1. Title:

The ecological impacts of a migratory bat aggregation on its seasonal roost in Kasanka National Park, Zambia.

2. Name of Authors:

Byng, J. W., Racey, P. A. & Swaine, M. D.

3. Full Postal Address:

School of Biological Sciences
University of Aberdeen
Aberdeen
AB24 3UU
United Kingdom

4. Email addresses:

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6. Name of corresponding author:

J. W. Byng

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Abstract

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The ecological impacts of migratory species on their seasonal environments are poorly known. The effects of several million straw-coloured fruit bats (*Eidolon helvum*), which migrate seasonally to Kasanka National Park, Zambia each year, on the small area of *mushitu* 'swamp' forest in which they roost, were investigated. The structure of the *mushitu* forest was profoundly altered by the presence of *E. helvum*, with increased roost tree mortality, lowering and opening of the forest canopy and a decrease in tree basal area. *E. helvum* are also thought to increase the severity of fires within their roost site because the structural changes result in a drier microclimate. The effects of increased nitrogen and phosphorous input were less apparent. These findings suggest that the ecological impact of this migratory bat species on its seasonal environment could ultimately threaten the long-term viability of its seasonal roost.

Introduction

Migration has evolved in several classes of vertebrates where species travel, often *en masse* and over long distances, to take advantage of the nutritional benefits associated with seasonally changing environments (Alerstam, Hedenstrom & Akesson, 2003; Fleming & Eby, 2003). Understanding the seasonal migration of tropical fruit bats is increasingly important because of their roles as seed dispersers in the world's tropical rainforests, pollinators of fruit crops, and vectors of newly emerging diseases (Polis, Anderson & Holt, 1997; Shilton *et al.*, 1999; Fleming & Eby, 2003; Messenger, Rupprecht & Smith, 2003). However, little is known about the impact migratory fruit bats have on their environments, particularly their seasonal roost sites.

Highly gregarious migratory bat genera such as *Pteropus* and *Eidolon* often defoliate and break branches of roost trees, resulting in reduced canopy foliage (Jones, 1972; Bonaccorso, 1998; Richter, 2004). Bonaccorso (1998) suggested that such defoliation might aid visual observations between bats and detection of approaching aerial predators or could be related to thermoregulation. Severe defoliation of roost trees could effect tree growth, composition and structure of roosts which may affect their long term viability (Richter, 2004). Large aggregations of bats are also likely to move significant amounts of energy and nutrients around their foraging areas (Polis, Anderson & Holt, 1997) and into roost sites, particularly as guano. Bat guano is rich in nitrogen and phosphorous and may benefit forest soils and play an important role in forest dynamics (Zielinski & Gellman, 1996).

This study was conducted in Kasanka National Park, Zambia where several million straw-coloured fruit bats, *Eidolon helvum* (Kerr, 1792), migrate each year. This large seasonal aggregation roosts in a stand of *mushitu* 'swamp' forest, defoliating trees and breaking branches (Richter & Cummings, 2006). In this paper the effects of this seasonal aggregation on forest vegetation and soil conditions in the *mushitu* forest were investigated, and the implications of these effects explored.

Methods

Study Site

This study took place between July – August 2007 in Kasanka National Park (KNP). KNP is located in Central Province, Zambia (12º 30'S 30º 14'E), and is one of the smallest national parks in the country, covering approximately 420 km^2, with a unimodal rainfall pattern of ca.1200 mm yr^{-1} and an average elevation of 1050 m (Smith & Fisher, 2001; Richter & Cummings, 2006). It consists of a mosaic of vegetation types including miombo woodlands, the dominant vegetation, seasonally flooded grasslands, small stands of wooded grassland known as chipya, mateshi dry evergreen forest, and riparian forest (Smith & Fisher, 2001). Associated with the riparian forest is a small area of *mushitu* 'swamp' forest which is the seasonal roost site for several million migratory *E. helvum*, from October to January (Richter & Cummings, 2006).

The *mushitu* 'swamp' forest in KNP is the only known roost site in the region for *E. helvum* and the population is thought to be an aggregation of several smaller colonies from further north in Africa (Richter and Cummings, 2006). The population in KNP has only been reported since the late 1980s (Richter, 2004) and previous descriptions by Darling (1960) and Ansell (1978) mentioned no large aggregations indicating that the population is of recent origin. Estimations in the size of the *E. helvum* aggregation varies from year to year as there has been no thorough systematic count over a long period of time, but estimates have ranged from 2-8 million individuals (Sorenson and Halberg, 2001; Richter, 2004; Richter and Cummings, 2006).

Mushitu 'swamp' forests are located predominantly in the higher rainfall areas of Zambia, are three-storeyed forests, easily fragmented and edaphically controlled (Fanshawe, 1969). The *mushitu* in KNP is approximately 0.4 km^2 and can be classified into two of Fanshawe's (1969) *mushitu* sub-types: seepage *mushitu* and seasonally flooded *mushitu* (Fig. 1a). The *mushitu* in KNP consists of three main areas: one large (referred to as the main *mushitu* forest) and two smaller *mushitu* 'island' groups (Fig. 1b).

Seepage *mushitu* has ground water all year at the level of the water table, whereas seasonally flooded *mushitu* has standing water only during the rainy season (Fanshawe, 1969). The seepage *mushitu* is dominated by few plant species notably *Syzygium cordatum* interspersed with *Ilex mitis, Ficus trichopoda* and *Maesa lanceolata* (Nomenclature follows Coates Palgrave, 2002). In contrast, the seasonally flooded *mushitu* is relatively species-rich particularly around termitaria with *Syzygium cordatum,* and *Khaya anthotheca* dominating the upper canopy and *Aporrhiza nitida, Rauvolfia caffra, Diospyros mespiliformis*, and *Maesa lanceolata* common in the understorey and thicket levels. Several fires have been reported in the *mushitu* in recent years, including a large peat fire in 2000 (E. Farmer, pers. comm.).

Mapping the forest

The *mushitu* forest in KNP was mapped using a GPS (Garmin GPS 60) to delineate its edge, the area of peat fire damage, and the roosts of *E. helvum*. Areas of fire damage were revealed by the presence of fire scars on tree trunks and roots and charcoal on fallen trees. Areas of *E. helvum* roosts were easily identified due to severe canopy loss and 'stag-headed' trees in these areas (Richter, 2004). An aerial survey was also carried out to confirm roosting areas and the forest margins.

Data Collection

Vegetation data were collected in 100 20 m x 20 m subplots (Table 1). Transects consisting of consecutive 20 m x 20 m subplots were laid out in areas of forest, which could be easily re-located (Fig. 2), but avoiding areas of above and below ground fire damage. Transects were 20 m wide and ranged from 20 m to 280 m long due to the shape and size of the *mushitu*. In each 20m x 20m subplot all trees ≥ 10 cm girth at breast height (GBH) were counted, identified, their girths measured and their basal areas calculated. Also, the height of the five tallest trees in each subplot were measured using a clinometer (Suunto PM-5), canopy openness quantified using hemisphere photography (Whitmore *et al*., 1993) every 20 m along each transect, and the percentage of herbaceous cover estimated, in increments of five, in each of the 100 20 m x 20 m subplots.

In every 20 m x 20 m subplot, four soil samples were collected in four 5 m x 20 m areas. There were 20 soil samples per 100 m resulting in one bulked sample (100 m x 20 m area). A 40g sub-sample was taken from this bulked soil sample after it had been well mixed and constituted one of the 20 samples used to measure nitrogen (N), carbon (C) and available phosphorus (P). Sub-samples were removed, air dried in metal pie trays, and analysed for N, C, and P at the Analytical Laboratory at the University of Aberdeen. Soil pH was measured using a pH meter (HI-98103 Checker) by taking a 20g sub-sample from each of the four soil samples collected in each 5 m x 20 m area, and mixing it with 200 ml of distilled water.

Statistical Analysis

Statistical analysis was carried out in Minitab (vers. 15). Analysis of variance (ANOVA) was applied to all forest vegetation and soil variables and transformed using Box-Cox, Log_{10} and square root where appropriate. Non-parametric Kruskall-Wallis tests were used for variables (mean herbaceous cover and number of dead roost trees) when the transformed data were still not normally distributed according to the Anderson-Darling normality test. The *mushitu* forest sub-type and bat presence were the two factors used in the analysis but the duration of bat roosting was not a factor. Two distinct seasonal roosting areas of *Eidolon helvum* were apparent due to different levels of defoliation: a short-term roost (≤ 3 years) in the seasonally flooded *mushitu* and a long-term roost (~20 years) in the seepage *mushitu*. Thus the vegetation and soil data were divided and consequently analysed in the four combinations shown in Table 1.

Results

Mapping the forest

Two distinct areas where *E. helvum* had roosted were mapped in the *mushitu*: a short-term roost (≤ 3 years, K. Farmer & L. Reynolds, pers. comm.) in the seasonally flooded main *mushitu* and a larger long-term roost (~ 20 years) in the seepage main *mushitu* (Fig. 1a). There was no evidence of bats roosting in either of the *mushitu* island groups. Evidence of severe peat fire damage was observed in areas of the main *mushitu* (Fig. 1b). The large peat fire which occurred in 2000 encompassed the central portions of the main *mushitu* causing many of the tall large trees, predominantly *Syzygium cordatum*, to fall. An increased abundance of *Maesa lanceolata* and *Ficus trichopoda* was apparent in some peat fire affected areas; woody species are completely absent in other areas which are now dominated by grassland vegetation or areas of open dry soil.

Changes in Forest Vegetation

Eidolon helvum roosting areas in both seasonally flooded and seepage *mushitu* subtypes were characterised by significantly reduced canopy height and significantly increased higher canopy openness (Table 2). There were also significantly lower tree basal areas, increased herbaceous cover of the forest (Table 2) and higher numbers of dead roost trees and tree species were associated with bat forest compared with non-bat forest (Table 2; Fig. 2). The mean number of trees and the extent of herbaceous cover were higher in seasonally flooded bat forest and lower in seepage bat forest when compared with their respective undisturbed forests (Fig. 2).

Forest type significantly influenced the mean number of species, herbaceous cover, and canopy openness (Table 2). The interaction between forest type and bats had a significant effect on the mean number of trees, species and canopy openness (Table 2) indicating that the effect of the bats differed between forest types.

Changes in Soil Conditions

The large seasonal bat roost had no significant effect on *mushitu* soil conditions, but soil N, C, P levels and soil pH were significantly higher in seepage *mushitu* compared with seasonally flooded *mushitu* (Table 3). The interactions between forest type and bats were significant for soil N and C content (Table 3). Although bats had no significant effect on soil conditions (Table 3), there were small increases in all four soil variables in bat areas compared with non-bat areas, which were particularly evident for N and C content (Fig. 3).

Discussion

Forest fires

Peat fires do not occur naturally in swamp forests because they are generally too wet. Exceptions are the peat swamp forests in Indonesia (Wosten *et al*., 2006), where such fires, occurring in disturbed or damaged areas of forest with open canopies, reduce tree crowns and increase fuel loads on the forest floors as a result of illegal logging (Dawson, Butt & Miller, 2000; Wosten *et al*., 2006). Another type of disturbance occurs in the *mushitu* swamp forest in KNP - the large seasonal aggregation of *E. helvum*, and a key issue is the extent to which this increases the fire risk. It is widely reported that logged areas of forests are more susceptible to fires than undisturbed areas because of their drier microclimate (Brown, 1988). The effects of bats on the forest structure, through increased canopy openness (Fig. 2) and increased fuel loads on the forest floor, due to the large number of fallen trees, suggests that bats could have similar effects to logging. The decrease in herbaceous cover in the long-term bat roost area compared with adjacent undisturbed forest also suggests that a drier microclimate could exist as a result of large canopy gaps. Thus bats could potentially increase the severity and frequency of peat and forest margin fires.

Changes in Forest Vegetation

The structure of the *mushitu* forest in KNP was substantially altered by roosting bats, with the primary roost trees, *S. cordatum*, affected in both roost areas, but particularly in the seepage *mushitu* which contained long-term bat roosts. *Syzygium cordatum* mortality was higher in both *E. helvum* roost areas resulting in a lower number of *S. cordatum* roost trees. As *E. helvum* prefer to roost in the taller trees, they are the first to become damaged resulting in lower basal areas in the remaining trees in both roost areas (Fig. 2).

Canopy patterns in roost areas were very different from undisturbed areas. This can be explained by the fact that *E. helvum* often roost at high densities in tall emergent trees (Rosevear, 1965; Funmilayo, 1976; Kingdon, 1984; DeFrees & Wilson, 1988). Funmilayo (1976) comments that the continued use of the same trees for roosting by

E. helvum prevents the regeneration of branches and leaves and this could be seen in KNP. This large *E. helvum* aggregation caused branches to break under their weight resulting in ‘stag-headed trees’ and a lowered canopy height (Fig. 2). This also reduced the foliage within the canopy and thus increased the canopy openness. Canopy gaps resulting from the fallen roost trees and defoliation have resulted in increased herbaceous cover on the forest floor and an increase in pioneer shrub species, particularly *Maesa lanceolata*, in the seasonally flooded *mushitu* containing short-term roosts. This response is similar to gaps caused by logging activities in other tropical forests (Webb, 1998). A dense herbaceous cover is characteristic of the seepage *mushitu* sub-type (Fanshawe, 1969), but with the increased canopy openness in the long-term *E. helvum* roost, herbaceous cover was lower in the seepage bat forest compared with its undisturbed counterpart (Fig. 2). The increase in canopy openness caused by the bats and possibly also the peat fire could have caused the soil to dry so it is unable to support a rich herbaceous cover (Brown, 1988; Webb, 1998).

A higher number of tree species were found in long-term bat seepage forest compared with non-bat seepage forest (Fig. 2) and this could be a result of site conditions, since it is not uncommon to see *mushitu* stands consisting of only one or two species (Fanshawe, 1969), or to the opening of the forest canopy leading to seeds in the soil seed bank germinating due to increased light levels (Uhl *et al*., 1988).

Changes in Soil Conditions

Soil conditions were not significantly different between *E. helvum* roost areas in either of the two forest sub-types and undisturbed stands of *mushitu* even though bat guano is rich in nitrogen and phosphorous (Shahack-Gross *et al.*, 2004; Emerson & Roark, 2007). There were small but non-significant increases in all soil variables measured, but particularly for nitrogen and carbon in bat areas (Fig. 3; Table 3). Thus roosting *E. helvum* may have some small effects on the soil conditions. There could be several explanations for this. Firstly *E. helvum* forage up to 30 km away from their *mushitu* roost in KNP (Richter, 2004; Richter & Cummings, 2006) and pteropodid bats have rapid intestinal passage times (Rosevear, 1965; Thomas, 1984; Shilton *et al.*, 1999). Thus much of the large potential nutrient input could be voided whilst foraging. Other possible explanations include changes in the height and position of the water table, which occurs in *mushitu* forests through the year, causing leaching of nutrients (Dahm *et al.*, 1998), or even increased nutrient uptake by plants and microbial consumption (Crawford, 1995).

Future Implications

An aggregation the size of that in KNP of *E. helvum* has not been reported elsewhere in Africa, therefore the damage and long-term consequences are difficult to predict. However, it is plausible that damage caused by roosting could render the bats' favoured roosting habitat in KNP unsuitable in the long-term, and the threat of forest fires could increase the likelihood of this happening. In KNP the *mushitu* used by bats for at least 20 years has been damaged by fire, and the majority of the large tall trees, notably the primary roost trees, *Syzygium cordatum*, have disappeared, resulting in a lowered and open canopy. *Eidolon helvum* prefer not to roost at lower levels and do so only when taller trees are not available. If *E. helvum* change roosts as a response to disturbance to their habitat (Kunz & Lumsden, 2003), then the loss of their preferred roost trees in the long-term seepage forest may have altered the suitability of the roosting area to such an extent that an alternative site where *S. cordatum* is locally abundant was occupied by part of the population. At present, bats continue to roost in both areas, even though they are separated, but the *mushitu* island groups are probably too far away from the main roost areas to be favoured as roost trees since *E. helvum* prefers to roost close together (Rosevear, 1965; Kingdon, 1984).

In the future, areas of the undisturbed seasonal flooded *mushitu* not previously used may be used for roosting, and this may be happening already (M. P. Kennedy, pers. comm.). If roosting in undisturbed seasonally flooded *mushitu* occurs in the future, with effects similar to those documented in the present study, combined with probable future fire damage and the increased loss of roost trees, then the use of the *mushitu* forest as a roost site for *E. helvum* in KNP could become untenable in the long-term. Alternatively, the bats may consistently roost on smaller trees and shrubs, which they do at present at KNP. Undisturbed bats populations have been reported doing this in Ibadan, Nigeria but this behaviour is considered rare (Funmilayo, 1976).

This study of the *E. helvum* roost in Kasanka National Park has revealed that the ecological impacts of a migratory species on its seasonal environments can be profound and perhaps irreversible. *E. helvum* have a major impact on forest dynamics and canopy patterns of its seasonal roost site and is also thought to increase fire risk and severity within the forest due to the structural changes it causes. These changes could ultimately threaten the long-term viability of their *mushitu* forest roost site.

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Table 1: The four forest combinations of *mushitu* sub-types studied in relation to seasonal *Eidolon helvum* roosts, the size of each area studied in hectares and number of subplots. All forest vegetation and soil data were analysed according to these combinations.

Mushitu Forest Type	Bat Roost Area	Area (ha.)	20m x 20m subplots n
seepage	no	0.52	13
seepage	yes (long-term)	1.00	25
seasonally flooded	no	1.48	37
seasonally flooded	yes (short-term)	1.00	25

Table 2: ANOVA results of mean forest vegetation variables per 20 m x 20 m subplots in KNP. The data were transformed by Box-Cox, Square root, Log $_{10}$, where appropriate when the residuals were non-normally distributed. Non-parametric Kruskall-Wallis tests were used (indicated by #) for variables where the data were transformed and still were not normally distributed. (ANOVA P-values = * indicates P< 0.05, ** indicates P< 0.01, and *** indicates P< 0.001; Kruskall-Wallis P-values = ** indicates P<0.005, *** indicates P<<0.0005; ns = non-significant).

Factors	No. of Species		No. of Trees		Basal Area		Canopy Height		Canopy Openness		# Herb Cover		# Dead Roost Trees	
	F (df)	P	F (df)	P	F (df)	P	F (df)	P	F (df)	P	χ^2 (df)	P	χ^2 (df)	P
Mushitu Forest Type (Seepage vs. Seasonal)	64.48 (1)	***	8.10 (1)	**	2.32 (1)	ns	4.15 (1)	*	11.43 (1)	***	30.48 (1)	***	0.05 (1)	ns
Bat Roosting Area	5.42 (1)	*	0.12 (1)	ns	19.66 (1)	***	117.38 (1)	***	179.47 (1)	***	28.71 (1)	***	10.43 (1)	**
Mushitu Type*Bat Roosting Area	8.19 (1)	**	21.31 (1)	***	1.52 (1)	ns	0.16 (1)	ns	3.97 (1)	*	---	---	---	---

Table 3: ANOVA results of mean *mushitu* soil pH per 20 m x 20 m subplots and mean soil nitrogen (N), carbon (C), and (P) per bulked 100 m plots in KNP. (P-values = * indicates P< 0.05, ** indicates P< 0.01, *** indicates P< 0.001, and ns = non-significant).

	pH		N Content		C Content		Available P	
Factor	F (df)	P	F (df)	P	F (df)	P	F (df)	P
Mushitu Forest Type	8.00 (1)	**	143.83 (1)	***	75.87 (1)	***	23.55 (1)	***
Bat Roosting Area	3.52 (1)	ns	1.47 (1)	ns	0.17 (1)	ns	0.45 (1)	ns
Forest Type*Bats	0.31 (1)	ns	18.82 (1)	***	9.46 (1)	**	0.18 (1)	ns

Figure 1: Maps of the *mushitu* ‘swamp’ forest in KNP showing areas of: (a) *Eidolon helvum* roosting in seepage *mushitu* (SM) and the seasonally flooded *mushitu* (SFM) (hatched) (The dotted lines show approximately where the divisions occur); and (b) peat fire damage (shaded) with the main *mushitu* and two *mushitu* island groupings.

Figure 2: Mean forest vegetation variables for each forest sub-type in bat roost areas (open bars) and non-bat areas (dark bars) ±SE. (a) no. of trees, (b) no. of tree species, (c) basal area, (d) canopy height, (e) herb cover, (f) no. of dead roost trees, and (g) canopy openness.

Figure 3: Mean forest soil variables for each forest sub-type in bat roost area (blue bars) and non-bat areas (orange) ±SE. (a) pH, (b) nitrogen content, (c) available phosphorous, (d) carbon content.

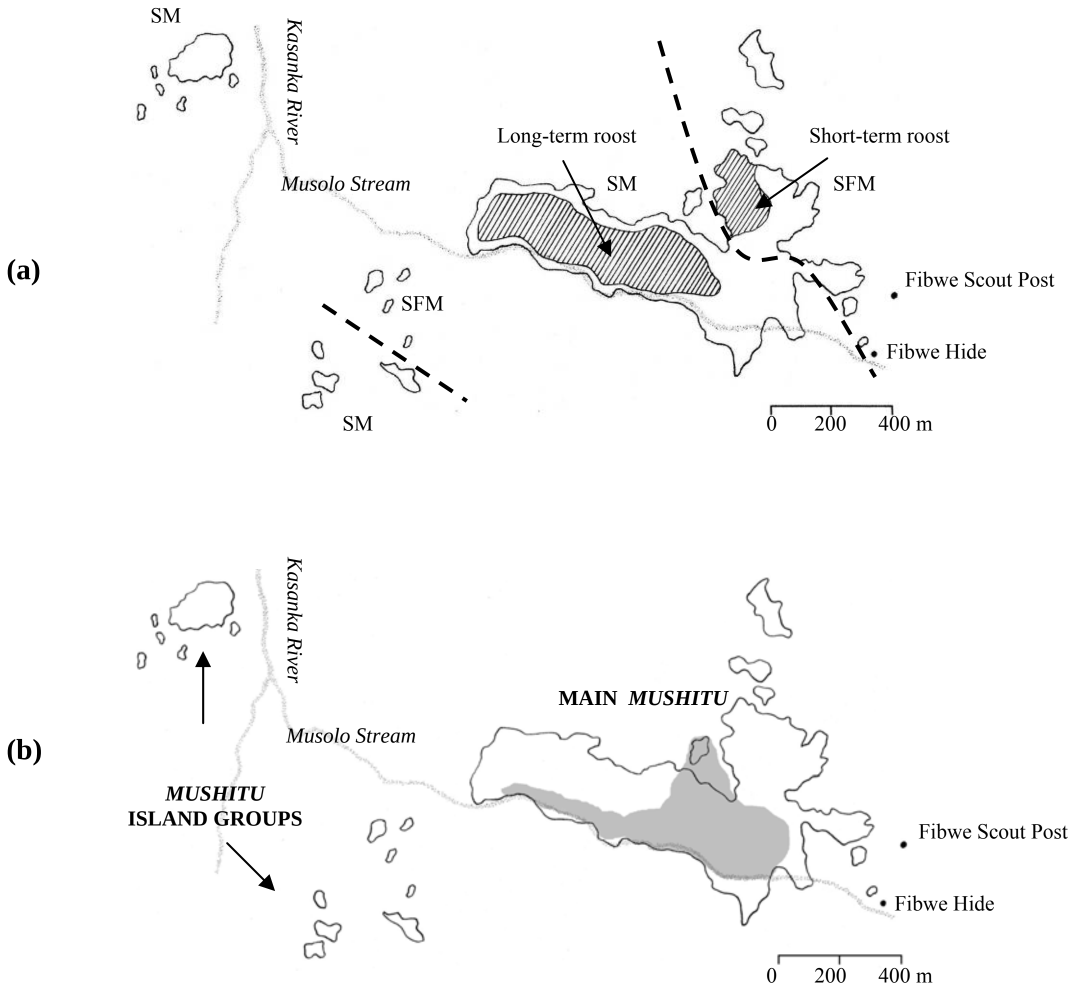
(a)
SM
Kasanka River
Musolo Stream
Long-term roost
SM
Short-term roost
SFM
SFM
SM
Fibwe Scout Post
Fibwe Hide
0
200
400 m
(b)
Kasanka River
Musolo Stream
MAIN *MUSHITU*
MUSHITU
ISLAND GROUPS
Fibwe Scout Post
Fibwe Hide
0
200
400 m

Figure 1

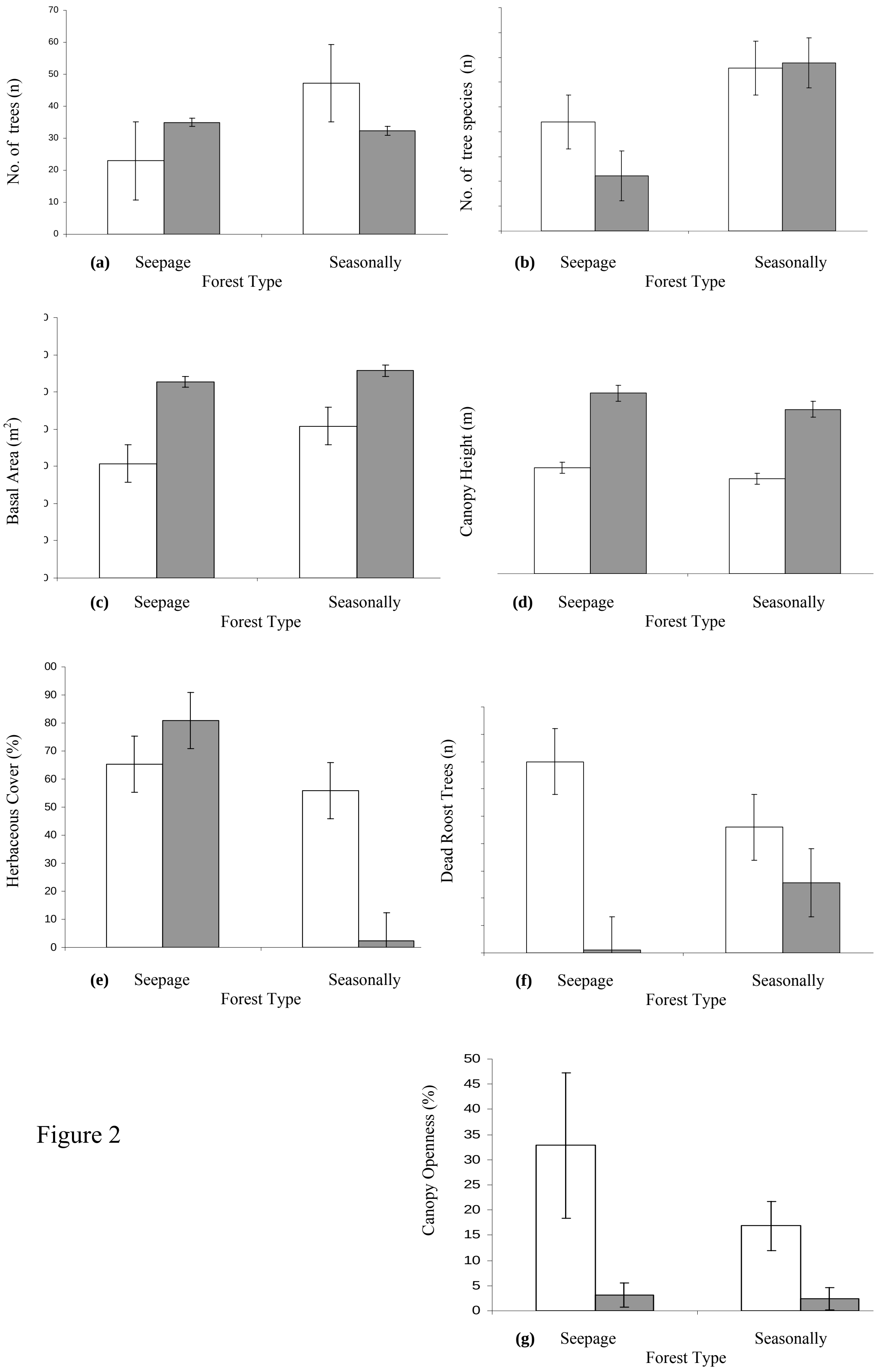
No. of trees (n)
70
60
50
40
30
20
10
0
(a)
Seepage
Seasonally
Forest Type
No. of tree species (n)
(b)
Seepage
Seasonally
Forest Type
Basal Area (m^2)
(c)
Seepage
Seasonally
Forest Type
Canopy Height (m)
(d)
Seepage
Seasonally
Forest Type
Herbaceous Cover (%)
00
90
80
70
60
50
40
30
20
10
0
(e)
Seepage
Seasonally
Forest Type
Dead Roost Trees (n)
(f)
Seepage
Seasonally
Forest Type
Canopy Openness (%)
50
45
40
35
30
25
20
15
10
5
0
(g)
Seepage
Seasonally
Forest Type

Figure 2

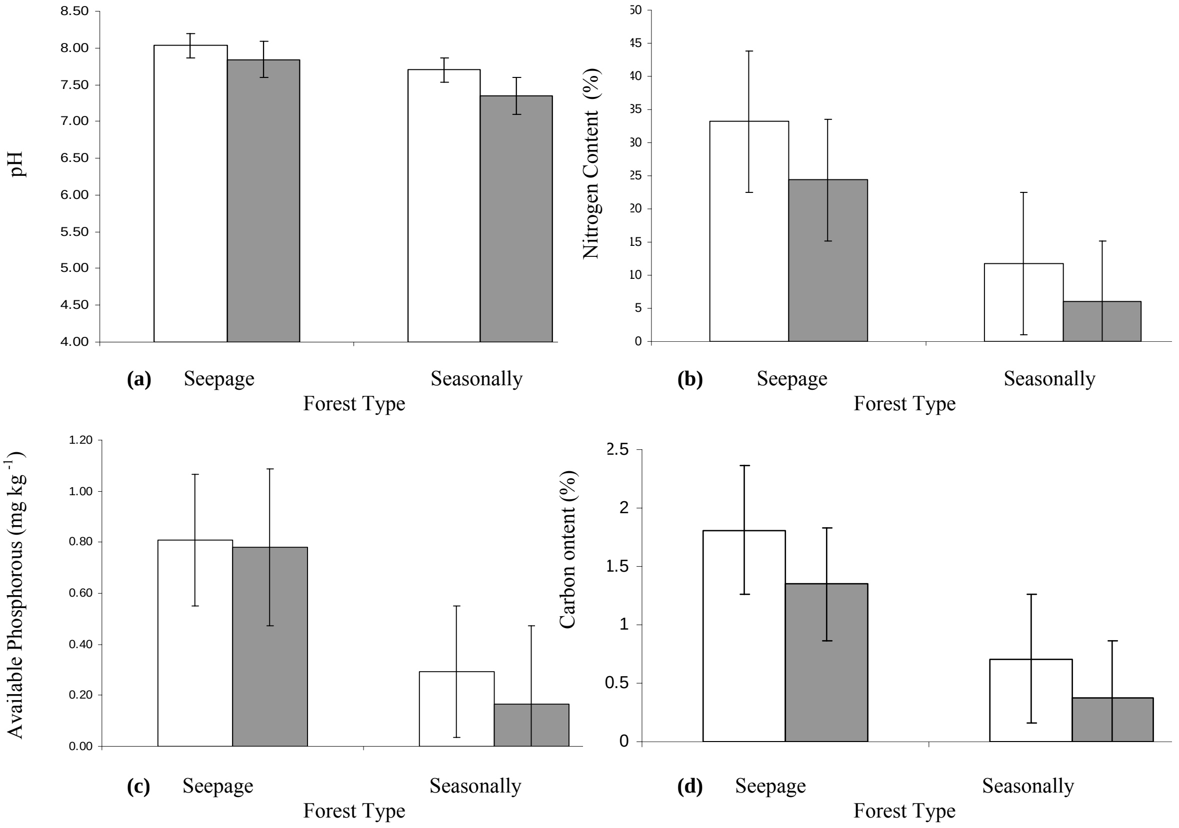
pH
8.50
8.00
7.50
7.00
6.50
6.00
5.50
5.00
4.50
4.00
(a)
Seepage
Seasonally
Forest Type
Nitrogen Content (%)
50
45
40
35
30
25
20
15
10
5
0
(b)
Seepage
Seasonally
Forest Type
Available Phosphorous (mg kg-1)
1.20
1.00
0.80
0.60
0.40
0.20
0.00
(c)
Seepage
Seasonally
Forest Type
Carbon ontent (%)
2.5
2
1.5
1
0.5
0
(d)
Seepage
Seasonally
Forest Type

Figure 3