Research Article

Ecological Characteristics That Enhance *Broussonetia papyrifera*’s Invasion in a Semideciduous Forest in Ghana

B. Kyereh,¹ V. K. Agyeman,² and I. K. Abebrese³

¹ Faculty of Renewable Natural Resources, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana
² Forestry Research Institute of Ghana, University P.O. Box 63, KNUST, Kumasi, Ghana
³ School of Natural Resources and Environmental Management, University of Energy and Natural Resources, P.O. Box 214, Sunyani, Ghana

Correspondence should be addressed to B. Kyereh; kyerehb@gmail.com

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*Broussonetia papyrifera* (L.) Vent. (Moraceae) was introduced to Ghana in 1969 and has since become second only to *Chromolaena odorata* as an invasive species in Ghanaian forests. This study determined its ecological traits that enhance its invasion of plant communities. Fruiting and viability patterns were studied through monthly monitoring of 985 trees (≥6 cm gbh) in one forest site. The effect of light on its seed germination was tested in light-proof boxes. Means of propagation were determined by tracking the origin of newly regenerated plants on a newly cleared plot of land that *B. papyrifera* had occupied. It fruited twice a year with one season (January–March) producing more fruits than the other (July-August). Fruiting occurred in trees as small as 9 cm gbh but the percentage of individuals fruiting in each size class increased with tree size. There was a clear pattern of seed viability during the January–March fruiting period. The species did not appear to have a naturally high seed viability with germination always below 50% of each weekly collection. Seed germination was depressed in dark. These results suggest that the species may be competitive in disturbed forest sites and therefore its spread may be aided by forest degradation.

1. Introduction

Of the important factors responsible for biodiversity loss in Ghanaian forests, species invasion is the least cited and investigated. This is despite the fact that the invasion of *Chromolaena odorata* for instance has been recorded in Ghana since 1972 [1] and is known to drive critical forest processes including fires [2]. Besides *C. odorata* another invasive species that has come up strongly is *Broussonetia papyrifera*, [3] a medium-size tree of the Moraceae family widely grown for paper production and native to Japan and Taiwan [4]. The species was introduced to Ghana by the Forestry Research Institute of Ghana (FoRIG) in 1969 to form part of an experimental programme to identify species for the local production of industrial cellulose [5]. It was planted in three forest reserves in the semideciduous forest zone on a trial basis, namely, Afram Headwaters, Bia-Tano, and Pra-Anum. From these three sites it has spread and invaded large canopy gaps and degraded farmlands in many parts of the forest zone. Its invasion has been most remarkable in the north west subtype of the moist semideciduous forest presumably due to its highly noticeable forest fragmentation. Viable populations of the species are found as far north as Dormaa Ahenkro near the Ghana-Cote d’Ivoire border. However, beyond the semideciduous forest zone reports of its invasion are not available possibly due to lack of recent inventories. The invasion of *B. papyrifera* in Ghana has been internationally acknowledged for more than a decade [6]. Elsewhere including 11 states in the United States of America and over a dozen countries, *B. papyrifera* is reported as an invasive species [7, 8].

There is a need to understand the extent to which it is a threat to natural ecosystems and how it can be controlled if necessary. However, no enough scientific information is available on the species in Ghana to make this achievable. At present what is known is that *B. papyrifera* normally occurs...
in degraded areas and large canopy gaps created as a result of logging and wildfires and that it is rarely found in forest shade [9]. More detailed information, for example, on attributes that enhance its colonizing abilities, conditions favouring its spread, and those that keep it in check, is required to inform decisions on its management and, if necessary, eradication. Important adaptive strategies that may enhance a plant’s successful establishment in a new environment and therefore invasive ability may be found in reproduction and germination [6]. This paper therefore is sought to determine the seed production and viability patterns of B. papyrifera, the ability of its seeds to reside in the soil seed bank, and the relative importance of its regeneration pathways.

2. Materials and Methods

2.1. Study Site. One of the three sites where B. papyrifera was first introduced in the country, Afram Headwaters Forest Reserve, was selected as the study site. Occupying an area of 201 km² the reserve is found in the dry semideciduous forest type and is mostly burnt with an open canopy and in some places resembles a pure stand of B. papyrifera. The site has a bimodal rainfall regime with the major peak in May–July and the minor in September–October. The mean annual rainfall is a little below 1500 mm and the length of the dry season expressed as the total months with less than 100 mm rainfall is 4-5 months [10].

2.2. Monitoring of Seed Production and Viability. Fruiting and viability patterns of B. papyrifera were studied through monthly monitoring of 985 trees (≥6 cm gbh) on 25 sampling plots each measuring 20 × 20 m. The plots were systematically established over an estimated area of about 6 ha in the research working circle of the reserve. The trees were simply observed for fruiting from December 2006 to December 2007. Trees found with fruits were counted, measured, and marked with a red oil paint. Finally all unmarked and therefore nonfruited trees were also counted and measured. Within each of the 25 plots one 1.5 × 1.5 m subplot was demarcated and cleared of debris and lined with polythene sheet for fruit collection at weekly intervals during the major fructifying period to assess seed viability. Seeds were removed from the fruits by washing in cold water and then air-dried under room temperature.

Seed viability was tested by germination. From each weekly collection 25 air-dried seeds were sown on two layers of 5.5 cm diameter Whatman Number 42 filter paper within Petri dishes. Eight Petri dishes (replicates) were used for the tests. The seeds were kept moist through regular watering. Possible seed dispersal agents were identified through informal interviews with local farmers and forestry technicians living close to the forest reserve where the studies were carried out. Following that bat droppings from the Kumasi Zoological Garden where a large colony of bats congregate during the day were cultured from January to March and monitored for seedling emergence.

2.3. Testing the Ability of Seeds to Reside in the Soil Seed Bank. The ability of B. papyrifera seeds to stay and germinate from the seed bank was tested in two ways, firstly by observing germination from soils collected from a forest site where the species had invaded and secondly by testing the effect of darkness on seed germination. For the soil seed bank experiments, approx. 800 cm² of top soil (2 cm depth) was collected from each of 12 sampling points located roughly 20 m from one another. The soil was thoroughly mixed and then divided into six portions and each portion thinly spread over white river sand in a wooden tray kept in a shade house with about 30% full irradiance. The soil was kept moist by regular watering at daily intervals. The emergence of seedlings from the soil was monitored for six weeks.

The effect of darkness on the germination of B. papyrifera was tested by sowing seeds as described above but this time the dishes were kept in a ventilated but light-proof box covered with black polythene as in [2]. The light treatment was of similar construction and design but used transparent polythene. Both treatments were placed under a shed with 8% ambient full sun irradiance. Germination in the dark treatment was assessed at night using a dim, green filtered torchlight [11]. Germinated seeds were counted at the emergence of the radicle. The study lasted for a period of 33 days.

2.4. Determining the Relative Importance of Natural Regeneration Pathways. About half of a hectare of B. papyrifera-invaded secondary forest was cleared to create an opening in the canopy. The resultant debris was removed allowing the exposure of the soil to sunlight and after 10 weeks B. papyrifera plants that emerged were sampled from 2 × 2 m plots. They were pulled out of the soil and their propagation origin was determined by examining the roots for any attachment. The plants were sorted into seedlings originating from seeds, sprouts originating from roots, and sprouts originating from stumps. The plants were counted and their dry weight was determined through the oven dry method. The relative importance (RI) of each regeneration pathway was estimated by the formula $RI = n_\text{es} \times 100\% / \sum n_i$, where $n_\text{es}$ is number of individual plants recorded for type of regrowth and $f_i$ is mean dry mass of plant regrowth.

2.5. Statistical Analyses. Chi-square tests were used to compare observed frequencies with those expected for differences in (i) seed germination between dark and light treatment; (ii) regeneration modes; (iii) seedling numbers of different tree species emerging from soil seed banks.

3. Results

3.1. Fruiting. B. papyrifera fruited twice a year with one season producing more fruits than the other. The major fruiting season was from January to March and the minor season occurred from July to September. Trees started fruiting from about 9 cm girth at breast height (gbh) but only 243 out of the 985 (24.7%) of all trees enumerated (≥6 cm gbh) were found to produce fruits. The likelihood of trees fruiting appeared to depend on size; for trees in stem girth size classes greater than
60 cm gbh, observed fruiting percentage ranged from 47.5 to 54.5%, but only between 12.8 and 26.5% of trees with stem girth sizes less than 60 cm gbh fruited (Figure 1). Thus, even though smaller trees were able to fruit, within each size class the proportion of trees that fruited increased with tree size.

3.2. Seed Dispersal and Viability Pattern. From the interviews conducted it came out that birds and bats are regular feeders on the species and possibly main dispersal agents over long distances. Accumulated droppings of bats cultured over a three-month period showed profuse germination of seeds of B. papyrifera along with other species (Table 1).

The first batch of fruits was collected in mid-January (Week 1) but these contained no developed seeds; that is, they were presumably aborted. Subsequent collections made between the 3rd week of January (Week 2) and the 3rd week of March (Week 11), however, contained mature seeds. The percentage of germination of these successive collections showed an initial low percentage, which rose to reach a peak in the last week of February (Week 7) and thereafter declined (Figure 2). Therefore there was a clear pattern of seed viability during the January–March fruiting period.

3.3. Effect of Light on Seed Germination. Light had a profound effect on the germination of B. papyrifera seeds. After 33 days of sowing seeds in neutral shade and darkness, 61 out of 200 seeds (30.5%) germinated in neutral shade whilst eight out of 200 seeds (4%) germinated in darkness. Seed germination of B. papyrifera was therefore significantly depressed in dark ($X^2 = 51.66, Df = 1, \text{Prob.} < 0.0001$).

3.4. Seed Germination from Soil Seed Bank and Plant Regrowth following Clearing of B. papyrifera. B. papyrifera was well represented in the soil seed bank. Of the 95 tree species seedlings that germinated from the soil seed banks B. papyrifera formed 45.3% (Table 2). A multinomial test showed that, compared with other tree species, the proportion of B. papyrifera seeds that germinated from the seed bank was significantly higher than what will be expected by chance ($X^2 = 22.011, Df = 3, \text{Prob.} < 0.0001$).

In the regrowth monitoring study, the mean number of B. papyrifera plants per m$^2$ that emerged 10 weeks after clearing was 15.5. They were derived from 3 main sources: seeds, roots, and stumps (Table 3).

Seedlings formed the highest proportion (73%) of regeneration followed by stem/stump sprouts (24%) and then

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**Table 1: Type of species and number of seedlings that emerged from bat droppings cultured from January to March.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of seedlings</th>
<th>% of total seedlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solanum spp.</td>
<td>233</td>
<td>54.82</td>
</tr>
<tr>
<td>Morus mesozygia</td>
<td>70</td>
<td>16.47</td>
</tr>
<tr>
<td>Broussonetia papyrifera</td>
<td>67</td>
<td>15.76</td>
</tr>
<tr>
<td>Alchornea floribunda</td>
<td>47</td>
<td>11.06</td>
</tr>
<tr>
<td>Trema orientalis</td>
<td>4</td>
<td>0.94</td>
</tr>
<tr>
<td>Ficus capensis</td>
<td>4</td>
<td>0.94</td>
</tr>
<tr>
<td>Total</td>
<td>425</td>
<td>100</td>
</tr>
</tbody>
</table>

**Table 2: Emergence of seedlings of Broussonetia papyrifera alongside those of other tree species from soil (9600 cm$^3$) collected from a forest site invaded by Broussonetia papyrifera. Monitoring of seedling emergence was for a period of six weeks.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of seedlings</th>
<th>% of total seedling population</th>
</tr>
</thead>
<tbody>
<tr>
<td>Broussonetia papyrifera</td>
<td>43</td>
<td>45.3</td>
</tr>
<tr>
<td>Trema orientalis</td>
<td>20</td>
<td>21.0</td>
</tr>
<tr>
<td>Musanga cecropioides</td>
<td>19</td>
<td>20.0</td>
</tr>
<tr>
<td>Ficus sp.</td>
<td>13</td>
<td>13.7</td>
</tr>
<tr>
<td>Total</td>
<td>95</td>
<td>100</td>
</tr>
</tbody>
</table>

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**Figure 1:** Percentage of the adult tree population that fruited in each girth class in the main fruiting season (January–March).

**Figure 2:** Seed germination pattern of B. papyrifera monitored over a period of 11 weeks during the major fruiting season (January–March).
root sprouts (3%). From a multinomial test on the plant population as recorded on the 2 × 2 m plots, the observed distribution frequency of the regeneration modes was different from that expected by chance ($X^2 = 44.247$, Df = 2, Prob < 0.0001). When size (biomass) is taken into consideration the “relative importance” of each regeneration mode, expressed as a proportion of total available biomass, was highest for stem sprouts (64.61%), followed by seedlings (27.54%), and finally root sprouts (7.85%).

4. Discussion

4.1. Seed Production and Dispersal. Broussonetia papyrifera regenerated from seeds, root suckers, and stumps; however, sexual reproduction was the most predominant. Its fecundity is high by virtue of its ability to fruit twice in a year and also achieving reproductive maturity at relatively small size (about 6 cm gbh in this study). Thus sexual reproduction may be the most important mode of reproduction that drives its invasiveness. This is supported by observations in the Pacific region, where, because only male clones of B. papyrifera were introduced and therefore no seed production takes place, the species invasive tendencies are not noticed [4]. Because B. papyrifera has separate male and female plants [12] not all healthy looking adult individuals would be expected to fruit at any fruiting event. This partly explains why only 24.7% of all trees enumerated were found to have fruited. In the present study the number of individuals which flowered but did not fruit was not taken into account. However, this information could have given an indication of the male : female ratio, an index that will be useful in future phenological studies of the species.

The results show that, even though trees start fruiting early, fruiting percentages increase with tree size. This may be due to the better crown exposure of large trees and therefore access to maximum sunlight required for the built up of the photosynthate necessary for fruiting. It also means older stands have a higher capacity to cause further spread of the species in adjacent forests. B. papyrifera was observed to produce mature seeds twice in a year, January to March and June to August, unlike the Budongo Forest in Uganda where this species is reported to fruit throughout the year [13]. The contrast may be explained by the often erroneous labeling of species that fruit more than once a year as having continuous or simply erratic seed production. The germination of B. papyrifera seeds from cultured bat droppings indicates the fruit bat feeds on the species and disperses its seeds. The fruit bat has been identified as an effective long-distance disperser of tropical seeds with no negative impact on seed viability [14]. Therefore high fecundity and effective seed dispersal may be some of the important adaptive traits in B. papyrifera for its prevalence in disturbed forest patches in Ghana.

4.2. Seed Viability. There was a clear pattern of increasing seed viability of B. papyrifera from January up to a peak in February followed by a decline in March during the major fruiting period. Similar seed viability patterns have been observed in a number of tropical forest trees whose seed viability patterns have been closely followed [2]. The results suggest that quality seeds of the species may be dispersed in February which incidentally is the time for land preparation for new farms in the forest zone of Ghana. This may contribute to B. papyrifera’s profuse germination in new farms. The results also imply that, as part of the control measures, the chances of germination from newly dispersed seeds can be minimized by clearing Broussonetia infested areas around December before seed maturation.

The duration of quality seed fall compares quite well with those of some Ghanaian forest trees. Generally for species that fruit twice in a year like B. papyrifera the period corresponding to mature and viable seed fall is quite brief, about eight weeks on the average. For those that fruit once in a year the period may extend to about 20 weeks, for example, Terminalia superba [11]. Two indigenous Ghanaian pioneer trees, which share similar characteristics with B. papyrifera, are Musanga cecropioides and Trema guineensis but detailed information on their seed production patterns is not available for comparison. The maximum percentage of seed germination was below 50. The species does not therefore appear to have naturally high seed viability in the January–March fruiting period. It is, however, possible that scarification of seeds is enhanced when seeds pass through the digestive systems of its dispersers as it is observed that passage through animal gut sometimes enhances seed germination especially in pioneer species [15].

4.3. Seed Germination and Residence in the Soil Seed Bank. The results of the study show that B. papyrifera seeds are positively photoblastic and will not germinate once buried in the soil or dispersed in deep shade. In photoblastic seeds red light promotes, and far red light and darkness inhibit, germination [16]. Among tropical forest trees light regulated germination has been reported for plants from many genera including Musanga, Nauclea, and Nauclea [2]. The effect of light on seed germination either directly or indirectly through temperature modification is an important aspect of forest dynamics and together with seedling response to light has been used as the basis for categorizing forest trees into ecological guilds, pioneers and nonpioneers. Pioneers depend on canopy gaps for seed germination and seedling establishment whilst nonpioneers can germinate and survive in forest shade [17]. Based on germination requirements and for that matter ability to reside in the seed bank and colonise disturbed forest sites, there are about five known

<table>
<thead>
<tr>
<th>Type of regrowth</th>
<th>Mean number of stems m$^{-2}$</th>
<th>Mean dry mass (gm$^{-2}$)</th>
<th>Estimated relative importance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seedlings</td>
<td>11</td>
<td>7.3</td>
<td>30</td>
</tr>
<tr>
<td>Stem sprouts</td>
<td>4</td>
<td>47.1</td>
<td>63</td>
</tr>
<tr>
<td>Root sprouts</td>
<td>0.5</td>
<td>45.8</td>
<td>7</td>
</tr>
<tr>
<td>Total</td>
<td>15.5</td>
<td>100.2</td>
<td>100</td>
</tr>
</tbody>
</table>
Ghanaian semideciduous forest trees that have comparative behaviour with B. papyrifera [2]. Three of them (Trema orientalis, Musanga cecropioides, and Ficus sp.) were found alongside B. papyrifera in the soil seed bank experiments in this study. The reasons why they have not been able to compete with the species in the invaded forests may be related to B. papyrifera’s possession of some superior characteristics in seed production and dispersal, growth, and survival in relation to the environment. For instance the size of the seed bank of B. papyrifera was much larger than those of the native species, an observation which has also been made on other invasive species [18, 19].

4.4. Regeneration of B. papyrifera following Clearing. The regeneration of the species after clearing is quite strategic employing sprouting from both stumps and roots as well as seedlings from the seed banks. This trait enables a high plant density to be achieved within a short time and is responsible for the relatively high mean plant density observed in the species. The large population of seedlings, however, contrasts with the low germination percentage. The degree of dominance of a species in regrowth vegetation appears to depend on whether the species regenerates from seedlings or resprouts [20]. The strength of either strategy may change with time and also the nature or extent of degradation of the site. Because B. papyrifera has both forms of regrowth, it may be more competitive than similar species that may regenerate from only seedlings or suckers. The ability to sprout after cutting is a favourable characteristic in invading species [6]. It ensures fast reestablishment after cutting due to the already well-established root network. Therefore early high recruitment rate coupled with more robust plants with high growth rate may lead to high rate of survival for B. papyrifera and consequently dominance over other competing species.

One lesson to be drawn from the recovery of the species after clearing is that attempts to reclaim forests invaded by it should adopt measures that seek to promote the establishment of indigenous tree species under the B. papyrifera stands rather than clearing the stand before revegetating. There are indications that this approach is feasible especially if nonpioneer species are used [9]. If manual clearing is adopted then it must incorporate treatment to kill the seedlings and saplings since they readily grow back.

5. Conclusions and Implications for Forest Management

In terms of germination requirements and presence in the soil seed banks B. papyrifera is a typical pioneer species and therefore highly competitive in disturbed forests or other open areas like roadsides and farms. Forest canopy opening will increase the abundance of B. papyrifera through an effect on germination as well as seedling growth whilst forest disturbance in general will promote the species’ invasion. On the other hand, the spread of the species may be of little threat to forests that are not severely disturbed. Inability to germinate in dark also implies that the species cannot regenerate effectively under its own shade once the canopy is dense and may allow some regeneration of shade tolerant species.

**Conflict of Interests**

The authors declare that there is no conflict of interests regarding the publication of this paper.

**References**


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