# Intratree Variation in Fruit Production and Implications for Primate Foraging

VIVAMUS

## Alain Houle · Colin A. Chapman · William L. Vickery

**Abstract** We tested the hypothesis that fruit quantity and quality vary vertically within trees. We quantified intratree fruit production before exploitation by frugivores at different heights in 89 trees from 17 species fed on by primates in Kibale National Park, Uganda. We also conducted a pilot study to determine if the nutritional value of fruit varied within tree crowns. Depending on the species and crown size, we divided tree canopies into 2 or 3 vertical layers. In 2-layered trees, upper crowns produced fruits that were 9.6–30.1% bigger and 0.52–140 times the densities of those from lower crowns, with one exception. Among 2-layered trees, upper crowns produced a mean of 46.9 fruits/m³ (median 12.1), while lower crowns produced a mean of 14.1 fruits/m³ (median 2.5). Among 3-layered trees, upper crowns produced a mean density of 49.9 fruits/m³ (median 12.5), middle crowns a mean of 16.8 fruits/m³ (median 6.6), and lower crowns a mean of 12.8 fruits/m³ (median 1.8). Dry pulp and moisture were systematically greater per fruit in the highest compared to the lowest canopy layers (22.4% and 16.4% respectively in 2-layered trees, 49.7% and 21.8% respectively in 3-layered trees). In 1 tree of *Diospyros abyssinica*, a pilot nutritional study showed that upper crown ripe fruit contained 41.9% more sugar, 8.4% more crude proteins, and 1.8 times less of the

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potentially toxic saponin than lower crown ripe fruit, but the result needs to be verified with more individuals and species of trees. We discuss the consequences of intratree variations in fruit production with respect to competition among frugivorous primates.

## Introduction

Frugivores respond to variation in fruit abundance and nutritional quality by changing metabolism and energy balance (Knott 1998), ranging behavior (Olupot *et al.* 1997; Remis 1997), and food selection (Peres 1994; Wrangham *et al.* 1998). Some female primates, such as chimpanzees (*Pan troglodytes*), establish social dominance among themselves (Wittig and Boesch 2003), which may provide high-ranking females access to high-quality fruit sites and translate to higher reproductive success (Pusey *et al.* 1997). From the individual's perspective, the problem becomes locating feeding sites that produce the highest nutritional gains (energy intake rate, amount of energy gained/minute), at a minimal cost of energy spent to get that energy, to locate these feeding sites when they are available at low predation risks, and at the lowest level of scramble and contest competition. Researchers had previously focused on how primates locate particular trees or patches (Snaith and Chapman 2005); however, selection may also operate on a smaller scale. We measured fruit production before primates and other frugivores exploited the fruit in 89 tree crowns from 17 species to compare the quality of foraging zones within trees.

Fruit development depends strongly on photosynthesis and light availability (Brady 1987; Raven *et al.* 1992; Taiz and Zeiger 1998). Variation in light availability can affect photosynthetic rate, photosynthate production, dry matter allocation, and various leaf phenotypic traits and physiology including leaf conductance, chloroplast size, and mean stomatal densities (Lynch and Gonzalez 1993; Mehrotra *et al.* 1998; Proietti *et al.* 2000; Raven *et al.* 1992; Sellin and Kupper 2005; Taiz and Zeiger 1998). Because leaves in the upper part of trees shade those below, one would expect a vertical stratification of light within the tree. Consequently, upper leaves are expected to produce more photosynthates than lower, shaded leaves. Zones of the canopy that receive more sunlight are expected to distribute more photosynthates locally, from the leaf to the adjacent fruit: local translocation of resources hypothesis (Lynch and Gonzalez 1993; Proietti *et al.* 2000; Raven *et al.* 1992; Taiz and Zeiger 1998). Thus, zones in a tree that receive more sunlight likely produce more food and nutritionally better foods for primates than other zones do.

Authors of previous studies have shown a vertical stratification of photosynthates in plants. Schaefer *et al.* (2002) found that fruit of various species were most abundant >16 m, rare at 4–12 m, and the caloric content of the standing crop differed among forest strata. They investigated fruit production among trees from species that differed in adult height; we propose to test variation of fruit production within the tree. Perica (2001) documented that, within a tree, leaves receiving more light

contained more nitrogen and therefore likely more proteins than other leaves. High-quality leaves might be important in determining leaf selection among folivorous primates, or could contribute to increase the quality of the diet of frugivorous primates during periods of fruit scarcity.

Measuring intratree variations in fruit production facilitates quantifying the nutritional benefits of primate social dominance, if it is possible to measure variation in food quality and its exploitation on a short time scale. We tested if food within tree crowns is patchily distributed, before frugivores begin to exploit it within a fruit cycle. Primates respond to food patchiness. Whitten (1983) showed that intraspecific rank-related differences in the diet of vervets (*Cercopithecus aethiops*) occurred when food items were clumped, but not when they were randomly distributed. We expected a similar pattern within tree crowns and if food items are patchily distributed, a situation that likely promotes contest competition within trees for foraging frugivores.

Energy intake may vary with feeding height and social dominance, which may have an effect on fitness. Among wild Malagasy indris (*Indri indri*), dominant females consistently fed higher in fruiting trees than subordinate males did, and they used aggressive displacements to force males to feed in the lower crown (Pollock 1977), suggesting short-time scale usurpation over high-quality food zones. Similarly, in Brazil, moustached tamarins (*Saguinus mystax*) are dominant to, and fed higher in trees than saddle-back tamarins (*S. fuscicollis*: Peres 1996), in a way similar to that of red-tailed monkeys (*Cercopithecus ascanius*) and blue monkeys (*C. mitis*) of Uganda (Houle *et al.* 2006). The fitness consequences are difficult to quantify; however, savannah yellow baboons (*Papio cynocephalus*) that feed on higher quality food during infancy obtain greater reproductive success (Altmann 1998). Interspecific and intraspecific dominance relationships determine feeding height selection of primate frugivores in Kibale National Park, Uganda (Houle 2004; Houle *et al.* 2006). Thus, we predict that dominant group members and infants from high-ranking mothers will feed higher in tree crowns, providing them a nutritional advantage, which will translate into higher fitness (energy allocation sensu Ellison 2003). We assess intratree foraging zone variations in fruit production, and in accordance with the local translocation of resources hypothesis, we predict that fruit crop size, fruit density, fruit moisture content, dry pulp per fruit, and nutritional quality will be higher in tree upper crowns than lower in the tree.

## Methods

### Study Area

We conducted observations from December 1999 to November 2000 and from June 2004 to July 2005 in Kibale National Park (795 km$^2$), in southwestern Uganda, near the foothills of the Ruwenzori Mountains (N 0° 7′ 48″–N 0° 24′ 36″ and E 30° 11′ 24″–E 30° 19′ 12″). Kibale contains moist, evergreen forest (57%), colonizing forest (20%), grassland (15%), swamp (4%), and open woodland (4%) (Chapman and Lambert 2000). The forest (altitude *ca.* 1500 m) receives a mean annual rainfall of 1722 mm (1990–2005) in 2 distinct wet (March–May, September–November) and

dry seasons. Mean daily minimum temperature is 14.9°C; mean daily maximum temperature is 20.2°C. (Chapman *et al.* 1997, 1999, 2000; Struhsaker 1997).

Tree Data

We evaluated variations in fruit density and fruit biomass in 89 individual trees from 17 species (mean diameter at breast height [DBH], or above buttresses, 99.9 cm, SD 72.4, range 15.7–244.2 cm; Table I). We accessed tree crowns via a modified version of Perry's single rope technique (Houle *et al.* 2004; Laman 1995; Perry 1978) 1) to evaluate fruit crop and fruit density from within the canopy, 2) to collect fruit to quantify moisture and dry pulp mass ($n$=14,359 fruits), 3) to increase crown height data accuracy (to estimate crown height and volume, via a 50-m tape, all data rounded to the nearest m), and 4) to collect fruit for a pilot study of nutritional quality in different canopy zones. Mean tree height is 22 m (SD 11.5, range 6–50 m), mean crown height is 11 m (SD 6.1, range 3–24 m), and crown volumes (used to quantify fruit density) average 2399 m$^3$ (SD 2381.1, range 28–6361 m$^3$). We computed crown volume as a sphere, and corrected for crown shape by multiplying the sphere volume by the ratio of twice the crown height divided by the sum of 2 crown diameter measures taken at 90° of each other. We also drew crown shapes on millimetric paper to increase accuracy of volume measurements.

For each tree, we divided the crown into 2 vertical zones of equal height: upper crown and lower crown ($n$=82 trees; Table I). After gaining experience it was possible to divide the crown of some trees into 3 vertical layers (upper, middle, lower crowns; $n$=7 trees; Table I). We defined canopy layers in 2-layered trees using the vertical middle point of the crown. In 3-layered trees, we also determined the volume of each vertical layer by first dividing the crown height into 3 vertical layers of equal heights.

We studied 17 tree species (Table I). We chose species because 1) they provided important food items for *Cercopithecus ascanius*, *C. mitis*, and *Lophocebus albigena* in 1999–2000 (Houle 2004) and *Pan troglodytes* in 2002–2005 (Houle, *unpublished*; Kahlenberg 2006), and 2) we could collect data in the trees before primates and other frugivores exploited them. Hence, the data represent fruit production, i.e., the food available within a tree for the primates, or competitors, during a fruit cycle.

Light, Temperature, and Humidity

It is possible that the putative intratree vertical stratification of fruit varies as a function of light availability or other factors. Although our objective was not to evaluate the validity of the local translocation of resources hypothesis, we collected data on light (200 measures during sunny days in 5 trees, 506 measures during cloudy days in 5 trees), temperature, and humidity (7 and 6 trees during sunny and cloudy days, respectively). We gathered light data in 6 trees from 3 species (*Diospyros abyssinica*, *Ficus exasperata,* and *Fagaropsis angolensis*), and temperature and humidity in 11 trees from 5 species (*Pouteria altissima*, *Ficus exasperata*, *F. sur*, *Mimusops bagshawei,* and *Pseudospondias microcarpa*).

We collected light availability in 1999–2000 via a LI-COR LI-250 attached to a LI-190SA quantum sensor. We conducted measurements between 1100 and 1300 h,

**Table I** Tree species sampled during two field seasons (1999–2000 and 2004–2005) in Kibale National Park, Uganda

| Date | Species (family) | Sample size (n trees) | DBH (cm) | Tree height (m) | Crown height (m) | Canopy volume (m³) |
|---|---|---|---|---|---|---|
| Trees for which the crown was divided in two canopy layers | | | | | | |
| Nov. 2004 | *Clausena anisata* (Rutaceae) | 6 | 15.7 | 6 | 3 | U 14 L 14 |
| Feb.–Mar. 2000 | *Diospyros abyssinica* (Ebenaceae) | 7 | 40 | 24 | 8 | U 230 L 236 |
| Apr.–Aug. 2000 | *Ficus exasperata* (Moraceae) | 10 | 142.8 | 29 | 11 | U 947 L 968 |
| Feb. 2000 | *Ficus natalensis* (Moraceae) | 1 | 213.3 | 29 | 19 | U 3,109 L 3,109 |
| May 2000 | *Ficus sansibarica* (formerly *brachylepis*) (Moraceae) | 1 | 119.1 | 26 | 19 | U 1,613 L 1,613 |
| Aug. 2000 | *Strychnos mitis* (Loganiaceae) | 5 | 40.6 | 15 | 8 | U 174 L 174 |
| Feb. 2005 | *Linociera johnsonii* (Oleaceae) | 12 | 29.3 | 8 | 5 | U 349 L 349 |
| Jun. 2004 | *Pseudospondias microcarpa* (Anacardiaceae) | 3 | 150.9 | 30 | 13 | U 2,670 L 2,670 |
| Jun. 2000–July 2005 | *Uvariopsis congensis* (Annonaceae) | 18 | 19.9 | 17 | 7 | U 87 L 87 |
| Mar. 2005 | *Cordia abyssinica* (Boraginaceae) | 1 | 202.0 | 29 | 10 | U 921 L 921 |
| Mar. 2005 | *Cordia millenii* (Boraginaceae) | 2 | 114.6 | 26 | 13 | U 2,249 L 2,249 |
| Mar. –Apr. 2005 | *Tabernaemontana* sp. (likely *johnstonii*) (Apocynaceae) | 16 | 16.1 | 9 | 4 | U 43 L 43 |
| Trees for which the crown was divided in 3 canopy layers | | | | | | |
| Mar. 2005 | *Ehretia cymosa* (Boraginaceae) | 1 | 69.6 | 17 | 13 | U 63 M 63 L 63 |
| Jan. 2005 | *Ficus natalensis* (Moraceae) | 1 | 244.2 | 21 | 10 | U 501 M 1,168 L 1,669 |
| Nov. 2004 | *Ficus sansibarica* (formerly *brachylepis*) (Moraceae) | 1 | 124.7 | 22 | 15 | U 1,014 M 1,353 L 1,014 |
| Nov. 2004 | *Ficus vallis-choudae* (Moraceae) | 1 | 35.2 | 8 | 6 | U 99 M 132 L 99 |
| Aug. 2004 | *Mimusops bagshawei* (Sapotaceae) | 1 | 83.5 | 33 | 12 | U 442 M 773 L 994 |
| Feb. 2005 | *Ficus sur* (formerly *capensis*) (Moraceae) | 1 | 99.9 | 24 | 21 | U 1,588 M 1,588 L 794 |
| Jun. 2005 | *Pouteria altissima* (formerly *Aningeria*) (Sapotaceae) | 1 | 136.5 | 50 | 24 | U 1,781 M 2,799 L 1,781 |

We sorted data first with species for which tree crowns are 2 canopy layered, then those with 3 layers. Fig names after Berg and Hijman (1989). U = Upper; M = middle; L = lower.

and averaged over 15 s (the unit took 2 measures/s). The light sensor was attached to a 2-m pole. Each set of light measurements consisted of 3 readings outside the canopy (direct sun light hitting the light sensor), 8 horizontal measures at 45° intervals at the same height as the climber, and 6 vertical measures ranging from 1 m below to 4 m above the climber's feet. We collected 3 consecutive sets of light measurements in the same tree, each 5 min apart. If the condition of the sky changed while we were taking measurements, we discarded the reading and took another. We later attributed each light measurement to either the upper crown or the lower crown.

We measured temperature and humidity data in 2004–2005. We attached an electronic thermometer and hygrometer to the tip of a 50-m tape line, and measured temperature (0.1°C of precision) and humidity (nearest 1%) in the middle of each of the canopy layers. We took the mean after 5 min. For a given tree, we made measurements in all canopy layers under the same light conditions, either uniformly cloudy or sunny.

## Fruit Ripeness and Biomass (Total, Dry Pulp and Moisture)

We defined ripeness stages by skin color change (determined visually), sometimes hardness (as determined by hand pressing, similar to what primates did), and based them on primate food selection (Houle 2004). One exception concerns *Ficus sansibarica,* which does not change color as it ripens, or so little to the human eye. We used this species in crop and density analyses, but could not use it in analyses requiring biomass data as a function of ripeness. For all other fruit species, we defined 5 visually continuous ripeness categories via skin color, and we discarded intermediate categories to get 3 (visually clear) discrete categories.

We measured the mass of fruits (with and without the seed) to the nearest mg for fruits <10 g, 0.01 g for all other larger fruits, except for the largest fruit of *Tabernaemontana* sp. for which we measured the whole fruit to the nearest g. We measured fruit mass ≤3 h after collection in the canopy and determined ripeness immediately on our return to the field station. We refrigerated the fruits until we measured their mass to slow down both ripening and evapotranspiration. We discarded fruit that had changed color while in the refrigerator, as well as those with signs of damage, e.g., insects, fruit squashed. We dried fruit at 40°C for ≤2 d in a propane-heated oven. We dried pulp and seed separately, in the same numbered tray, until the dry mass of both items no longer varied on the electronic balance. We measured moisture by subtracting the dry pulp mass from the fresh pulp mass of each fruit. It was not possible to get the fresh pulp from *Ehretia cymosa* because we could collect only immature (very small and darkest green), and the fresh pulp was stuck to the fresh seed. However, once the whole fruit was dried we were able to remove the dry pulp from the dry seed. We provide data on 8196 fruits collected before frugivores started to exploit the tree. We treated the remaining 6163 fruits collected after primates had exploited the tree in a separate paper (Houle *et al.* 2006).

## Crop Size, Fruit Density, and Nutritional Analyses

We estimated fruit density (number of fruit/m$^3$) separately for unripe, ripening, and ripe fruit, and for each canopy layer. There was no horizontal variation in 3 preliminary tests (comparison between 2 zones of the same horizontal layer, in 3

different layers in *Ficus natalensis*, *t*-test, *p>*0.05); thus we assessed only vertical variation. We calculated fruit counts as the product of 1) the number of fruit of a given ripeness stage in a small region within a canopy layer and 2) the number of times a region of similar volume and fruit density was present in the canopy layer, as estimated visually while in the tree, and based on the mean of 4 counts. We then divided this product by the volume of the canopy layer to obtain the fruit density. We counted 1 ripeness category at a time in 1 crown layer to minimize counting errors. Moreover, we always counted the fruits via binoculars, even when fruit were close to the observer, because it enhanced the color differences of the skin among the unripe, ripening, and ripe fruit. Repeated counts of the same sample volume yielded a margin of error ranging from 3.5% to 5.8% (mean coefficient of variation: 4.8%, *n*=10).

We conducted a pilot study to determine if the nutritional value of the fruits could also vary within tree crowns. We collected *ca.* 20 fruits for each canopy layer (upper crown, lower crown) and ripeness category (unripe, ripening, ripe) in 1 tree of *Diospyros abyssinica*, 1 of *Strychnos mitis*, and 3 of *Uvariopsis congensis*. We assessed the protein (nitrogen) content of fruit using Kjeldahl procedures (Chapman and Chapman 2002; Gallaher *et al.* 1975; Horowitz 1970). Saponins are surfactants and have a soaplike foam-forming property in aqueous solutions, hemolyze red blood cells on contact, irritate the digestive tract, and can serve as a steroid hormone precursor (Phillips-Conroy 1986). We indexed the quantity of saponins in a sample via the froth test (Fong *et al.*, *unpublished*) via a 300-s criteria. Finally, we assessed 80% ethanol-soluble carbohydrates (mono- and oligosaccharides: sugars) per Danish *et al.* (2006).

## Statistical Analyses

We used *t*-tests for independent samples to compare fruit biomass among crown layers when the tree crown was 2 layers and ANOVA for independent samples to contrast upper, middle, and lower crown layers when the tree crown was 3 layers. We used nonparametric Wilcoxon tests for paired samples to contrast fruit crop (number of fruits/layer) and fruit density (number of fruits/m$^3$ per crown layer) in 2-layered tree crowns, and Friedman tests for paired samples to contrast fruit data in 3-layered tree crowns. We used nonparametric tests for crop size and fruit density because variances were heterogeneous, even after transformation. We performed multiple comparisons *post hoc* in 3-layered crown analyses. We used comparisons *post hoc* that assumed equal variances in fruit biomass contrasts (on log-transformed data, large sample sizes, the fruit as the unit of analysis) and tests *post hoc* that did not assume equal variances after nonparametric tests to contrast crop size and fruit density (on natural —untransformed— data, small sample sizes, the canopy layer as the unit of analysis). Many fruit biomass data ranged between 0 and 1, and therefore we multiplied all by 100 before we made log transformations (Sokal and Rohlf 1995). We also used nonparametric tests to contrast availability of light, temperature, and humidity in upper and lower crowns.

In fruit biomass analyses, graphs show 95% confidence intervals with the mean (Figs. 1, 2, 3, 4, 5 and 6). In other analyses, they show box plots with the median and interquartile ranges (Figs. 7 and 8). We omitted outliers to increase box lengths and ease the visualization of canopy differences. We set our tests as 2-tailed and α at 0.05, and used SPSS 8.0 for statistical procedures (SPSS Inc. 1998).
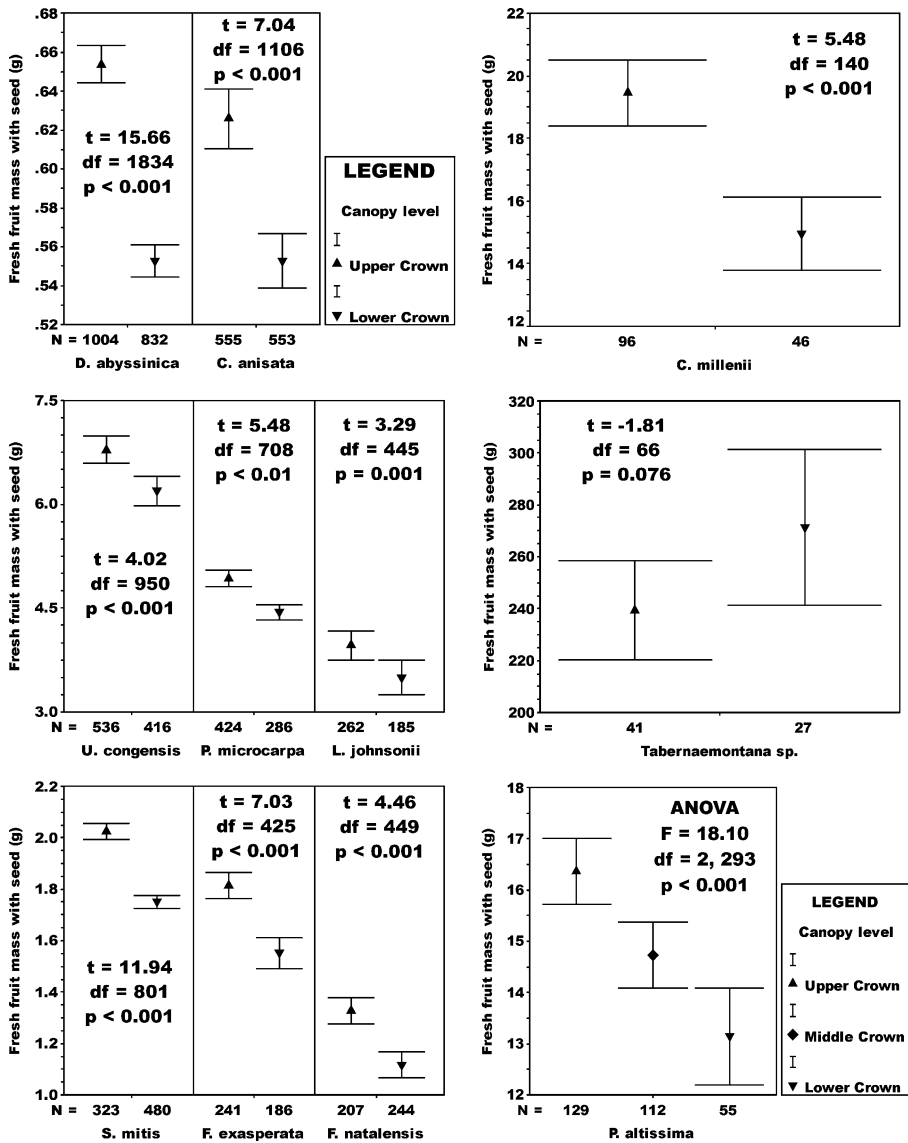
**Fig. 1** Intratree variation in fresh fruit mass (with the seed, g) in primate food trees in Kibale National Park, Uganda. *N* is the number of fruits, and fruit species with similar scales are pooled on the same graph. Species tested but not shown include *Mimusops bagshawei* (ANOVA, $F_{2, 222}=8.06$, $p<0.001$), *Ficus natalensis* (ANOVA, $F_{2, 497}=15.91$, $p<0.001$), and *F. sur* (*t*-test, $t_{166}=-3.65$, $p<0.001$, lower crown fruit not available).

## Results

### Intratree Variation in Light, Temperature, and Humidity

The upper crown receives almost twice as much sunlight (65% of incident light available above the canopy) as the lower crown does (35%). Light availability differs
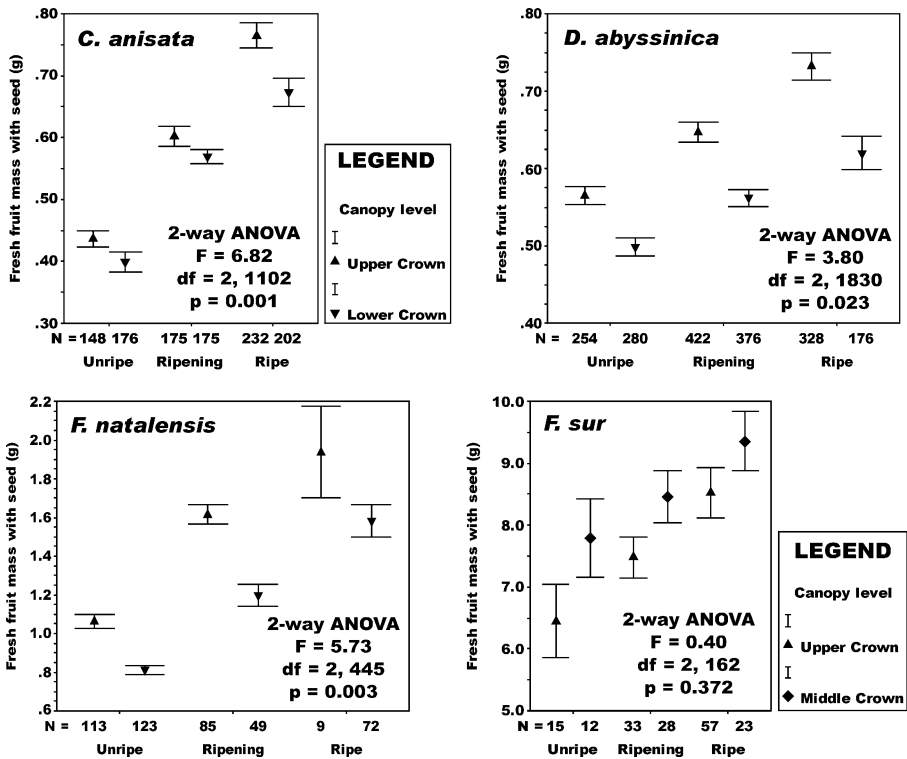
**Fig. 2** Intratree variation in fresh fruit mass (with the seed, g) per ripeness categories and vertical canopy layers in primate food trees in Kibale. Species tested but not shown include 2-layered trees: *Ficus exasperata* (2-way ANOVA, $F_{2, 421}$=3.86, $p$=0.022), *Linociera johnsonii* ($F_{2, 441}$=3.01, $p$=0.050), *Pseudospondias microcarpa* ($F_{2, 704}$=13.19, $p$<0.001), *Srychnos mitis* ($F_{2, 797}$=2.52, $p$=0.071), *Cordia millenii* ($F_{2, 136}$=0.29, $p$=0.751), *Uvariopsis congensis* ($F_{2, 946}$=0.99, $p$=0.372) and 3-layered trees: *Pouteria altissima* ($F_{4, 248}$=0.940, $p$=0.442), *F. natalensis* ($F_{4, 491}$=0.56, $p$=0.690).

between the upper crown and lower crown (Wilcoxon test for paired-samples, $Z$= –2.293, $p$=0.022, upper crown mean for 5 trees in sunny days and 5 trees in cloudy days=832.5 μmol of photons/s/m$^2$=*ca.* 46,250 lux, median=675.3 μmol/s per m$^2$; lower crown mean=454.7 μmol/s per m$^2$=*ca.* 25,261 lux, median=335.5 μmol/s per m$^2$). Similarly, temperature varies between the crown layers ($Z$=−2.313, $p$=0.021, upper crown 26.6°C, and lower crown 25.4°C), as does humidity ($Z$=−1.94, $p$=0.05, upper crown 44.3%, lower crown 49.7%). Overall, the upper crown represents a sunnier, warmer, and drier microhabitat than that of the lower crown.

Intratree Variation in Fresh Fruit Biomass

Among 2-canopy-layered crowns ($n$=82), upper crown fruits with seeds are on average 16.3% bigger than lower crown fruits (range 9.6–30.1%). There is 1 exception, the subcanopy tree *Tabernaemontana* sp. (mean 8.6 m high, SD 1.55, range 5–11 m, $n$=16), for which fruits are the same size (Fig. 1; not all tree species are represented in this and subsequent figures, but when species are not shown graphically, their statistics appear in the legend). The same pattern occurs among
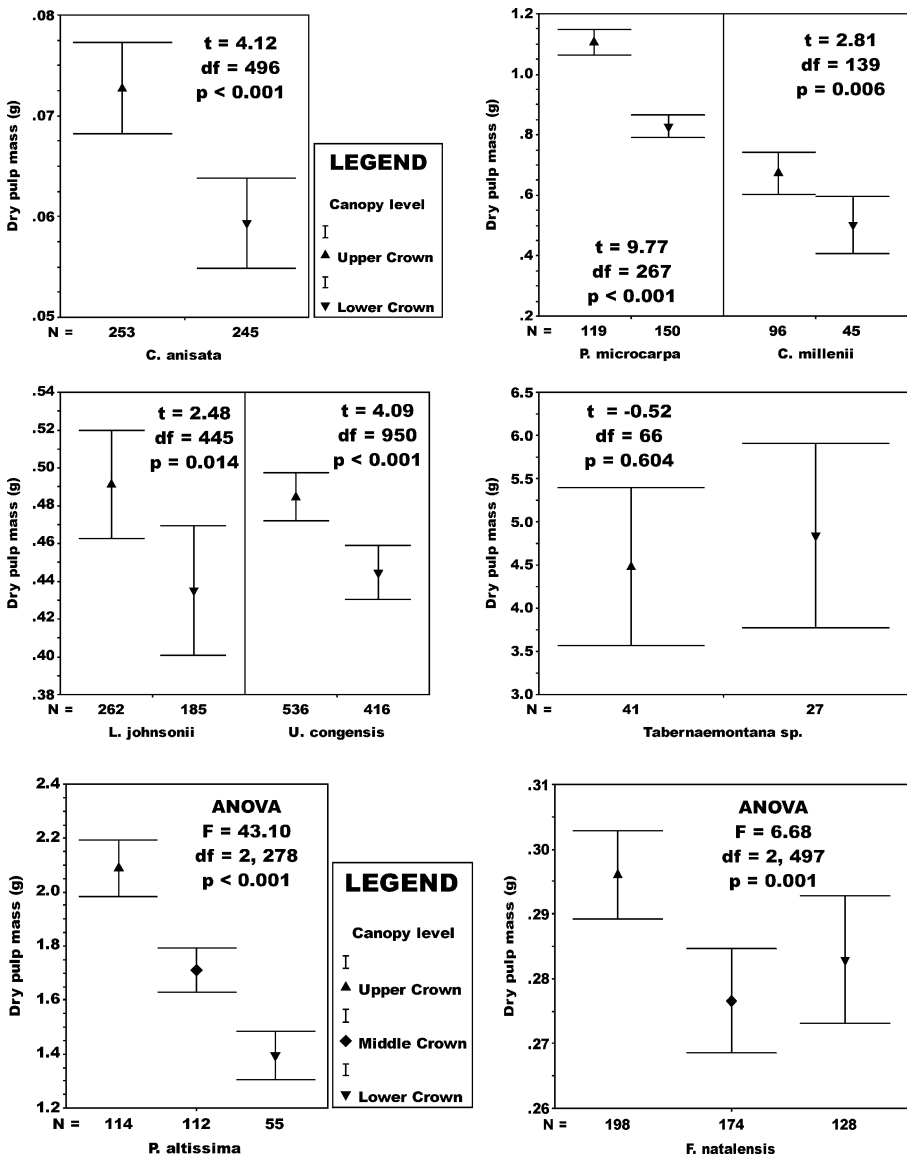
**Fig. 3** Intratree variation in dry pulp (g) in primate food trees in Kibale. Species tested but not shown include *Mimusops bagshawei* (ANOVA, $F_{2,\ 220}$=5.99, $p$=0.003), *Ehretia cymosa* (ANOVA, $F_{2,\ 59}$=9.95, $p$<0.001, green/immature fruit only), and *Ficus sur* (*t*-test, $t_{166}$=−0.598, $p$=0.551, lower crown fruit not available).

fruit species ($n$=7) for which tree crowns are 3-vertical-layered, with upper crown fruits being larger than lower crown fruits, but middle crown fruits vary as to whether they are larger, smaller, or of the same size as fruits from the other 2 layers. In 1 case (*Pouteria altissima*), multiple comparisons *post hoc* suggest that fruits from each canopy layer differ in biomass, with upper fruits being 11.1% larger than middle fruits, and middle fruits 12.0% larger than lower fruits (Fig. 1). In *Mimusops*
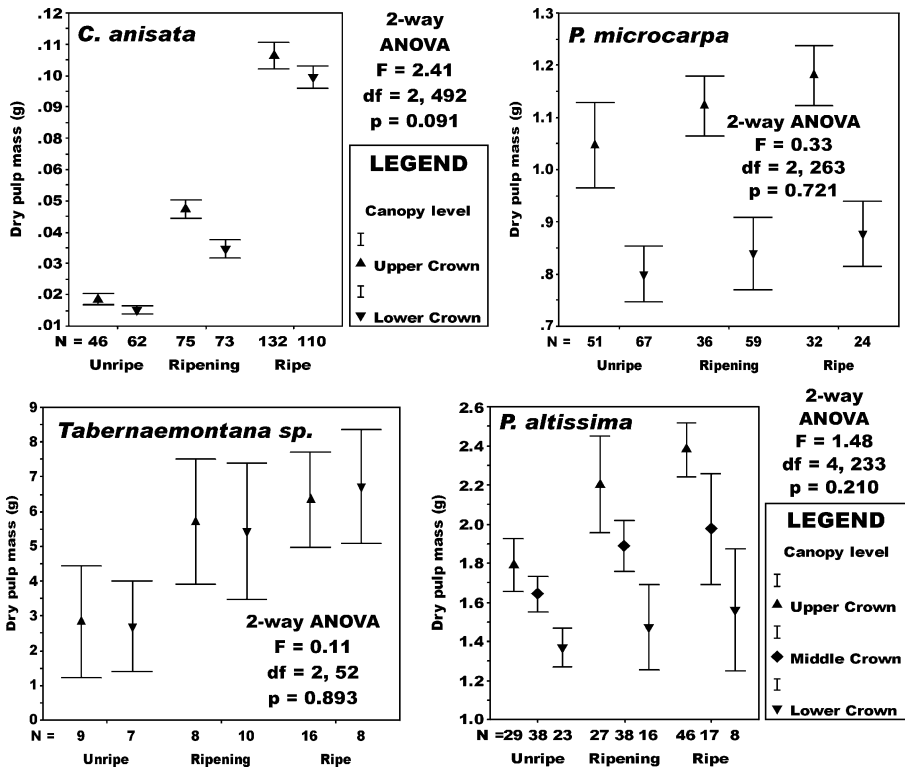
**Fig. 4** Intratree variation in dry pulp (g) per ripeness categories and vertical canopy layers (5 more species tested, all *p*>0.05) in primate food trees in Kibale.

*bagshawei*, middle crown fruits do not differ statistically from upper crown fruits (2.1% of difference), but are significantly larger than lower crown fruits (3.4% larger). In *Ficus natalensis*, middle fruits are smaller than upper fruit (6.7%), but the same size as lower fruits (2.1%). Finally, although we could not collect lower crown fruits in *Ficus sur* because they were still small and immature, middle crown fruits were larger than upper crown fruit (8.8%).

The difference in fruit biomass between canopy layers increases as fruit ripens in some species, but not in others. For trees that are split into 2 canopy layers, this is true for *Clausena anisata*, *Diospyros abyssinica*, *Ficus exasperata*, *F. natalensis*, *L. johnsonii*, *Pseudospondias microcarpa*, and marginally significant for *Strychnos mitis*. However, this is not the case in *Cordia millenii* and *Uvariopsis congensis*. No species shows such a pattern in 3-layered trees: *Pouteria altissima*, *Ficus natalensis*, and *F. sur* (4 species are shown in Fig. 2). In *Ficus sur* the pattern of larger fruit in the middle canopy holds for each ripeness category (Fig. 2).

Intratree Variation in Dry Pulp Biomass and Moisture

Among 2-canopy-layered trees, upper crown fruits produce a mean of 22.4% more dry pulp per fruit than lower crown fruits (range 9.0–34.0%), except in *Tabernaemontana* sp., for which fruit in different canopy layers had the same
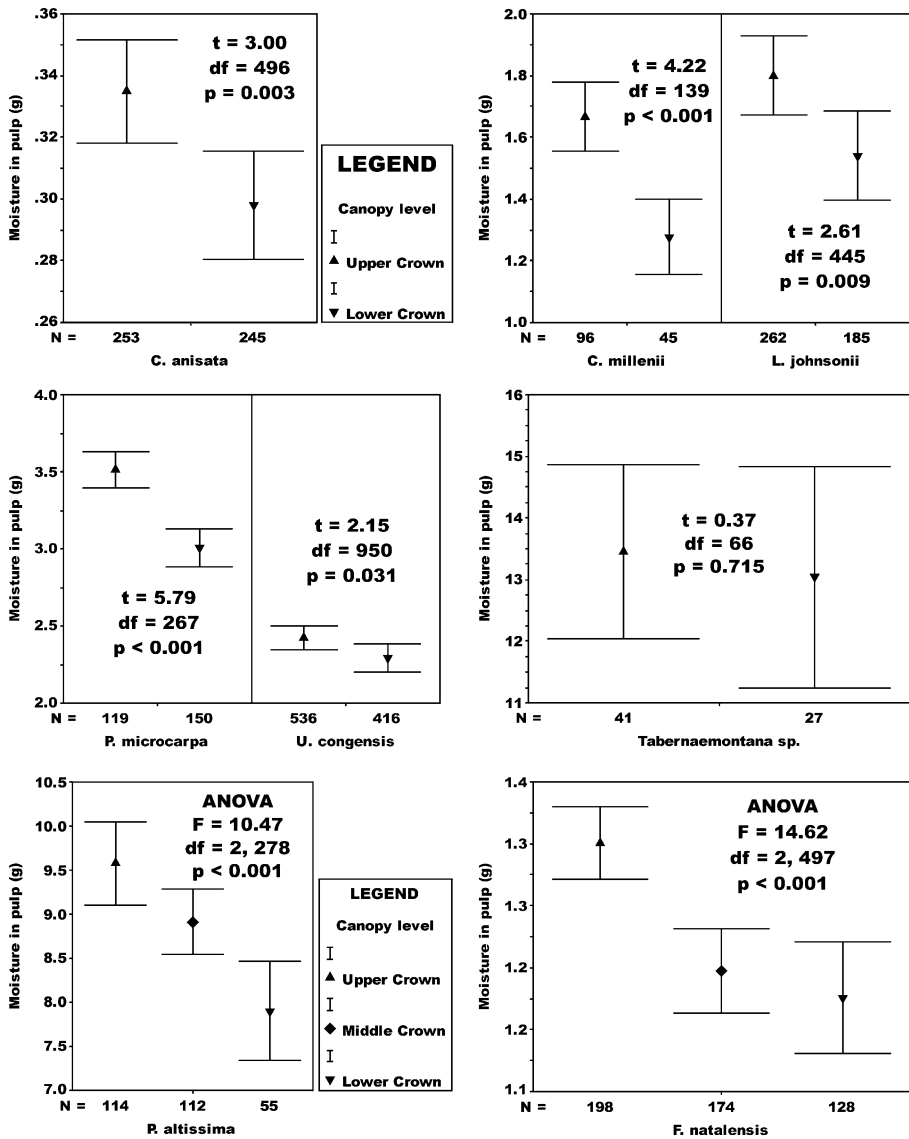
Fig. 5 Intratree variation in moisture (g) in primate food trees in Kibale. Species tested but not shown include *Mimusops bagshawei* (*t*-test, $t_{148}=-1.03$, *p*=0.306) and *Ficus sur* (*t*-test, $t_{166}=-3.37$, *p*=0.001, lower crown fruit not available).

amount of dry pulp (Fig. 3). Among 3-layered trees, upper crown fruits in *Pouteria altissima* produce 22.2% more dry pulp than middle crown fruits, the latter 22.5% more than lower crown fruits, and upper fruits 49.7% more than the lowest fruits (Fig. 3). In *Mimusops bagshawei*, dry pulp biomass differs among the 3 layers, but multiple comparison tests *post hoc* suggest that upper and middle fruits produced the same amount of dry pulp (1.2% of difference, *p*>0.623), while middle fruits significantly produce 7.2% more dry pulp than lower fruits (*p*=0.006, Fig. 3). The
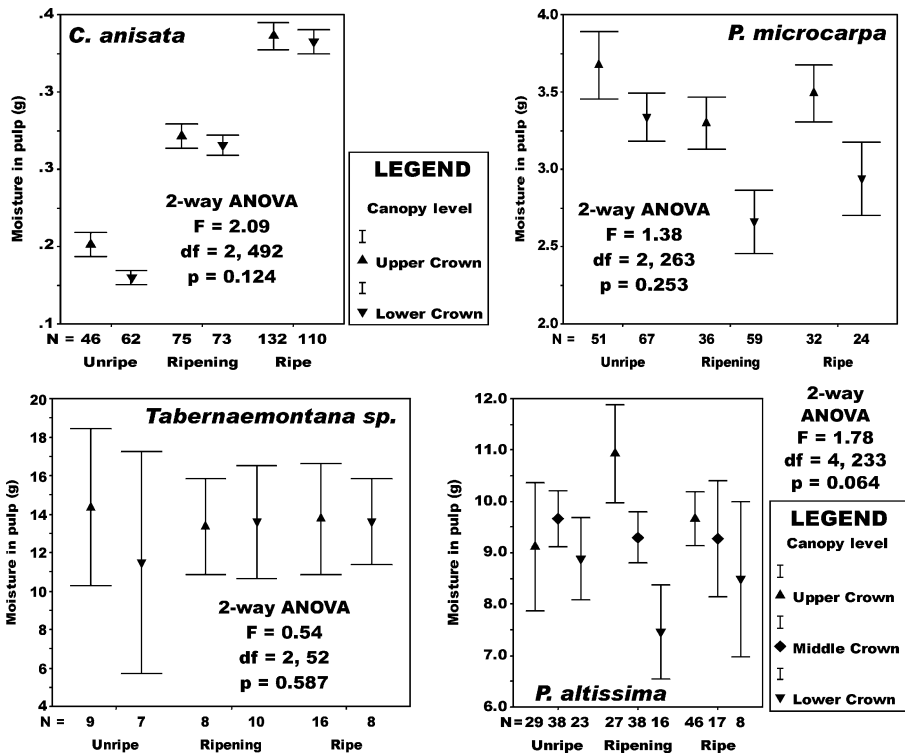
Fig. 6 Intratree variation in moisture (g) per ripeness categories and vertical canopy layers (5 more species tested, all $p>0.05$) in primate food trees in Kibale.

opposite occurs in *Ficus natalensis*, for which upper fruits produce 7.1% more dry pulp per fruit than that of middle fruits ($p<0.002$), while middle and lower fruits produce the same amount of dry pulp (2.3% of difference). In *Ficus sur*, although the biomass of the whole fruit is significantly larger in the middle crown versus the upper crown, there is no statistical difference in the amount of dry pulp produced by the 2 layers (2.1%, Fig. 3). Finally, in *Ehretia cymosa*, for which we could collect only small green immature fruit, upper immature fruits produce 22.8% more dry pulp per fruit than that of middle immature fruits ($p<0.002$), while middle and lower fruits produce the same amount of dry pulp (4.8% of difference). There is no interaction between the canopy layers and ripeness categories for dry pulp biomass (Fig. 4, 2-way ANOVA, 9 fruit species tested, all $p>0.05$); thus, differences in dry pulp do not change as fruit ripens.

Among 2-canopy-layered trees, upper crown fruits contain an average of 16.4% more moisture per fruit than that of lower crown fruit (range 5.7–30.5%), except in *Tabernaemontana* sp., for which fruit contain the same amount of moisture (3.1%, Fig. 5). Among 3-layered trees, multiple comparisons *post hoc* suggest that upper crown fruits in *Pouteria altissima* contain 7.4% more moisture than middle crown fruits, the latter 12.8% more than lower crown fruits, and upper fruits 21.8% more than the lowest fruits (Fig. 5). In *Mimusops bagshawei*, upper and lower crown fruits contained the same amount of moisture (2.3% of difference; we lost middle crown
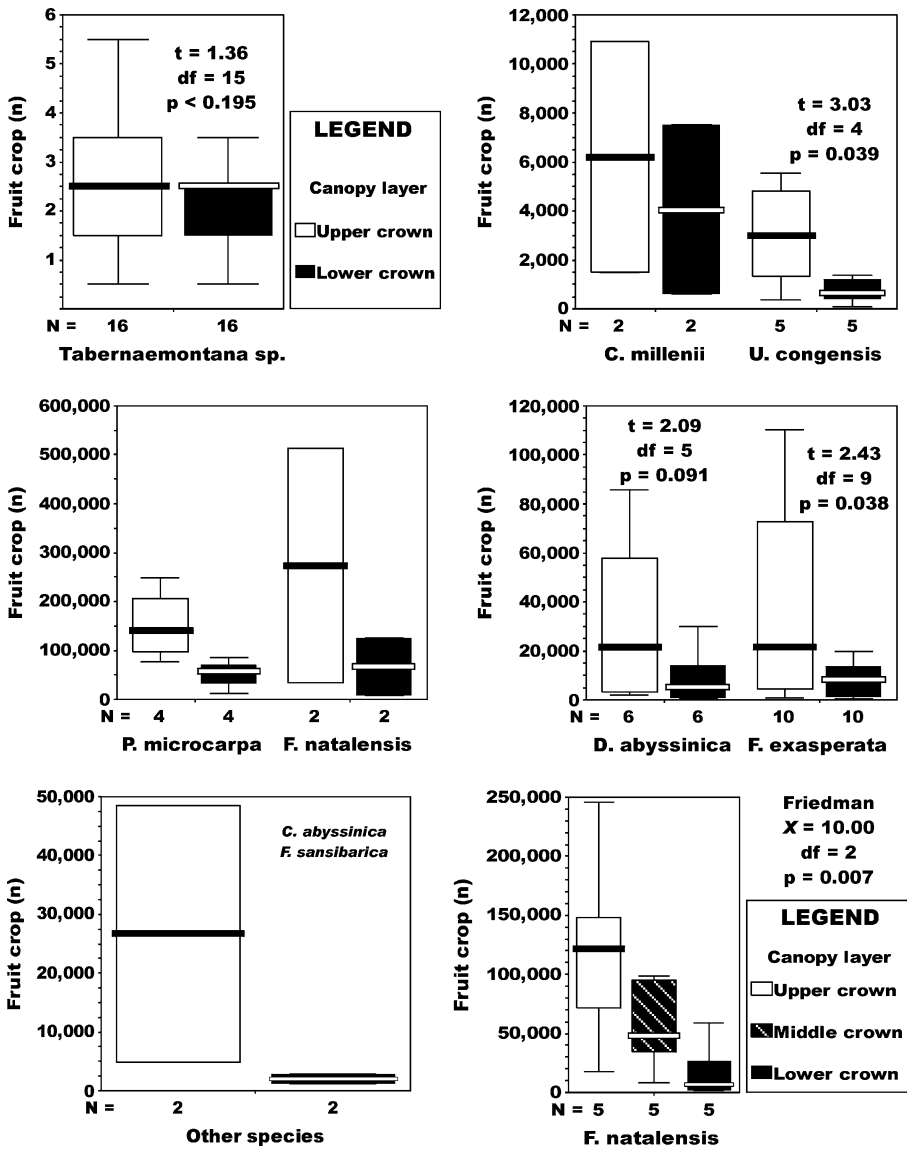
**Fig. 7** Intratree variation in crop size (*n* fruits) in primate food trees in Kibale. *N* is the number of trees, and tree species with similar scales are pooled on the same graph. Additional statistics: all 2-layered tree species with a sample size <5 trees are pooled (shown here: 4 trees of *Pseudospondias microcarpa*, 2 *Cordia millenii*, 2 *Ficus natalensis*, 1 *F. sansibarica*, 1 *C. abyssinica*): *t*-test for paired samples, $t_9$=2.32, $p$=0.046. All 3-layered trees with a sample size <5 trees are pooled (not shown: 1 tree each of *Pouteria altissima*, *Mimusops bagshawei*, *Ficus exasperata*, *F. sansibarica*, *F. vallis-choudae*): Friedman, $X_2$=10.0, $p$=0.007. If crop size data are presented here per canopy layer, layers of the same tree crown did not necessarily have the same volume because the crown was divided into vertical zones of equal height and tree crowns had occasionally irregular shapes.
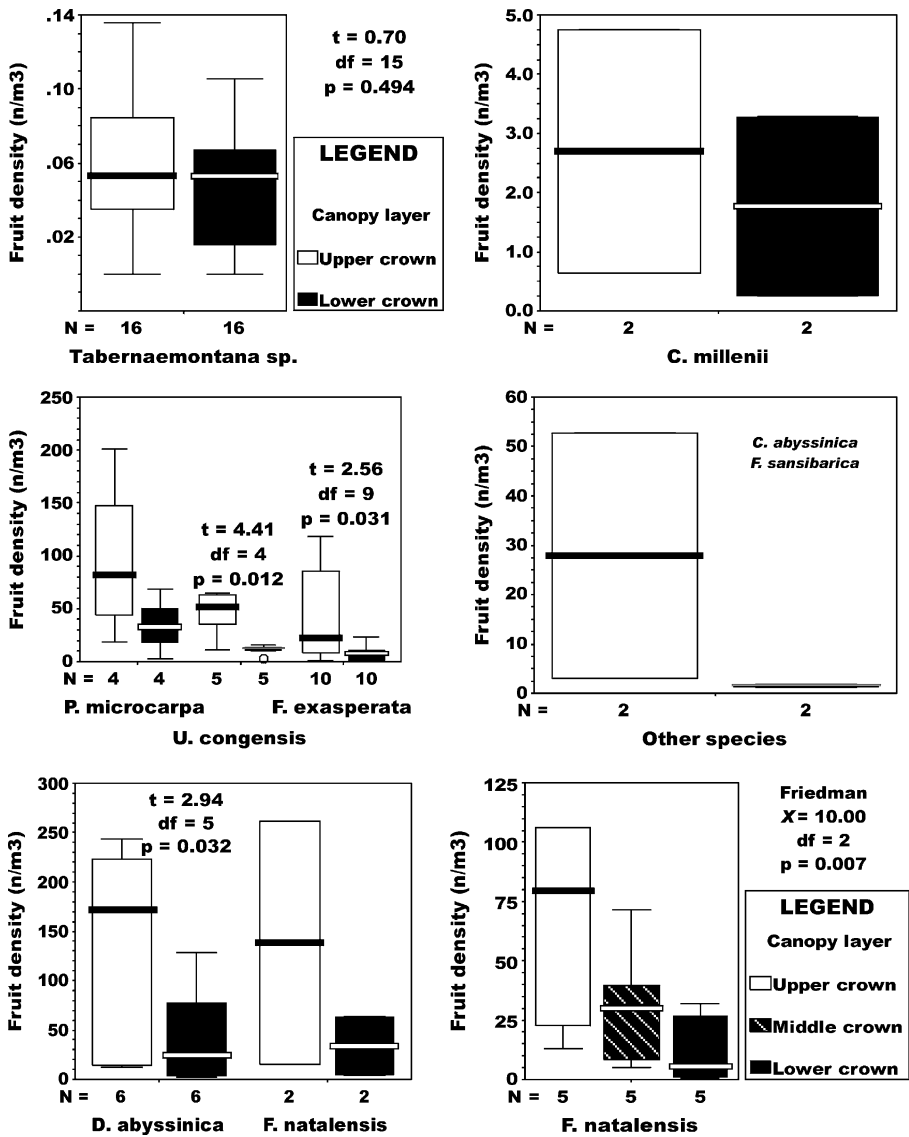
**Fig. 8** Intratree variation in fruit density ($n$ fruits/m$^3$) in primate food trees in Kibale. Additional statistics: all 2-layered tree species with a sample size <5 trees pooled (4 trees of *Pseudospondias microcarpa*, 2 *Cordia millenii*, 2 *Ficus natalensis*, 1 *F. sansibarica*, 1 *C. abyssinica*): $t$-test for paired samples, $t_9$=2.46, $p$=0.036. All 3-layered trees pooled (not shown: 1 tree each of *Pouteria altissima*, *Mimusops bagshawei*, *Ficus exasperata*, *F. sansibarica*, *F. vallis-choudae*): Friedman, $X_2$=10.0, $p$=0.007.

data). In *Ficus natalensis*, upper crown fruits contained 8.6% more moisture per fruit than middle crown fruits ($p<0.003$), while middle and lower fruits contained the same amount of moisture (1.8% of difference, $p>0.299$). In *Ficus sur*, the biomass of the whole fruit (fresh with the seed) is larger in the middle crown versus the upper crown (statistics in Fig. 1 legend), but both upper and middle layers produce the same amount of dry pulp (statistics in Fig. 3 legend), which could partly be

explained by the fact that middle crown fruits contained more moisture than that of upper crown fruits (8.7%, statistics in Fig. 5 legend).

There is no interaction between the canopy layers and ripeness categories for moisture (2-way ANOVA, 9 fruit species tested, all $p>0.05$; 4 species in Fig. 6). Differences in moisture content do not change as fruit ripens. Thus the increasing difference in fresh mass between canopies as fruit ripens is not due to increased moisture or dry pulp. We surmise that it must be due to differential seed growth.

Intratree Variation in Crop Size, Fruit Density, and Nutrients

Crop size and fruit density are greater in higher crown layers than in lower ones, in both 2-layered trees and 3-layered trees (Figs. 7 and 8), except in *Tabernaemontana* sp., for which both crop size and fruit density do not vary vertically within trees. Crop size per species range from 0.52 to 130 times more in upper than lower crowns. It is important to recall that canopy layers of the same tree crown do not necessarily have the same volume because the crown is divided into vertical zones of equal height.

Mean fruit densities per species are 0.52–140 times larger in upper than lower crowns (range zero to 262 fruits/m$^3$). Among 2-layered trees, upper crown fruit density has a mean of 46.9 fruits/m$^3$ (median 12.1) and lower crown fruit density has a mean of 14.1 fruits/m$^3$ (median 2.5). Among 3-layered trees, upper crown fruit density has a mean of 49.9 fruits/m$^3$ (median 12.5), middle crown has a mean density of 16.8 fruits/m$^3$ (median 6.6), and lower crown has a mean of 12.8 fruits/m$^3$ (median 1.8).

Our pilot study on nutrient variation within a tree crown reveals that upper crown ripe fruit contained a mean of 19.8% more sugars (*Strychnos mitis* 0.4%, *Uvariopsis congensis* 17.2%, *Diospyros abyssinica* 41.9%) than that of lower crown fruit. Moreover, upper crown fruits of *Diospyros abyssinica* produced 8.4% more crude proteins and 63.6% less saponin than those of lower crown fruits (Table II). Our sample size is not large enough for statistical testing; however, it suggests that upper crowns might produce not only more food but also possibly higher nutritional quality food than lower crowns.

**Table II** Intratree nutritional variation in proteins, saponin, and sugar in one tree of *Diospyros abyssinica* (April 8, 2000) in Kibale National Park, Uganda

| Ripeness | Canopy layer | Sugar (% DM) | Proteins (% DM) | Saponin (300 s) |
|---|---|---|---|---|
| Ripe: red | Upper | 32.01 | 5.27 | 4 |
| Ripe: red | Lower | 22.56 | 4.86 | 11 |
| Ripening: orange | Upper | 33.25 | 5.81 | 6 |
| Ripening: orange | Lower | 23.50 | 6.06 | 15 |
| Ripening: yellow | Upper | 16.29 | 6.73 | 6 |
| Ripening: yellow | Lower | 11.54 | 7.14 | 15 |
| Unripe: green | Upper | 6.44 | | |
| Unripe: green | Lower | 3.85 | | |

DM = dry matter. Sample size = *ca.* 20 fruits per ripeness category and canopy layer (total = *ca.* 160 fruits).

## Discussion

The upper crown represents a sunnier, warmer, and drier microhabitat than the lower crown. Upper crowns produce fruit that are bigger, more abundant, and in higher densities than those in lower crowns. Moreover, upper crown fruits possibly contain more sugars, more crude proteins, and less potentially toxic saponin than in lower crown fruits, but nutritional differences need to be verified with more individuals and species of trees. Our results are coherent and consistent with 2 exceptions, *Tabernaemontana* sp. and *Ficus sur*. We have no quantitative datum on fruit density of *Ficus sur*, but visual estimations support the statement that more fruit are produced in the middle of the crown ($n=2$ trees). However, it is less clear whether the upper crown or the lower crown produces more fruit. In any case, *Ficus sur* displays a vertical stratification of fruit production like most other species, except that the middle layer is a better feeding site. In *Tabernaemontana* sp. ($n=16$ trees), there is equality in biomass, crop size, and fruit densities among the canopy layers, possibly because it is one of the smallest understory species (<9 m high) with a very small crown height (4 m). From the behavioral ecological perspective, fruits of *Tabernaemontana* sp. are rare (<5 per tree) but large ($\leq$10 cm in diameter) and offer the highest amount of dry pulp per fruit (mean 6.5 g; median 6.8 g; range 2.2–11.8 g).

Our discovery has implications for studies of contest competition among primates. All 17 species of fruit trees tested in Kibale produce feeding sites that can be monopolized or usurped or both: 15 species in which the upper crown produces more food than elsewhere in the tree, 1 species (*Ficus sur*) in which the middle crown produces more food than elsewhere in the tree, and 1 species (*Tabernaemontana* sp.) that shows no stratification but produces rare big fruits that do not ripen all at the same time. Feeding sites in it can be usurped but not monopolized (spatial occupation *sensu* Isbell and Young 2002). A similar case could be the rare big fruits of *Monodora myristica*, also exploited by monkeys and chimpanzees.

Vertical stratification of fruit quality and quantity within trees may affect the behavior of primates that exploit them. Goodall (1986) stated that in large fruiting trees dominant individuals occupy the best feeding sites, though she did not define a best feeding site. We suggest that frugivores find the best feeding sites in the upper canopy and that individuals distribute themselves within trees according to dominance order. Further, dominant individuals may acquire more nutrients at lower costs because they occupy and ursup higher quality feeding sites, which potentially affects their health and fitness.

Vogel (2005) showed that dominant white-faced capuchins (*Cebus capucinus*) have higher energy intake rate relative to subordinate members, probably because dominant capuchins monopolized trees that produced food with higher energy content. We suggest that such interactions can occur within a tree, in a predictable manner (seasonal intertree variation in fruit production are very difficult to predict), such that high-ranking individuals use the best feeding sites to their advantage. This could explain the higher reproductive success among dominant Gombe chimpanzee females (Pusey *et al.* 1997). Assuming the high-ranking chimpanzee females fed in and monopolized the highest (higher quality) canopy strata, they gained more

energy, which possibly helped them to achieve greater reproductive success. Preliminary analyses showed that high-ranking chimpanzee males and females in Kibale feed higher in fruit trees than low-ranking males do (Kahlenberg 2006), a result similar to ours among 3 frugivorous monkey species in the same forest (Houle 2004). Although the species varied greatly in body mass, they could access all fruit in the tree even on slender terminal branches. When necessary primates folded branches toward themselves or broke them to obtain fruit (Houle *et al.* 2006).

The quality of leaves may also be vertically stratified within a tree. Lynch and Gonzalez (1993) showed that in *Borojoa patinoi*, nitrogen biomass per unit leaf area (nitrogen levels correlate with protein content) and volumetric nutrient allocation both correlate with incident photosynthetically active radiation. Perica (2001) found that leaves from the sunnier side of olive trees (*Olea europaea*) contain 12% more nitrogen (thus proteins) than leaves growing on the shadowed side. If the discoveries apply generally, primates feeding on leaves might also experience intratree variation in food density and nutritional quality that could trigger competition. However, in a study comparing canopy versus understory leaves, Dominy *et al.* (2003) showed that canopy leaves were tougher and featured greater quantities of protein, phenolics, and tannins than those in the understory. This is in contrast with our findings on fruit that suggested more nutritious and less toxic food in the upper canopy. However, the study of Dominy *et al.* (2003) is different from ours because they compared the canopy and understory leaves from different trees of the same species, which could greatly affect their results because leaves from different trees of the same forest differ greatly in their nutritional values (Chapman *et al.* 2003). Further, the difference might be expected because fruits are being produced to be attractive to seed dispersers, but plants are attempting to prevent leaves from being consumed by folivores, and the leaves in the upper canopy that are the most photosynthetically active may be the most valuable leaves, thus warranting the best protection. Preliminary analyses (*unpublished*) have shown that seed from fruits that grew in the upper canopy were heavier; this could affect seed and seedling survival after seed dispersal.

We propose that vertical variations in food production will mean that the upper canopy is a more profitable zone than the lower canopy for foragers (and more predictable to human observers). The stratification of the fruit and the leaf in tree crowns provides an opportunity for dominant species and group members to monopolize and usurp the best feeding sites, which could affect their intragroup social relationships (*cf*. Isbell and Young 2002; Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980). The variation within tree crowns and the response that it evokes in primates can contribute to understanding better the mechanisms of coexistence among species with similar diets (Houle *et al.* 2006) and intraspecific relationships (Houle 2004; Kahlenberg 2006).

Our discovery also triggers new questions about predation risks, e.g., how does a primate trade between the quality of a food zone like the upper crown and predation rates from birds of prey? How do predation risks perceived by the forager vary as a function of food zone quality? The framework of Brown and colleagues (Brown 1988, 1992; Brown *et al.* 1992, 1994; Kotler *et al.* 1991, 1993; Olsson *et al.* 2002) applied to primates will contribute to answer these questions.

The vertical stratification of food items alters the potential for scramble, contest, and passive competition (in cases subordinates defer without resistance to dominants

in feeding contexts). In passive competition, it may provide a novel tool to evaluate dominance hierarchies in species in which aggression is rare, i.e., the same individuals systematically monopolize the best intratree feeding sites without apparent agonistic interactions. Examples might be muriquis (*Brachyteles arachnoides*; Strier *et al.* 1999, 2002), bonobos (*Pan paniscus*; Furuichi and Ihobe 1994; Ihobe 1992; Stevens *et al.* 2005), eastern chimpanzee females (Kahlenberg 2006; *pers. obs.*: AH), and many folivores (Saj *et al.* 2007; Struhsaker 1975) in which cases agonistic relationships are relatively rare. Finally, intratree variation in food production could be used in ecological studies to evaluate the effect of food competition on social relationships at times when preferred food is rare, e.g., among folivores feeding on fruit during leaf scarcity, or frugivores feeding on leaves during fruit scarcity (dominance regimes of folivores and frugivores compared: Sterck and Steenbeek 1997).

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