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WHAT IS THE IMPACT OF DISTURBANCE ON TROPICAL DRY FOREST REGENERATION?

Systematic Review Protocol

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1. BACKGROUND

It is estimated that of the total global extent of tropical forest, tropical or subtropical dry forest accounts for 42 % of total global forest cover (Murphy & Lugo 1986). They have been exposed to severe, large-scale changes, through the cutting of valuable trees, creation of pastures, accidental or intentional fires (Gerhardt & Hytteborn 1992) and as a source of fuel wood (Murphy & Lugo 1986) and virtually all of the tropical dry forests that remain are currently exposed to a variety of different threats, largely resulting from human activity (Miles et al., 2006). However, despite their over-exploitation there have been relatively few studies of tropical dry forest and even fewer studies done on their regeneration pathways, which can provide knowledge crucial to the restoration of these forests (Vieira & Scariot, 2006).

Tropical dry forests have particular natural regeneration attributes which are not currently well understood (McLaren & McDonald, 2003b; Vieiria & Scariot, 2006). Unlike tropical moist forests, regeneration in gaps is not the primary mechanism; and the availability of moisture plays a major role in successful establishment of seedlings. The timing and duration of rainfall is crucial as there is a high probability that a given seedling will be left stranded in a drying soil and there is therefore a low probability of successful regeneration from seeds (Ewel 1980). The pronounced seasonality affects patterns of seed production, germination, survival and seedling development (Khurana & Singh 2000). Seeds of a majority of dry tropical species mature in the dry season and they are dispersed at the beginning of the rainy season when sufficient moisture is available for germination and seedling growth (Singh & Singh 1992; McLaren & McDonald, 2005). The favourable growing period is restricted to short rainy seasons when seeds are expected to germinate and seedlings establish. The deciduous state of some or most tree species allows for an increase in irradiance that in the absence of moisture exacerbates desiccation in seedlings and hence higher rates of mortality (e.g. Gerhardt 1996a).

Vegetative regeneration may well be the primary regeneration mechanism in disturbed dry forest sites, where stem and roots remain in place (Ewel 1977; Murphy & Lugo 1986; Murphy et al. 1995; McLaren & McDonald, 2003b). In the wet tropics, where large-scale disturbance occurs as a result of clearing, burning and extensive storm damage, regeneration from stem coppice is also important (e.g. Byer & Weaver 1977; Ewel 1977; Stocker 1981; Uhl et al. 1981; Putz & Brokaw 1989; Kauffman 1991; Bellingham et al. 1994). It may however, be more important in dry forest sites where resprouting offers considerable resilience to disturbance in dry forests where successful regeneration by seed is highly susceptible to rainfall seasonality (Ky-Dembele et al., 2007; McLaren & McDonald, 2003c; Vieira et al., 2006; Vieira & Scariot, 2006). Also, because trunk bases are less subject to rapid decay in the dry tropics, trees in seasonally dry forests are much more prone to reproduce vegetatively through coppicing (Ewel 1980) in response to disturbance. However, the different abilities of species to produce shoots will affect long-term species diversity in disturbed forests.

The sensitivity to moisture availability renders the regeneration of the dry forests highly vulnerable to predicted climate change effects. Most predictions of the response of tropical forests to rising CO_2 concentrations and temperatures and changing precipitation patterns have concluded that changes in precipitation will have the most impact, in that drying trends will remove drought-sensitive species from the forest (e.g. Condit, 1998). However, a recent assessment of neotropical rain forests over a 20 year period showed an increase in faster-growing species to the detriment of slower-growing sub-canopy species, apparently irrespective of their light or moisture requirements (Laurance et al., 2004). This may be due to the fertilising effect of rising CO_2 concentrations. However, this is uncertain, and strong droughts have been shown to cause shifts in tree-community composition in Panama (Condit et al., 1996) and niche differentiation with respect to soil water availability has been shown to determine distributions of tropical trees at both local and regional scales (Engelbrecht et al., 2007). Körner (1998) postulated that changing plant water relations could become the most important of all elevated CO_2 effects on tropical forests, as water is always a selective driver of plant growth. The length of dry periods is among the key determinants of the species structure of communities (Condit, 1998; Körner, 1998). 97% of the remaining global dry forest is estimated to be 'at risk', and in the Americas this is mostly from climate change (Miles et al., 2006). Most studies on the effects of climate change in the tropics have been centred on tropical rainforest with a noticeable absence of work in tropical dry forest (Körner, 1998). Given that seasonally dry forests are so heavily impacted in the neotropics, and largely surrounded by agricultural landscapes, it is unlikely that they will be able to spread their range in the face of hotter and drier climates because of the lack of habitat in anthropogenic landscapes (Pennington et al., 2004). Mayle et al., (2004) demonstrated that dry forest species merely shift their ranges rather than expand them in the face of drier climates in the Bolivian Chiqitano region. If this is generally true, then the future of the seasonally dry forests is very bleak as they will "die where they stand" (Pennington et al., 2004).

Drying trends in a dry forest environment may create conditions similar to those more usually found in xeric tropical environments where plants are more drought-tolerant and seedling survival is enhanced by both the direct effects of habitat amelioration by shade, and the indirect effects of shaded plants attaining greater size before the onset of extreme conditions (Hastwell & Facelli, 2003). This is regarded as facilitation, the positive effect of plants on the establishment or growth of other plants (Holmgren et al., 1997). In the last decade, plant ecologists have focused more on the occurrence of positive plant-plant interactions than ever before, especially in severe environments. These studies have shown that facilitative effects are stronger in these environments, leaving little doubt of their generality and importance and raising questions about the assumed ubiquity of competition as the dominant interaction between neighbouring plants. Postulated relationships between facilitation and stress (Bertness & Callaway, 1994; Callaway & Walker, 1997) propose that, as conditions for plant growth becomes increasingly adverse, facilitation becomes 'usually common' (Bertness & Callaway, 1994) or that the 'importance' and intensity of facilitation increases. Dormann and Brooker (2002) suggest a model of plant interactions whereby the importance of facilitation increases along a gradient of increasing environmental harshness, while the importance of competition decreases (Figure 1). They apply this model to harsh environments, such as the Arctic, where species removal experiments tend to find facilitative rather than competitive effects. This phenomenon has also been recorded in more mesic environments which encounter periods of environmental severity, particularly drought. Hastwell and Facelli (2003) found that the relationship between facilitation and environment severity is more complex than previously thought, as neither the intensity nor the importance of facilitation necessarily increases as conditions become severe. Maestre and Cortina (2004) found that competitive interactions dominated at both extremes of an environmental gradient and suggested that a shift from facilitation to competition under high abiotic stress conditions is likely to occur when the levels of the most limiting resource are so low that the benefits provided by the facilitator cannot overcome its own resource uptake.

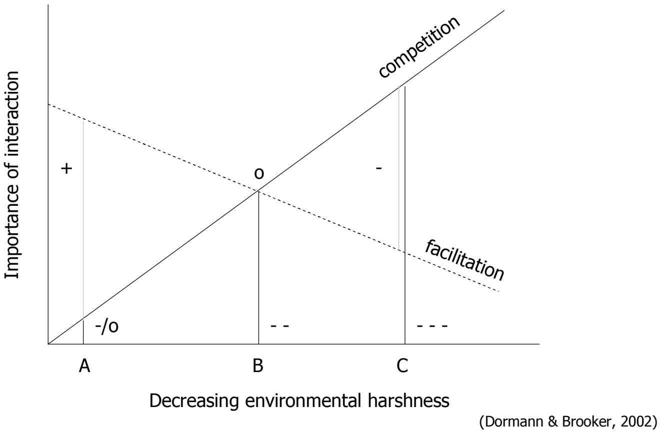

Figure 1. Intensity of facilitation and competition along a gradient of decreasing environmental harshness adopted from Brooker and Callaghan (1998). (A) Facilitation outweighs competition, leading to a negative effect of neighbour removal (grey vertical lines and symbols, indicating positive (+), neutral (o) or negative (-) net effects. In (B) both interactions cancel each other out and in (C) competition is dominant over facilitation, leading to positive effects of neighbour removal.

Thus, the relationship between facilitation and environmental severity is more complex than previously recognised, and clarification of this relationship is central for further progress in plant facilitation research (Brooker et al., 2007). The relationship is likely to be particularly complex in seasonally dry forests in a changing climate where the balance between competition and facilitation is confounded by a decrease in stomatal conductance and increased water use efficiency in response to increasing CO_2 concentrations (Lewis et al., 2004). McLaren and McDonald (2003a) observed that, in shaded plots, seedling density and survival were higher than in unshaded plots, also reflected in higher mortality rates in the unshaded plots. However, competition for moisture between adult trees and seedlings was indicated in the shaded plots by negative growth rates in the seedlings, and mortality in the shaded plots was observed to be higher in the wet season. Thus, it would appear that the facilitative effects of the canopy are stronger in drier periods, and that alleviation of the moisture stress switches the effect of the interaction from facilitative to competitive (Holmgren et al., 1997; McLaren & McDonald, 2003a). A number of other studies have confirmed the importance of shading on tree seedling survival in dry tropical forests where shading significantly improved dry season survival (Gerhardt, 1993, 1996a,b, 1998; Gerhardt & Fredriksson, 1995, Hammond, 1995; Ray & Brown, 1995; McLaren & McDonald, 2003b). However, the advantages of being below the canopy at a given location may change with seasonal or transient weather conditions (Greenlee & Callaway, 1996; Tielbörger & Kadmon, 2000; Hastwell & Facelli, 2003; McLaren & McDonald, 2003b). Smith and Huston (1989) hypothesized that the response of plants to the combined effects of irradiance (Photosynthetic Active Radiation (PAR)) and water is characterized by a trade-off between drought tolerance and shade tolerance. They proposed a trade-off model, which they used to predict the growth and survival of plants along gradients of PAR and water availability. While this model was supported by empirical studies, the results of field studies on one or a few species did not support the hypothesis (e.g. Hastwell & Facelli, 2003; Holmgren, 2000; Sack & Grubb, 2002; Tielbörger & Kadmon, 2000). Holmgren (2000) therefore expressed the need to test the model using a large set of species as an essential next step in understanding positive plant-plant interactions and these data could also be used to explain species' responses to a drying environment. Hence, it is difficult to predict the impact of drying trends on species' interactions in tropical dry forests. Species within these environments are already drought tolerant and facilitation does occur, consequently the importance of facilitation may increase at least up to a certain threshold level of drought (Maestre and Cortina, 2004). As well as reduced consumption and demand for water, differential responses of growth to CO_2 fertilization between species can be predicted (Körner, 1998). How will this then modify or affect the interaction between plants? Different species have different climatic responses, so they will respond individualistically to climate change. Consequently, not only would one expect biome shifts (e.g. replacement of rainforest by seasonally dry forest or savannah) but also significant reassortment of species within plant communities in response to such changes (Mayle et al., 2004). Furthermore, relatively little is known about how different tropical forest types will respond to future climate changes (Enquist, 2002).

2. OBJECTIVE OF THE REVIEW

2.1 Primary question

What is the importance of facilitation and vegetative regrowth in the regeneration of tropical dry forests?

Table 1. Definitions of components of the primary systematic review question

Subject	Intervention	Outcome
Tropical Dry Forests	Disturbance (natural or anthropogenic) • **Low intensity** (e.g. tree fall) • **Medium intensity** (e.g. logging, partial canopy alteration, charcoal production) • **High intensity** (e.g. hurricanes, clearance for agriculture, fire) Climate change (dry season length)	Regeneration by seedlings: 1) Growth rate of Seedlings 2) Percentage of recovery accounted for by seedlings 3) Canopy facilitation Vegetative regrowth: 1) average number of shoots per stem 2) percentage of stems with shoots 3) Average diameter or height of shoots 4) Percentage of diameter or height recovered by shoots 5) growth rate of shoots Species regeneration composition

2.2 Secondary question

The secondary question will assess the relative contribution of either seedlings or vegetative regrowth to the recovery of the site in terms of growth rates, %DBH recovered, %height recovered, %BA recovered, and %of the species recovered, i.e. a direct comparison of which contributes the greatest to the recovery of structure and floristics.

3. METHODS

3.1 Search strategy

The following computerised databases and web engines will be searched:
1. ISI Web of Knowledge
2. Science Direct
3. Directory of Open Access Journals (DOAJ)
4. Copac
5. Scirus
6. Scopus
7. Index to Theses Online (1970-present)
8. Digital Dissertations Online
9. JSTOR
10. CABI Databases
11. googlescholar.com

Plus, communications to Forestry Departments, Research Institutions and individual experts

The following search terms will be used:

1. (Tropical dry forest*) AND facilitation
2. (Tropical dry forest*) AND competition
3. (Tropical dry forest*) AND seed dispersal
4. (Tropical dry forest*) AND regeneration
5. (Tropical dry forest*) AND resprouting
6. (Tropical dry forest*) AND coppicing
7. (Tropical dry forest*) AND burning
8. (Tropical dry forest*) AND climate change
9. (Tropical dry forest*) AND disturbance
10. (Tropical dry forest*) AND carbon dioxide
11. (Tropical dry forest*) AND clearance
12. (Tropical dry forest*) AND herbivory
13. (Tropical dry forest*) AND shifting cultivation
14. (Tropical dry forest*) AND drought
15. (Tropical dry forest*) AND dry season length

Identified experts and authors of review papers will be consulted. Where appropriate, authors of papers will be contacted to request data.

3.2 Study inclusion criteria

- **Relevant subject(s):**

Seasonally dry tropical forest (pan-tropical)

- **Types of intervention:**

Disturbance (see Table 1 for list of relevant types)

- **Types of comparator:**

Undisturbed forest (mature forests that indicate no signs of anthropogenic or natural disturbance) varyingly described in the literature - including terms such as unlogged, mature, closed forest.

- **Types of outcome:**

Regeneration by seedlings, vegetative regrowth and species regeneration composition

- **Types of study:**

Studies where inventories of seedling regeneration and composition have been taken on control (no disturbance) and experimentally disturbed forest (plot or stand level). Before and after study designs. Different lengths of dry season.

- **Potential reasons for heterogeneity:**

1. Age of seedlings/saplings
2. Age of sprouts
2. Basal area of overstorey prior to disturbance
3. Basal area of the overstorey after disturbance
4. Intensity of disturbance
5. Time elapsed since previous disturbance
6. Time elapsed between disturbance and assessment
7. Composition of overstorey
8. Soil type and geology
9. Herbivores
10. Climate (especially dry season length)
11. Ground vegetation

3.3 Study quality assessment

Articles will be considered at full text and quality will be assessed by reviewers according to a hierarchy of evidence (Stevens & Milne 1997, Pullin & Knight 2003, e.g. a randomised control trial would be weighted higher than a site comparison study) admitting or excluding them from the study. A minimum of 25% of the articles will be considered by two of the reviewers and tested statistically to ensure agreement of quality is sufficiently high. Disagreement will be resolved by a third reviewer.

3.4 Data extraction strategy

Study characteristics, design, quality, results and reasons for heterogeneity will be extracted and recorded on specially designed data extraction forms. These may be modified in consultation with a statistician after piloting the method. Attempts will be made to collect primary data from authors where appropriate.

3.5 Data synthesis

A narrative thesis summarising the data will be produced including study characteristics, design, quality, tabulated results and reasons for heterogeneity. After consultation with a statistician, any data suitable for statistical analysis will be analysed using appropriate techniques for the type of data extracted; this may include meta-analysis.

4. POTENTIAL CONFLICTS OF INTEREST AND SOURCES OF SUPPORT

No conflicts of interest to be declared. This systematic review is funded by Bangor University and the University of the West Indies.

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