAD chlorophyll content and Quantum yield of photosystem II (QY_{PSII}), root and shoot dry weight and leaf senescence. SPAD chlorophyll content was measured with a CCM plus (Apogee Instruments). QY_{PSII} was measured with Chlorophyll fluorescence meter (PARFluor 100, Photon System Instruments, Czech) from 11:00 am to 2:00 pm. Temperature and Relative humidity (RH) within the screen-house was monitored with a hygrothermograph (Brune, Germany). The soil moisture content at a depth of 20 cm was monitored with a TDR sensor (Field Scout, USA).

2.4.2.1 Determination of relative water content

The leaf relative water content of the papaya accessions was determined based on the method of Barrs and Weatherley [22] with minor modifications. Ten leaf discs were bored with a 1 cm inner diameter leather punch, quickly placed in plastic containers which were kept in an insulated container before taken to the laboratory to determine the fresh weight (FW) with a balance (brand, city). The leaf discs were then floated on distilled water in covered 10 cm diameter petri dish for 24 h. Before determining the turgid weight (TW), the leaf disc were removed from the distilled water, surface blotted between two layers of three-ply tissue paper folded in two with a flat bottom constant weight of 500 g placed on it on a flat ceramic tile. Following determination of the turgid weight, the leaf discs were placed inside a folded aluminium foil and dried in a hot air oven at 70℃ to a constant weight to determine the dry weight (DW). The RWC of the plants were determined by the formula:

$$RWC = [(FW - DW)/ (TW-DW)] \times 100$$

2.4.2.2 Determination of root to shoot ratio

Root to shoot ratio was determined at the end of the experiment by first immersing the planting bags with seedlings in a big bowl of water for 15 min to loosen the soil. The whole plant was then carefully pulled out of the soil before washing the roots to remove any attached soil particles. After the water was allowed to drain, each plant was separated into its components, i.e. tap (main) root, lateral (fibrous) roots, stem and leaves and placed in an envelope. The samples were dried in a hot air oven at 70℃ to a constant weight in order to determine the plant biomass. The root to shoot ratio was found by dividing the dry weight of the root (tap and lateral roots) by the weight of the shoot (stem and leaves).

2.5 Micro-climate within Screen-house

The mean temperature and relative humidity in the screen house during the experimental period are presented in Table 1.

Table 1. Mean daily minimum and maximum temperature and relative humidity (RH) in the screen house during the period of the experiment

Month	Temperature (℃)		RH (%)	
	Min	Max	Min	Max
February	23.0	36.2	47.3	91.2
March	24.1	36.8	44.4	89.7
May	23.7	37.0	48.9	96.8
June	24.0	36.2	50.3	95.9
July	23.7	32.8	51.7	87.6
August	23.0	31.9	54.2	88.3

2.6 Data Analysis

Analysis of Variance (ANOVA) was used to compare block means whereas Pairwise comparison was performed for treatment means for the various parameters. Data was analyzed with SPSS version 16.0.

3. RESULTS AND DISCUSSION

3.1 Experiment 1: Rapid Screening of Papaya Accessions for Tolerance to Flooding

3.1.1 Growth parameters before and after flooding

Flood stress (90% partial flooding) significantly ($p < .001$) reduced the growth potential of seedlings of most of the papaya accessions (Table 2). There were reductions in number of leaves of flood-stressed seedlings over the one week long flood stress compared to the non-stressed plants, some of which (VR-02) increased their number of leaves by about 33% during the same period. This reduction was due to increased rate of leaf senescence in the flood-stressed seedlings. The rate of increase in height and diameter were also reduced by flood stress. For example the non-stressed plants of CR-05A recorded a 6.5 cm increase in height whereas its flood-stressed counterpart recorded no increase in height (Table 2).

3.1.2 Percent leaf senescence and relative growth rates (height and diameter) under flood stress

Most flood-stressed papaya seedlings had significantly ($p < .001$) reduced growth rate in height and stem diameter compared to the non-stressed seedlings (Table 3). Non-stressed papaya seedlings increased the number of leaves and had significantly ($p < .001$) lower percentage leaf senescence compared to the flood-stressed seedlings some of which (AR-03) lost as much as 75.9% of leaves after one week under stress.

Plants subjected to flooding often exhibit low growth rate compared to non-flooded plants which usually results from a drop in photosynthesis at the leaf and plant level [23]. Therefore accessions with a slower growth rate under flood stress compared to the non-stressed plants can be said to be relatively less tolerant to flooding. Chlorosis and early leaf shedding observed in this study for flood-stressed papaya plants are similar to that reported by Campostrini and Glenn [24] also for papaya plants. Early leaf senescence has also been reported as a response of other plants to flooding [25] which in combination with other factors such as reduced leaf area often lead to a decline in carbon fixation at the plant level [8]. These may possibly result in reduced plant growth rate as observed in this study.

Considering the fact that the observations made in this study are for 90% partial flooding, accessions which recorded lower growth rate in either plant height or stem diameter or both in addition to higher percentage leaf senescence when compared to the control plants may be highly intolerant to complete flooding.

Table 2. Growth parameters of flood stressed (F90) and non-stressed (NS) seedlings of papaya accessions before (initial) and one week after imposition of flood stress

Treatment / Accession	Initial (before flooding)						After 1 week under flood stress					
	Height (cm)		Diameter (mm)		No. of leaves		Height (cm)		Diameter (mm)		No. of leaves	
	NS	**F90**	**NS**	**F90**	**NS**	**F90**	**NS**	**F90**	**NS**	**F90**	**NS**	**F90**
AR-01	30.3	23.7	7.6	9.1	11.0	7.7	35.8	25.7	10.7	9.5	11.0	4.3
AR-02A	29.7	34.3	8.8	11.7	9.0	9.7	34.7	35.0	12.3	12.0	11.0	4.3
AR-02B	31.7	27.7	9.1	7.9	11.3	11.0	36.7	28.0	11.6	9.8	14.3	5.0
AR-03	34.0	27.3	8.4	6.8	10.7	9.7	38.8	27.7	12.6	8.0	9.7	2.3
AR-04	35.7	28.0	9.0	6.8	11.0	11.7	38.3	29.0	13.9	8.5	11.3	7.7
CR-02	29.5	25.0	8.5	7.4	11.0	10.7	33.7	26.2	12.4	9.7	10.3	5.3
CR-03	34.3	29.3	8.3	8.3	8.7	10.7	42.2	29.7	11.1	10.2	10.3	6.0
CR-04	31.5	33.7	10.4	7.3	10.7	9.3	40.3	34.8	13.2	8.5	10.7	4.7
CR-05A	16.7	16.7	8.8	5.7	10.0	11.0	23.2	16.7	10.7	6.6	10.0	2.7
CR-05B	36.7	23.3	10.3	7.6	12.3	9.0	44.3	25.0	13.6	8.7	11.0	8.7
CR-06A	29.7	28.3	8.1	7.4	11.0	11.3	39.5	30.7	11.7	10.5	11.0	8.0
CR-07A	27.7	32.0	8.8	7.5	10.3	10.0	38.7	33.0	12.2	9.8	10.3	6.7
ER-02A	36.3	30.3	9.2	7.0	12.0	12.7	38.7	31.0	13.1	8.8	11.0	4.3
ER-03	29.7	23.7	8.9	7.8	12.3	10.3	33.2	24.7	14.1	9.2	12.0	6.0
ER-04	37.3	25.0	9.4	7.4	12.3	10.7	41.7	25.2	12.1	8.0	12.0	3.3
ER-05	38.3	31.0	10.9	8.5	11.0	9.0	48.0	32.0	13.2	9.5	11.7	7.7
ER-07	33.3	24.8	9.3	7.3	11.0	8.3	38.3	26.8	12.1	9.5	11.0	6.3
ER-11	29.7	25.3	10.5	6.8	10.3	11.3	35.5	26.2	14.3	8.1	11.7	5.3
GA-02	31.3	30.3	8.4	7.3	10.0	12.7	34.4	30.0	12.4	7.9	11.0	4.0
GA-05	40.2	25.7	9.4	7.3	10.7	10.3	45.3	30.0	11.8	8.7	11.0	7.3
GA-06	38.0	25.7	9.3	7.4	9.3	11.3	43.2	26.7	11.2	9.5	9.7	7.3
GA-07	34.8	20.7	10.0	7.0	9.7	11.7	41.5	25.3	13.8	11.1	11.3	8.0
VR-02	36.7	20.0	7.8	4.8	10.0	10.0	44.3	21.0	12.0	6.6	13.3	5.7
VR-03	35.3	23.0	9.5	6.8	12.3	9.3	41.0	24.3	12.3	8.3	12.0	6.7
VR-04	31.3	28.3	7.5	7.7	11.0	9.7	37.0	29.7	11.9	8.8	12.0	5.0
VR-07	37.0	29.3	9.4	7.5	11.3	9.3	45.8	29.8	12.7	8.8	10.3	4.3
VR-10	34.3	28.3	8.6	7.6	11.3	12.7	38.3	29.0	11.7	8.4	12.0	3.7
VR-12	33.3	27.0	7.5	8.2	10.0	8.7	36.3	30.2	9.9	10.2	10.0	6.0
VR-13	30.3	28.3	7.3	7.1	10.0	8.0	33.3	30.1	10.1	8.8	10.0	5.0
VR-15	34.3	27.0	9.1	6.1	10.7	10.0	41.7	29.7	12.2	8.0	11.0	7.3
S.E	1.61		0.43		0.41		1.63		0.43		0.55	
Sig. Treatment (T)	.000		.000		.001		.000		.000		.000	
Block (B)	.000		.000		.000		.000		.000		.000	
T x B	.000		.000		.000		.000		.000		.000	

3.1.3 Percent leaf senescence and relative growth rates post release from flood stress

Following release from flood stress, growth rate of flood-stressed seedlings improved relative to the non-stressed seedlings over a period of 1 week (Table 4). Flood-stressed seedlings of GA-07 had significantly higher ($p < .001$) growth rate in height (0.022 cm/d) compared to the non-stressed seedlings (0.015 cm/d). Accession CR-07A recorded the highest growth rate in height (0.034 cm/d) whereas its control plants increased in height at the rate of 0.017 cm/d. No leaf senescence was observed in the non-stressed leaves whereas leaf senescence continued in all the flooded plants (although at a slower rate) with the exception of ER-07 which rather recorded a 7% increase in number of leaves.

Recovery after release from flood stress is another important criterion for determination of flood tolerance potential of plants [26,27]. Papaya plants that are able to survive flooding do not recover well [28] since flooding may possibly cause irreversible damage to plants. This implies that plants that are able to recover well post-flooding compared to the control plants could be described as being relatively tolerant to flooding.

3.1.4 Flood tolerance score of papaya accessions

The mean total Flood Tolerance Scores (FTS) of the papaya accessions based on pairwise comparison between flood-stressed and non-stressed seedlings of each accession for the parameters measured as well as severity of flood stress symptoms observed are presented in Fig. 1. Accessions with FTS ≥ 6 had the highest flood tolerance potential. The thirty (30) papaya accessions could be ranked according to their Flood Tolerance Potential as follows:

High tolerance (FTI ≥ 6 points): none
Medium/moderate tolerance (4 ≤ FTI < 6 points): *CR-06A, CR-07A, ER-05, ER-07, ER-11, GA-06, GA-07, VR-12,* and *VR-15*
Low tolerance (FTI ≤ 3 points): *AR-01, AR-02A, AR-03, AR-04, CR-02, CR-03, CR-04, CR-05A, CR-05B, ER-02A, ER-03, ER-04 GA-02, GA-05, VR-02, VR-03, VR-04, VR-07, VR-10,* and *VR-13.*

None of the accessions tested exhibited high flood tolerance potential. About 60% of the accessions fell within the low flood tolerance category. This further buttresses the argument that papaya plants cannot tolerate hypoxia as has been observed by Marler et al. [16].

3.2 Experiment 2

Based on the results of Phase I, the six accessions selected for Phase II flood experiments were: CR-06A, CR-07A, ER-05 and GA-07 (medium tolerance group); CR-05A and VR-10 (low tolerance group).

Table 3. Relative growth rate in height and diameter (cm d^{-1}) and percentage leaf senescence of flood stressed (F90) and non-stressed (NS) seedlings of papaya accessions after 1 week of flooding

Treatment / Accession	Height (cm d^{-1})		Diameter (cm d^{-1})		% Leaf senescence	
	NS	**F90**	**NS**	**F90**	**NS**	**F90**
AR-01	0.024^{*}	0.011	0.050^{**}	0.005	-4.7	45.9^{**}
AR-02A	0.022^{***}	0.002	0.048^{***}	0.003	-23.3	55.2^{***}
AR-02B	0.021^{***}	0.002	0.036	0.033	-26.5	49.3^{**}
AR-03	0.019^{***}	0.002	0.059^{***}	0.025	10.4	75.9^{***}
AR-04	0.010^{**}	0.005	0.064^{**}	0.034	-2.6	29.5^{*}
CR-02	0.020^{*}	0.007	0.054	0.040	5.6	51.8^{***}
CR-03	0.030^{***}	0.002	0.043^{**}	0.028	-19.4	44.4^{**}
CR-04	0.035^{*}	0.005	0.035	0.020	-1.7	49.0^{**}
CR-05A	0.046^{***}	0.001	0.029	0.024	0.0	75.6^{***}
CR-05B	0.029	0.009	0.040^{**}	0.019	9.9	4.2
CR-06A	0.041^{**}	0.012	0.054	0.052	0.3	28.3
CR-07A	0.050^{**}	0.004	0.046	0.041	0.0	29.2
ER-02A	0.009^{**}	0.003	0.052^{**}	0.034	6.6	64.7^{***}
ER-03	0.016^{*}	0.006	0.069^{*}	0.022	2.8	43.4^{**}
ER-04	0.016^{***}	0.001	0.035^{*}	0.012	2.6	68.8^{***}
ER-05	0.032^{**}	0.004	0.028	0.016	-9.2	12.8^{*}
ER-07	0.022^{*}	0.011	0.040	0.039	-1.4	20.7^{**}
ER-11	0.026^{**}	0.005	0.047	0.026	-14.1	49.2^{**}
GA-02	0.015^{*}	0.001	0.056^{*}	0.015	-11.1	69.0^{***}
GA-05	0.017	0.024	0.033	0.025	-3.7	28.5^{***}
GA-06	0.019	0.006	0.026	0.038	-5.0	35.4^{**}
GA-07	0.026	0.029	0.047	0.063	-17.8	27.8^{**}
VR-02	0.027^{**}	0.007	0.061^{*}	0.047	-33.3	43.3^{**}
VR-03	0.022^{*}	0.008	0.037^{*}	0.028	1.6	27.5^{*}
VR-04	0.023^{***}	0.007	0.067^{***}	0.021	-9.7	48.6^{***}
VR-07	0.032^{**}	0.002	0.043^{**}	0.023	8.6	56.8^{**}
VR-10	0.016^{**}	0.003	0.044^{**}	0.015	-5.6	70.5^{***}
VR-12	0.012	0.017	0.040	0.031	0.0	32.1^{***}
VR-13	0.013*	0.009	0.047	0.029	-0.3	31.4
VR-15	0.029*	0.014	0.045	0.041	-2.8	27.7
S.E	0.002		0.004		5.86	
Sig.: Treatment (T)	.000		.000		.000	
Block (B)	.000		.000		.000	
T x B	.000		.000		.000	

*Means followed by *,** and *** are significantly higher than the corresponding values at p < .05, p < .01 and p < .001 respectively as determined by pairwise t-test between flood-stressed and non-stressed plants.*

Table 4. Relative growth rate in height and diameter (cm d^{-1}) and percentage leaf senescence of flood stressed (F90) and non-stressed (NS) seedlings of papaya accessions at one week post release from flood stress

Treatment / Accession	Height (cm/d)		Diameter(cm/d)		% senescence	
	NS	F90	NS	F90	NS	F90
AR-01	0.013	0.013	0.032	0.015	-9.2	21.5*
AR-02A	0.018**	0.007	0.036**	0.006	-41.9	49.2***
AR-02B	0.018*	0.010	0.035***	0.016	-0.3	28.3**
AR-03	0.024***	0.005	0.038	0.019	-18.9	60.9***
AR-04	0.021	0.016	0.035**	0.025	-16.7	40.2***
CR-02	0.019	0.014	0.031	0.028	-3.8	23.7**
CR-03	0.023	0.012	0.041	0.023	-34.3	55.0**
CR-04	0.023**	0.003	0.030	0.021	-3.3	33.9*
CR-05A	0.026***	0.001	0.033	0.017	-26.7	53.8***
CR-05B	0.024	0.016	0.030*	0.021	15.6	58.7**
CR-06A	0.025**	0.014	0.037	0.039	-3.9	23.5**
CR-07A	0.034*	0.017	0.031	0.029	-22.7	29.5***
ER-02A	0.018	0.012	0.049*	0.016	-10.0	36.5**
ER-03	0.025*	0.015	0.033**	0.019	5.6	36.0**
ER-04	0.017*	0.009	0.031*	0.013	-5.1	34.8***
ER-05	0.020	0.012	0.032	0.014	-7.9	56.4***
ER-07	0.021**	0.011	0.034	0.023	-22.9	-7.0
ER-11	0.015	0.011	0.024	0.042**	-13.5	33.9**
GA-02	0.021*	0.006	0.019	0.013	-17.2	49.6**
GA-05	0.022*	0.013	0.032***	0.029	-15.3	34.3**
GA-06	0.016	0.021	0.038	0.022	-30.0	32.6***
GA-07	0.015	0.022***	0.032	0.034	-24.4	30.4**
VR-02	0.016	0.024	0.029	0.037**	-13.3	23.3*
VR-03	0.035	0.036	0.028	0.031	10.6	28.3**
VR-04	0.016	0.019*	0.034	0.023*	-9.2	50.5***
VR-07	0.024**	0.016	0.042*	0.018	11.5	21.3*
VR-10	0.016	0.011	0.040**	0.010	-5.8	62.6***
VR-12	0.018	0.017	0.045**	0.026	-20.0	15.5**
VR-13	0.030**	0.015	0.039*	0.024	-19.8	35.8**
VR-15	0.025*	0.017	0.034	0.039*	-16.0	12.4***
S.E	0.002		0.003		3.98	
Sig.: Treatment (T)	.000		.000		.000	
Block (B)	.000		.002		.000	
T x B	.000		.000		.000	

Means followed by *,** and *** are significantly higher than the corresponding values at $p< .05$, $p< .01$ and $p < .001$ respectively as determined by pairwise t-test between flood-stressed and non-stressed plants.

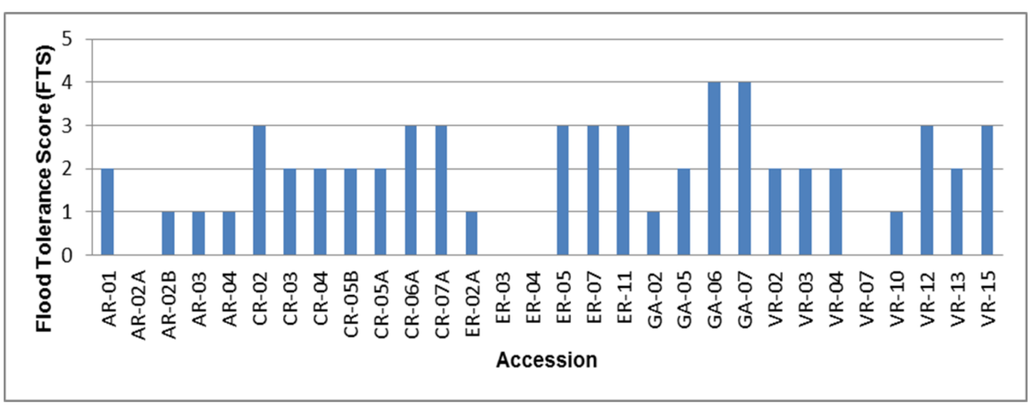

Fig. 1. Flood tolerance scores of papaya accessions subjected to partial flooding at the juvenile stage

3.2.1 Growth parameters before, under and post flood stress

All the papaya plants (including accessions belonging to the medium tolerance group) subjected to complete (100%) flooding (F100) 'collapsed' by the third day of treatment and could not be resume normal growth even after release from flood-stress, confirming the general intolerance of papaya to flooding as has been reported by Marler et al. [16], Morton [18], and Orwa et al. [29]. However the partial (50%) flooding treatments survived up to the end of the flood stress period (5 weeks) and were able to continue growth after release from stress. Data on flooding experiments are shown in Tables 5 – 8.

Accessions CR-06A, CR-07A and GA-07 generally had taller plants than other accessions and this translated into significant increases in height than the other accessions (Table 5). Partial (50%) flooding resulted in significant differences in height ($p < .001$) but not in stem diameter ($p = .89$) between the flood-stressed plants and the non-stressed plants.

3.2.2 Relative growth rate under flood stress and post release from stress

Similar to the results of Experiment 1, papaya plants subjected to 50% flood stress recorded lower growth rate than the control plants for all the growth parameters measured during the stress period, although most of the reductions were not significant (Table 6). The non-stressed plants of GA-07 significantly ($p < .001$) increased in height (0.114 cm/week) compared to the flood-stressed plants. Following release from flood stress, relative growth rates of the flooded plants were comparable to the non-stressed plants for all the growth parameters except GA-07 which recorded higher rate of increase in stem diameter compared to the control plants. Flood-stressed seedlings of CR-05A had significantly ($p < .01$) higher growth rate both in height and stem diameter compared to the control plants.

A possible explanation for this observation could be that, the 50% partial flooding may not have resulted in complete depletion of the oxygen in the soil and thus the papaya plants were able to continue normal growth in the upper part of the soil where hypoxia was low to negligible.

3.2.3 Physiological parameters

Fifty percent (partial) flooding stress (F50) did not have any significant effect on leaf relative water content (RWC) between treatments and between accessions (Table 7). Both flood-stressed and non-stressed plants had high RWC with the flood-stressed plants of ER-05 having significantly higher ($p < .001$) SPAD chlorophyll

Table 5. Growth parameters (height – H, stem diameter – D, length of petiole and central vein) of seedlings of papaya accessions subjected to 5 weeks of partial flooding and subsequent release from flood stress

Treatment	Accession	Initial		5 weeks under flood stress		6 weeks after release from flood stress			
		Height (cm)	Diameter (cm)	Height (cm)	Diameter (cm)	Height (cm)	Diameter (cm)	Petiole length	Vein length
NS	ER-03	35.3	1.41	63.0	2.66	70.3	2.83	18.7	20.1
	ER-04	40.7	1.08	68.3	2.37	77.0	2.42	20.1	15.8
	ER-11	40.3	1.14	76.0	2.35	87.3	2.42	22.3	17.7
	GA-02	26.0	0.90	77.5	2.39	88.0	2.56	21.8	19.0
	CR-05A	40.7	1.51	72.0	2.53	82.7	2.60	20.9	17.7
	VR-10	29.0	1.00	62.0	2.24	70.7	2.36	18.9	15.5
F50	ER-03	23.7	0.97	37.0	2.20	45.3	2.57	19.5	16.6
	ER-04	39.3	1.55	59.0	2.40	67.7	2.60	21.2	15.9
	ER-11	47.7	1.20	73.0	2.44	81.0	2.44	21.8	15.7
	GA-02	40.0	0.96	75.7	2.55	84.0	2.78	20.2	15.6
	CR-05A	45.0	1.44	62.3	2.66	66.0	2.59	20.4	15.6
	VR-10	35.3	0.87	59.5	2.25	70.0	2.63	19.9	16.2
S.E		3.09	0.14	2.13	0.062	2.29	0.059	0.74	0.49
Sig.	Treatment (T)	.08	.94	.000	.89	.000	.046	.93	.000
	Block (B)	.000	.001	.000	.000	.000	.000	.002	.000
	T x B	.003	.046	.000	.000	.000	.000	.40	.000

Table 6. Relative Growth Rate (RGR) of papaya seedlings of papaya accessions after 3 weeks (vein, petiole, leaf width) and 5 weeks (height, stem diameter) under flood stress and at 6 weeks post release from flood stress

Treatment	Accession	Relative growth rate (RGR) under flood stress (cm/wk)				RGR at 6 weeks post release from flood stress (cm/wk)			
		Height	Diameter	Petiole	Vein	Height	Diameter	Petiole	Vein
NS	CR-05A	0.117	0.128	0.384	0.082	0.018	0.014	0.209	0.078*
	CR-06A	0.104	0.160	0.472	0.080	0.020	0.012	0.204	0.035
	CR-07A	0.137	0.146	0.429	0.058	0.023	0.017	0.211	0.054
	ER-05	0.260	0.214	0.644	0.198	0.021*	0.015	0.209	0.046
	GA-07	0.114***	0.106	0.417	0.107	0.023	0.015***	0.148	0.032
	VR-10	0.156	0.164	0.467	0.108*	0.022	0.012	0.194*	0.037
F50	CR-05A	0.092	0.175	0.417	0.091	0.034**	0.026**	0.217	0.037
	CR-06A	0.083	0.107	0.341	0.077	0.023	0.010	0.215	0.031
	CR-07A	0.085	0.142	0.434	0.075	0.024	0.018	0.215*	0.033
	ER-05	0.129	0.197	0.556	0.093	0.019	0.015	0.197	0.034
	GA-07	0.067	0.132	0.436	0.101	0.019	0.013	0.167	0.036
	VR-10	0.105	0.200	0.436	0.061	0.027	0.026***	0.168	0.033
S.E		0.022	0.022	0.37	0.024	0.002	0.001	0.01	0.006
Sig.	Treatment (T)	.000	.66	.13	.10	.005	.000	.94	.000
	Block (B)	.000	.003	.000	.03	.02	.000	.000	.001
	T x B	.16	.24	.18	.11	.000	.000	.21	.007

*Means followed by *, ** and *** implies significantly higher values at p < .05, p < .01 and p < .001 respectively as determined by pairwise t-test between flood-stressed and non-stressed plants.*

content (40.5%) than their non-stressed plants (32.1), implying an advantage of the 50% partial flooding treatment. On the other hand the non-stressed plants of CR-07A, GA-07 and VR-10 significantly lost more leaves than their flood-stressed counterparts did.

In general, chlorophyll fluorescence (QYPSII) was not significantly ($p = .24$) affected by partial flooding treatment, although highly significant differences ($p < .001$) were observed within the block. However, interaction between treatment and block was highly significant, implying that the papaya accessions had genetic differences which might have affected their QY_{PSII} values under partial flooding stress.

These observations in the physiology of papaya seedlings under 50% partial flooding stress deviate from what pertains in the literature. Generally, complete inundation of roots and part of the stem results in reduced chlorophyll content, increased leaf senescence and reduced QY_{PSII} which leads to a dip in photosynthetic efficiency [10-12]. However, in this experiment, the papaya roots were inundated up to 50% of their height. Although through capillary action, the water was spread throughout the soil, the anoxia at the upper half of the soil may have been lower or negligible, enabling the papaya roots within that region to continue normal growth processes, making up for the damage caused by anoxia within the lower portion of the roots.

The effect of hypoxic conditions on plant water status varies between species [23] and between seasons of occurrence [30]. As observed in this study, 50% partial flooding did not have negative effects on plant water status as measured by the leaf RWC. In fact, flood-stressed plants of ER-05 had significantly higher ($p < .001$) RWC (91.8%) than the control plants (86.8%). A similar observation was made by Mollard et al. [31] where *Paspalum dilatatum* plants subjected to complete inundation recorded higher plant water status as measured by leaf water potential (Ψ_w) on dates with higher air vapour pressure deficit (VPD_{air}). On the other hand Striker et al. [32] found that in flood tolerant the legume, Lotus tenuis, flooding negatively affected plant water status as measured by the leaf water potential almost a week after flooding.

3.2.4 Plant biomass

Non-stressed plants of CR-05A had the highest total plant biomass (45.4 g), which was significantly different from its partially flooded counterparts (34.0 g) (Table 8). Similarly, partially flooded seedlings of ER-05 and GA-07 recorded higher shoot and total plant dry matter than the non-stressed plants. Among the partially flooded plants, CR-07A produced the highest total plant biomass (37.7 g) and this was not significantly different from the control plants (38.2 g). VR-10 had the highest root to shoot ratio (0.57) for both flood-stressed and non-stressed plants.

Table 7. Percentage leaf senescence and other physiological parameters (relative water content – RWC, SPAD chlorophyll content and fluorescence – QY_{PSII}) of papaya accessions during 5 weeks of flood stress

Treatment	Accession	RWC (%)	SPAD chlorophyll content	Chlorophyll fluorescence (QY_{PSII})	% leaf senescence
NS	CR-05A	90.4	35.8	0.78	40.1**
	CR-06A	93.6	25.5	0.79	42.7
	CR-07A	93.5*	28.3	0.77	46.7***
	ER-05	86.8	32.1	0.77	23.1
	GA-07	87.9	42.9	0.79	38.5**
	VR-10	88.4	39.3	0.77	42.0***
F50	CR-05A	89.0	44.7	0.78	30.8
	CR-06A	92.3	27.2	0.79	27.1
	CR-07A	89.4	40.5*	0.77	20.6
	ER-05	91.8***	40.5***	0.78*	14.5
	GA-07	89.3	41.2	0.78	25.0
	VR-10	88.0	37.2	0.78**	11.0
S.E		1.93	4.0	0.002	3.93
Significance	Treatment (T)	.89	.05	.24	.000
	Block (B)	.12	.004	.000	.000
	T x B	.28	.35	.000	.03

Means followed by $*$, $**$ and $***$ implies significantly higher values at $p < .05$, $p < .01$ and $p < .001$ respectively as determined by pairwise t-test between flood-stressed and non-stressed plants. Chlorophyll fluorescence, SPAD chlorophyll, Leaf RWC, leaf senescence were measured 2, 3, 4 and 5 weeks respectively after initiation of flood stress.

Table 8. Plant biomass (dry weight) of seedlings of papaya accessions after release from flood stress

Treatment	Accession	Shoot biomass (g)			Root biomass (g)			Total plant biomass	Root to shoot ratio
		Stem	Leaf	Total	Main	Lateral	Total		
NS	CR-05A	19.8*	9.87	29.7*	13.2**	2.55	15.7*	45.4*	0.53
	CR-06A	18.6*	4.84*	23.5	7.08*	2.32	9.4	32.9	0.39
	CR-07A	22.2	5.81*	28.0	6.91	3.32	10.2	38.2	0.37
	ER-05	22.3	7.19**	29.5*	7.75**	3.17	10.9	40.4*	0.37
	GA-07	24.3***	6.30	30.6*	8.86*	3.93	12.8*	43.4*	0.42
	VR-10	15.8	4.97	20.8	8.74*	2.72	11.5	32.2	0.57
F50	CR-05A	15.4	7.81	23.2	6.57	4.27**	10.8	34.0	0.46
	CR-06A	15.9	4.60	20.5	3.88	4.39***	8.3	28.8	0.41
	CR-07A	22.4	5.38	27.7	4.69	5.29**	10.0	37.7	0.35
	ER-05	22.0	5.31	27.3	4.22	5.18**	9.4	36.7	0.34
	GA-07	21.6	5.96	27.5	5.87	3.98	9.8	37.4	0.35
	VR-10	17.1	5.68	22.8	6.27	6.82**	13.1	35.8	0.57
S.E		0.84	0.58	1.18	0.85	0.38	1.05	1.97	0.036
Sig.	Treatment (T)	.004	.04	.002	.000	.000	.015	.002	.19
	Block (B)	.000	.000	.000	.000	.002	.001	.000	.000
	T x B	.009	.16	.02	.13	.000	.06	.01	.79

Means followed by $*$, $**$ and $***$ implies significantly higher values at $p < .05$, $p < .01$ and $p < .001$ respectively as determined by pairwise t-test between flood-stressed and non-stressed plants.

A consequence of the negative effects of flood stress on photosynthesis is reduction in carbon fixation at the plant level [8]. This will ultimately affect biomass accumulation, as evidenced by reduced total plant dry mass [33,34].

Generally, partial (50%) flood stress induced production of more lateral (secondary) roots compared to the control. All the accessions with the exception of GA-07 produced significantly higher lateral root biomass than their corresponding non-stressed plants did. Although flooding is known to induce root decay and thus have a deleterious effect on root formation [35] it also induces formation of adventitious roots as a mechanism of coping with the flood stress [11,23,36,37]. The higher lateral root biomass observed in this study for partially flooded plants could be as result of increased production of adventitious roots in the flood stress plants, although this was not directly measured in this study. The lower tap (main) root biomass observed for flood-stress plants could be due to root decay which resulted from hypoxia in the lower half of the soil.

4. CONCLUSION

Out of the thirty accessions, none had high flood tolerance potential. Majority (about 60%) fell within the low flood tolerance category. Ninety percent partial flooding significantly reduced plant growth in height and stem diameter, as well as increased the rate of leaf senescence of the flood stressed plants compared to the control. None of the six accessions which were used in the second experiment could tolerate complete inundation for more than three days. Plants subjected to 50% partial flooding did not have any significant reductions in leaf relative water content and quantum yield of photosystem II (QY_{PSII}) compared to the control. On the other hand, leaf senescence was lower under 50% partial flooding than the non-stressed plants whereas SPAD chlorophyll content after three weeks of partial flood stress was higher than the non-stressed plants. At the end of the experiment 50% partially flooded plants had higher lateral root biomass compared to the control, although non-stressed plants had higher tap (main) root and total root biomass as well as higher total plant biomass compared to the partially flooded plants.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Pimentel P, Almada RD, Salvatierra A, Toro G, Arismendi MJ, Pino MT, Sagredo B, Pinto M. Physiological and morphological responses of *Prunus* species with different degree of tolerance to long-term root hypoxia. Scientia Horticulturae. 2014;180:14-23.
   Available:http://dx.doi.org/10.1016/j.scienta.2014.09.055
2. Bailey-Serres J, Voesenek LA. Flooding stress: Acclimations and genetic diversity. Annual Review of Plant Biology. 2008; 59:313–339.
3. Licausi F, van Dongen JT, Giuntoli B, Novi G, Santaniello A, Geigenberger P, Perata P. HRE1 and HRE2, two hypoxia-inducible ethylene response factors, affect anaerobic responses in *Arabidopsis thaliana*. Plant J. 2010;62:302–315.
4. Chen H, Qualls R, Blank R. Effect of soil flooding on photosynthesis, carbohydrate partitioning and nutrient uptake in the invasive exotic *Lepidium latifolium*. Aquat. Bot. 2005;82:250–268.
5. Hossain Z, López-Climent M, Arbona V, Pérez-Clement R, Gómez-Cadenas A. Modulation of the antioxidant system in citrus under waterlogging and subsequent drainage. J. Plant Physiol. 2009;166:1391–1404.
6. Pezeshki SR, DeLaune RD. Responses of seedlings of selected woody species to soil oxidation–reduction conditions. Environmental & Experimental Botany. 1998;40:123–133.
7. Mielke MS, Almeida A–AF, Gomes FP, Aguilar MAG, Mangabeira PAO. Leaf gas exchange, chlorophyll fluorescence and growth responses of *Genipa americana* seedlings to soil flooding. Environmental & Experimental Botany. 2003;50:221–231.
8. Striker GG, Insausti P, Grimoldi AA, Ploschuk EL, Vasellati V. Physiological and anatomical basis of differential tolerance to soil flooding of *Lotus corniculatus* L. and *Lotus glaber* Mill. Plant & Soil. 2005;276:301–311.
9. Medina C, Sanches MC, Tucci MLS, Sousa CAF, Cuzzuol GRF, Joly CA. *Erythrina speciosa* (Leguminosae-Papilionoideae) under soil water saturation: Morphophysiological and growth responses. Annals of Botany. 2009;104:671–680.
10. Falqueto AR, Cassol D, Magalhães Júnior AM, Oliveira AC, Bacarin MA. Physiological analysis of leaf senescence of two rice cultivars with different yield potential. Pesqui. Agropecu. Bras. 2009; 44:695–700.
11. Patel PK, Singh AK, Tripathi N, Yadav D, Hemantaranjan A. Flooding: Abiotic constraint limiting vegetable productivity. Advances in Plants & Agriculture Research. 2014;1(3):00016.
    Available:http://dx.doi.org/10.15406/apar.2014.01.00016
12. Yordanova R, Christov K, Popova L. Antioxidative enzymes in barley plants subjected to soil flooding. Environmental & Experimental Botany. 2004;51:93–101.

13. Krause GH, Weis E. Chlorophyll fluorescence and photosynthesis: the basics. Annual Review of Plant Physiology and Plant Molecular Biology 1991;42:313-349.

14. Misra AN, Misra M, Singh R. Chlorophyll fluorescence in plant biology, biophysics, Dr. Prof. Dr. Misra AN, editor. InTech; 2012.

Available:http://www.intechopen.com/books/biophysics/chlorophyll-fluorescence-in-plant-biology (Accessed 18 March 2013)

15. Ministry of Food and Agriculture (MOFA). Review of agriculture sector performance. In: Medium Term Agricultural Sector Investment Plan (METASIP) 2011 – 2015, Government of Ghana; 2010.

16. Marler TE, George AP, Nissen RJ, Andersen PC. Miscellaneous tropical fruits. In: Schaffer B, Andersen PC, editors. Sub-tropical and tropical crops. Handbook of environmental physiology of fruit crops, vol. 2. Boca Raton: CRC Press; 1994.

17. Kruger JA, Mostert PG. Irrigation. In: de Villiers EA, editor. The cultivation of papaya. South Africa: ARC LNR; 1999.

18. Morton JF. Papaya. In: Morton JF, editor. Fruits of Warm Climates. Miami: Creative Resource Systems, Inc; 1987.

19. Khondaker NA, Ozawa K. Papaya plant growth as affected by soil air oxygen deficiency. Acta Hort. 2007;740:225-232.

20. Torres-Netto A. Atributos fisiológicos e relações hídricas em genótipos de mamoeiro (*Carica papaya* L.) na fase juvenil. Campos dos Goytacazes, Universidade Estadual do Norte Fluminense. DSc thesis; 2005. Portuguese

21. Ewusie JY. The soil in tropical ecology. In: Elements of tropical ecology: With reference to the African, Asian, Pacific and New World tropics. Heinemann; 1980.

22. Barrs HD, Weatherley PE. A Re-examination of the relative turgidity technique for estimating water deficits in leaves. Australian Journal of Biological Sciences. 1962;24:519-570.

23. Striker GG. Flooding stress on plants: anatomical, morphological and physiological responses, Botany. Mworia J, editor. InTech; 2012.

Available:http://www.intechopen.com/books/botany/flooding-stress-on-plants-anatomical-morphological-and-physiological-responses (Accessed 02 April 2015)

24. Campostrini E, Glenn DM. Ecophysiology of papaya: A review. Brazilian Journal of Physiology. 2007;19(4):413–424.

25. Grassini P, Indaco GV, López Pereira M, Hall AJ, Trápani N. Responses to short–term waterlogging during grain filling in sunflower. Field Crops Research. 2007;101:352–363.

26. Malik AI, Colmer TD, Lambers H, Setter TL, Schortemeyer M. Short–term waterlogging has long–term effects on the growth and physiology of wheat. New Phytologist. 2002;153:225–236.

27. Striker GG, Izaguirre RF, Manzur ME, Grimoldi AA. Different strategies of *Lotus japonicus*, *L*. *corniculatus* and *L*. *tenuis* to deal with complete submergence at seedling stage. Plant Biology; 2011.

DOI: 10.1111/j.1438–8677.2011.00493.x

28. Office of the Gene Technology Regulator (OGTR). The biology of *Carica papaya* L. (papaya, papaw, paw paw). Version 2, February, 2008. Australian Government, Department of Health and Ageing; 2008. Available:http://www.ogtr.gov.au

29. Orwa C, Mutua A, Kindt R, Jamnadass R, Simons A. *Carica papaya*. In: Agroforestree Database: A tree reference and selection guide version 4.0; 2009.

Available:http://www.worldagroforestry.org/af/treedb/

30. Lenssen JPM, Van de Steeg HM, de Kroon H. Does disturbance favour weak competitors? Mechanisms of altered plant abundance after flooding. Journal of Vegetation Science. 2004;15:305–314.

31. Mollard FPO, Striker GG, Ploschuk EL, Vega AS, Insausti P. Flooding tolerance of *Paspalum dilatatum* (Poaceae: Paniceae) from upland and lowland positions in a natural grassland. Flora. 2008;203:548–556.

32. Striker GG, Insausti P, Grimoldi AA. Effects of flooding at early summer on plant water relations of *Lotus tenuis*. Lotus Newsletter. 2007;37:1-7.

33. Lopez OR, Kusar TA. Flood tolerance of four tropical tree species. Tree Physiology. 1999;19:925-932.

34. Dias-Filho MB. Tolerance to flooding in five *Brachiaria brizantha* accession. Pesqui. Agropecu. Bras. 2002;37(4):439–447.

35. Kozlowski TT. Responses of woody plants to flooding and salinity. Tree Physiology Monograph 1; 1997. Available:http://www.heronpublishing.com/tp/monograph/kozlowski.pdf (Accessed 01 June 2015)
36. Yamamoto F, Sakata T, Terazawa K. Physiological, morphological and anatomical responses of *Fraxinus mandshurica* seedlings to flooding. Tree Physiology. 1995;15:713-719
37. Steffens B, Wang J, Santer M. Interactions between ethylene, gibberellins and abscisic acid regulate emergence and growth rate of adventitious roots in deep water rice. Planta. 2006;223(3):604-612.

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