studies on terrestrial invertebrates from Central Amazonian floodplains, in particular the seasonal inundation forests (*cf.* Adis & Schubart 1984, Adis 1997).

The study site was situated on the lower course of the Rio Tarumã Mirím (03°02'S, 60°17'W), a tributary of the Rio Negro, about 20 km upstream from Manaus. The seasonal blackwater inundation forest (for definition see Prance 1979) was situated on a slope and extended from the non-inundated upland area (= *terra firme*) with a constant decline (< 5%) to the bare sandy shoreline of the Rio Tarumã Mirím (see map in Adis 1992). The central part of the study site was covered annually by up to 3.35 m of floodwater between March/April and August/September (= aquatic phase). Further information on the study site is given in Adis (1981, 1984, 1992).

Distribution of Diplura in the non-flooded soil was studied between September 1981 and February 1982. Once a month, six soil samples were taken at random along a transect with a split corer (= steel cylinder with lateral hinges; diameter 21 cm, length 33 cm) which was driven into the soil by a mallet. Each sample of 14 cm depth was then subdivided into four subsamples of 3.5 cm each. Animals were extracted from subsamples during two weeks following a modified Kempson method (Adis 1987). The combined area of the six samples represented 0.21 m^2. Calculated average abundances per m^2 are given below with sample standard deviation.

The presence of Diplura in the flooded soil was studied at the end of each aquatic phase in 1984–86. Twelve soil samples were taken at 3-week intervals under water to a soil depth of 8 cm as described above. Each of the subsamples was kept moist for 10–14 days on a grid inside a bucket, which was covered by a cotton screen (sealed by a plastic snap ring) and contained aqueous picric acid at the bottom. Animals were subsequently extracted with a modified Kempson apparatus. In addition, Diplura were obtained alive from soil samples which were taken to a soil depth of 25 cm under water in August 1988 (end of aquatic phase) and March 1990 (early aquatic phase) as described above and subsequently extracted within one day by means of a flotation method via sugar water (for methodology, see Adis *et al.* 1989). Flotation was also used to study the reaction of diplurans to flooding. For this purpose, 14 soil samples each were taken to 3.5 cm depth at 10, 30, and 50 m from the

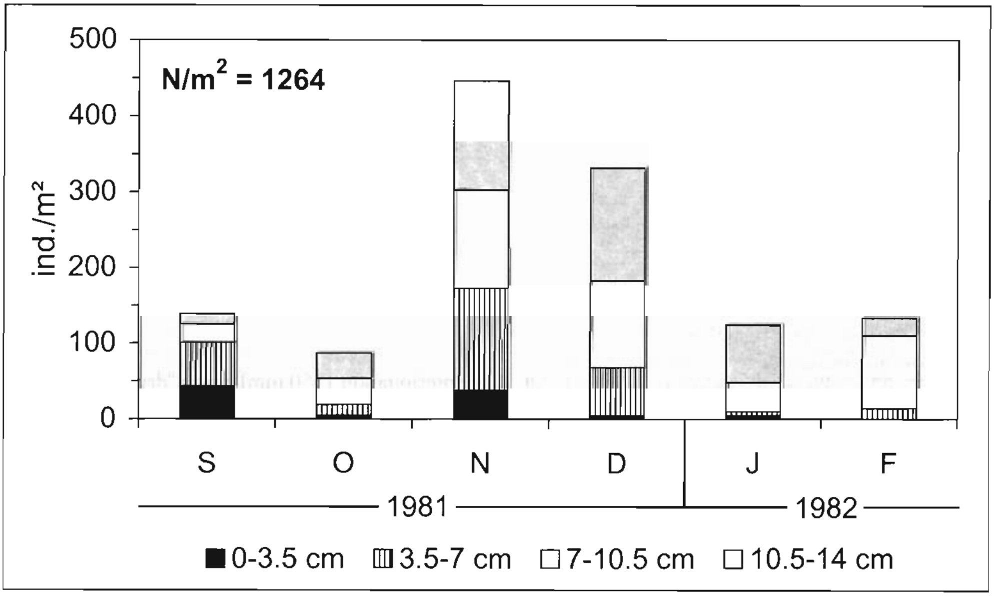

FIG. 1. Temporal occurrence and abundance of *Parajapyx* (*P.*) *adisi* (ind./m^2) in the soil (0–14 cm depth). Monthly samples taken between September 1981 and February 1982 (terrestrial phase) at Rio Tarumã Mirím. N = total number of specimens.

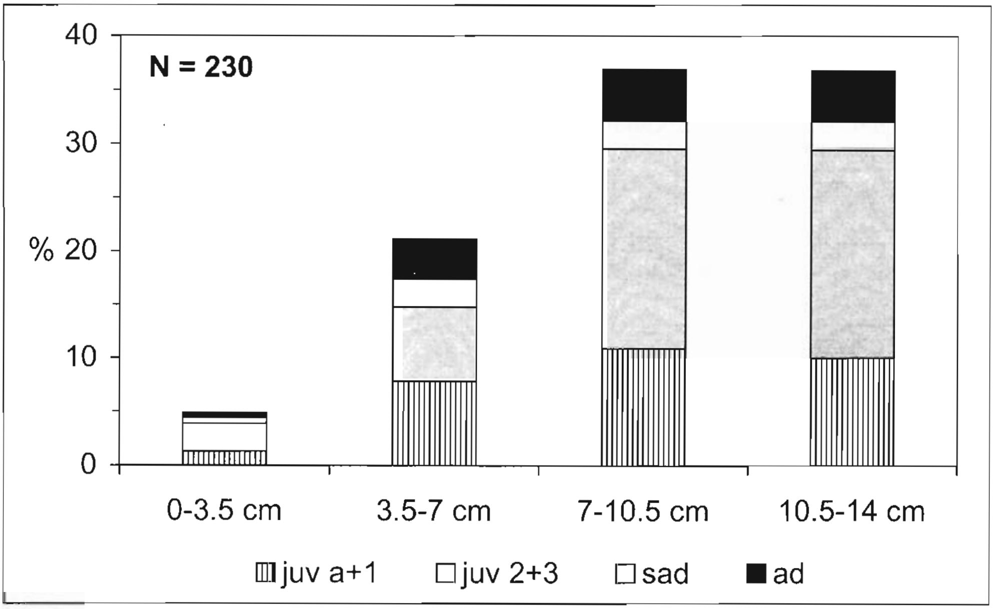

FIG. 2. Depth distribution of developmental stages of *Parajapyx* (*P.*) *adisi* in the soil at Rio Tarumã Mirím. Monthly samples taken every 3.5 cm to a depth of 14 cm between September 1981 and February 1982 (terrestrial phase); total number of specimens (N) = 100 %; juv = juvenile, sad = subadult, ad = adult, a = asexual stage III, 1–3 = sexual stages 1–3.

rising waterline inside the inundation forest in March 1990.

The activity density of Diplura on the forest floor was monitored with 8 ground photo-eclectors after Funke (= emergence traps) during the non-inundation period (terrestrial phase) in 1976/77. Trunk ascents and descents were detected at 1- or 2-week intervals with arboreal photo-eclectors (= funnel traps) on three tree trunks of each of the dominant tree species (*cf.* Adis 1984) between December 1975 and May 1977. The killing / preserving agent used in all traps was an aqueous picric acid solution (without detergent), which is known to be mostly neutral in terms of attraction or repellence in temperate zones (Adis 1979). All capture devices are fully described by Adis (1981) and Funke (1971), who also explain their mode of utilization and function. Trunk ascents of Diplura and their activity on the ground were additionally monitored with funnel traps on one tree, and with 1–4 emergence traps on the forest floor, during the terrestrial phase in 1982/83 and 1983/84.

The presence of Diplura in tree crowns was tested by fogging canopies with pyrethrum in the early dry season (July 1977, 1979), when the inundation forest was completely flooded (*cf.* Erwin 1983, Adis *et al.* 1984). Bromeliads, 5–25 m above ground, were also sampled and checked for terrestrial invertebrates in August 1979 (forest not flooded) and June 1981 (forest flooded).

Seasonal inundation forests in Central Amazonia are subject to a rainy season (December to May: average precipitation 1550 mm), and a "dry" season (June to November: average precipitation 550 mm, but every month has some rain events; *cf.* Ribeiro & Adis 1984). Vertical distribution of Diplura in relation to changing conditions of soil moisture content, temperature, and pH was statistically evaluated with the linear, parametric correlation test (Cavalli-Sforza 1972), using the original field data.

Material. The collection and evaluation of field data for this paper was carried out by J. Adis, the identification of the material by J. Pagés. The stages of the

Parajapygidae sampled were determined according to Pagés (1952, 1998) and tentatively classified as juveniles (asexual stage III, sexual stages 1–3 [$♂_{1-3n}$, ♀ st. 1–3]), subadults ($♂_{4n}$, ♀ st. 4) and adults ($♂_{5n}$, ♀ st. 5, 6).

RESULTS AND DISCUSSION

A total of 399 Diplura was sampled in the blackwater inundation forest under study. Sixty-four animals (16%), representing the Campodeidae, were captured in trunk traps at the beginning of the aquatic phase (March 1976: n = 7, April/May 1977: n = 57). Diplurans were obtained neither from the canopy (during fogging or in epiphytes) nor the soil surface (with pitfall and emergence traps). The remaining 335 specimens were collected from soil samples. Two of them belonged to an undescribed species of a new genus in the Japygidae. The bulk (333 ind., 83% of the total catch) represented *Parajapyx* (*P.*) *adisi* (Parajapygidae). Eighty-seven percent of these animals (291 ind.) could be identified to their developmental stages. The majority (73%, 212 ind.) were juveniles, 17% were adults (49 ind.), and 10% subadults (30 ind.). Phenology and life cycle of this parajapygid species are tentatively discussed, since the bionomics of representatives of this family is totally unknown.

P. adisi reaches 4 mm in length (Pagés 2000). It passes the aquatic phase in dormancy inside a whitish, non-transparent silken cocoon (*cf.* Adis *et al.* 1989). The 61 animals obtained from soil samples taken under water during the aquatic phase (Fig. 4) comprised juveniles (54%; mostly sexual stage 3), adults (28%), and subadults (18%). The sex ratio of the total female to male developmental stages was 1.1:1. Five asexual juveniles (stage III) were obtained by soil extraction. They presumably derived from females that laid eggs during the extraction procedure which had lasted about four weeks. If soil samples taken under water were put directly into the extraction apparatus without being kept moist for two weeks beforehand, no specimens of *P. adisi* were obtained. One possible explanation may be that, as in Japygidae (Gyger 1960, Pagés 1967), females take care of their brood. In this case, the asexual juvenile stages I and II stayed with their mother and presumably died when being exposed to high soil temperatures in the extraction apparatus (up to 59 ° C; *cf.* Adis 1987). The

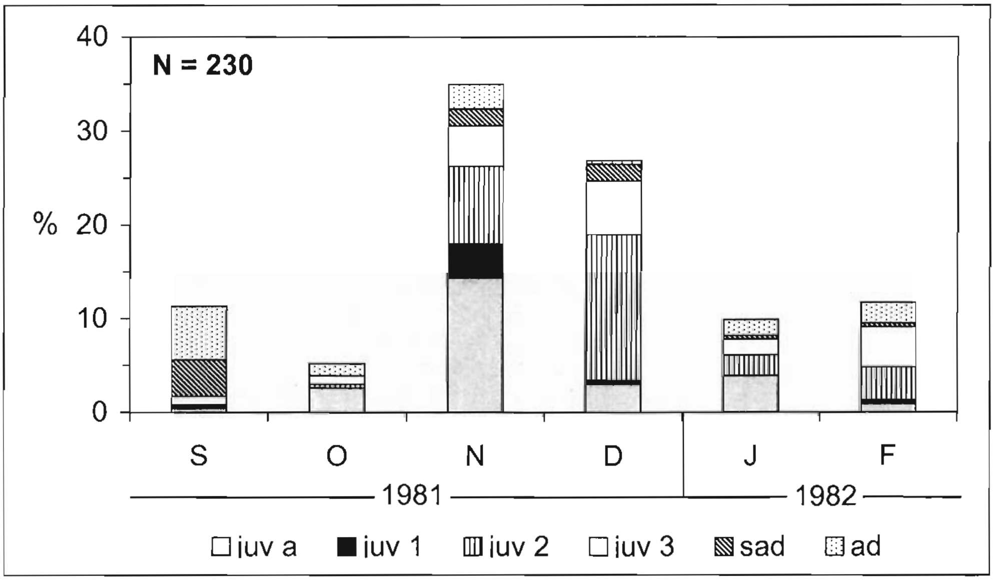

FIG. 3. Percentage of temporal occurrence and developmental stages of *Parajapyx* (*P.*) *adisi* in the soil (0–14 cm depth). Monthly samples taken between September 1981 and February 1982 (terrestrial phase) at Rio Tarumã Mirím; total number of specimens (N) = 100 %; juv = juvenile, sad = subadult, ad = adult, a = asexual stage III, 1–3 = sexual stages 1–3.

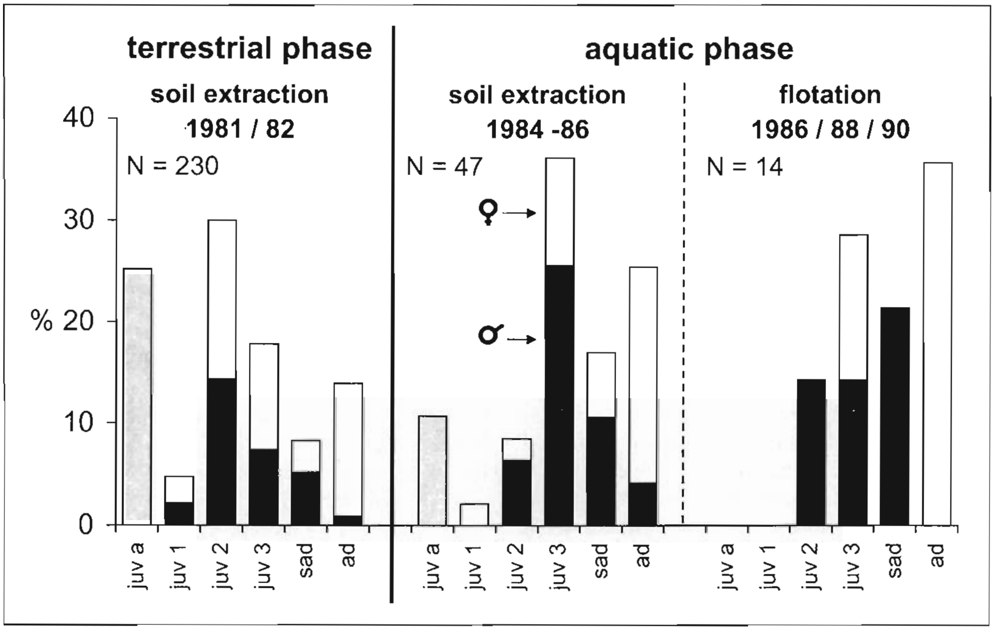

FIG. 4. Percentage of developmental stages and sex of *Parajapyx* (*P.*) *adisi* obtained between 1981 and 1990 during the terrestrial and aquatic phases by soil extraction (0-14 cm depth) and flotation (0-25 cm depth) at Rio Tarumã Mirím; total number of specimens (N) per extraction or flotation = 100 %; juv = juvenile, sad = subadult, ad = adult, a= asexual stage III, 1-3 = sexual stages 1-3 (see text for further explanations).

existence of asexual stages I and II in the Parajapygidae was reported by Smith (1961) for *Parajapyx* (*P.*) *isabellae*. All sexual developmental stages of *P. adisi* obtained with the flotation method to 25 cm soil depth (Fig. 4) were found inside their cocoon.

P. adisi is considered terricolous and euedaphic since 70% of all specimens obtained during the terrestrial phase in 1981/82 by soil extraction were caught below 7 cm soil depth (*cf.* Figs. 1, 2). About 23% were taken at 3.5–7 cm and only 7% in the top 3.5 cm. It is not known if this species occurs below 25 cm soil depth. Japygids have been observed to live up to 60 cm depth (Hairstone & Byers 1954).

The highest abundance of *P. adisi* (447 ind/m^2) was recorded during the dry season (Fig. 1: in November). The average population density (211 ± 144 ind./m^2/month) was higher than the average obtained for Japygidae and Parajapygidae from a mixedwater inundation forest (136 ± 28 ind./m^2; Morais 1995).

Data on developmental stages indicated that reproduction took place during the early part of the terrestrial phase. In 1981, first juveniles of asexual stage III occurred from September onwards (Fig. 3), about four weeks after the forest floor had dried. We presume that they derived from females that had passed the aquatic phase in the flooded soil. In cultures at about 20 °C, *Dipljapyx humberti* (Japygidae) needed about 21 days to reach the free-living asexual juvenile stage III near Dijon in France (Pagés 1967). In *P. adisi*, the bulk of these asexual juveniles occurred in November (Fig. 3). Most specimens sampled during the following month had attained an advanced sexual juvenile stage (2 & 3). The sex ratio of the total female to male developmental stages was 1:1.5. Without rearing individuals of this species it is impossible to know whether females tentatively classified as "subadults" possibly lay eggs, and how often both sexes molt after they have reached the "adult" stage. The latter has been described for Campodeidae and Japygidae (Marten 1939, Orelli 1956, Pagés 1967, Bareth 1968). Nevertheless, the data suggest that *P. adisi* has a univoltine life cycle like most terricolous invertebrates that inhabit blackwater inundation forests of Central Amazonia (*cf.* Adis 1997).

During the period of highest abundance (Fig. 2), at the end of the dry season, the abundance of *P. adisi* increasing with greater soil depth correlated negatively with a decreasing soil moisture content (November: 47% soil humidity in the top 3.5 cm compared to 25% at 14 cm depth; $P < 0.05$, $r = -0.9582$ for the total catch and $r = -0.9565$ for the total sexual juveniles, $n = 4$). No correlation was found with soil temperature (25 °C on average). Data on preferred microclimatic conditions in diplurans are only known for the japygid *Dipljapyx humberti*, which is considered a xero- to mesophilic species (Pagés 1967, 1978; Eisenbeis & Wichard 1985).

Grain size and mineral composition of the soil seem to be especially important for the vertical distribution of terricolous arthropods in seasonal inundation forests (*cf.* Adis *et al.* 1996). First analyses of soil data (Adis & Irion unpubl.) indicated that the abundance of *P. adisi* increasing with soil depth in November/December was correlated negatively with a decreasing amount of grains 250–500 mm in size in lower soil layers (from 36.4% in 0–3.5 cm to 28.3% at 10.5–14 cm depth; total catch: $P < 0.01$; total of sexual juvenile females (stages 1–3): $P < 0.05$), and with a decreasing amount of silt from 14.6% in the top 3.5 cm to 10.8% at 14 cm soil depth ($P < 0.05$ for total catch as well as total of sexual juvenile females [stages 1–3]). In addition, increasing abundance correlated positively with pH increase at lower soil depths (December: pH 3.5 in the top 3.5 cm to pH 3.8 at 14 cm; $P < 0.05$, $r = +0.9518$ for the total catch, $n = 4$).

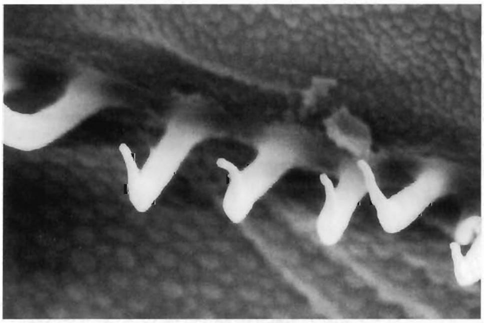

FIG. 5. Spinning bristles located at the posterior margin of the first abdominal segment in an adult *Parajapyx* (*P.*) *adisi* representing one side of the spinning apparatus or "spinnerets"; SEM 1:10,000 (photo B. Messner).

Gut contents suggest that *P. adisi* feeds on roots in the soil. Parajapygidae are presumed to feed on plant material (Pagés, unpubl.), despite the presence of abdominal forceps which are used by the predatory Japygidae and other Japygoidea families to catch and hold prey (Kosaroff 1935, Schaller 1949). *P. isabellae* has been reported to be a potential pest in sugarcane plantations in the Hawaiian islands (Zwaluwenburg 1934).

During the first weeks of the aquatic phase, *P. adisi* started to build its cocoon which served as a retreat. The waterproof spinning threads were produced by two secretory glands and released by two rows of hollow spinning bristles (Fig. 5), both located on the first abdominal segment (Adis *et al.* 1989). The cocoon is filled with air and attached to roots, leaves, and soil material to prevent it drifting away on the flood. Fifty meters away from the advancing waterline, the 21 animals sampled alive in March 1990 with the flotation method were still free-living, partly inside roots. Thirty meters away from the waterline, 84% of the animals obtained (n = 34) were inside their cocoons and actively spinning. Only four animals were free-living. About ten meters away from the waterline, the majority of the 20 animals, all found inside their cocoons, were immobile and had entered a dormant stage. Due to the anoxic conditions during the aquatic phase (*cf.* Adis & Messner 1991), *P. adisi* is presumed to make anaerobic respiration. However, accumulation of lactate was not found and the presence of other metabolites (e.g., ethanol, alanine, succinate) has not yet been tested for. Animals which were sampled alive with the flotation method at the end of the aquatic phase became active shortly after the cocoon had surfaced and been taken out of the sugar water. For this reason, the dormant stage is considered to represent a quiescence, in the sense of Denlinger (1986), which is ended as soon as the forest floor dries up. This kind of "survival strategy" was also found in other terricolous arthropods (Adis 1997), which represent the "non-migrating terricolous animals" that pass the aquatic phase of Central Amazonian floodplains in naturally available retreats (roots [Symphyla], logs [Coleoptera: Oedemeridae]), by means of self-made retreats (wax protection [Homoptera: Pseudococcidae, Cicadidae]) or as eggs (Acari, Collembola, Archaeognatha: Meinertellidae). Spinning bristles are present in all species representing the Parajapygidae. It therefore remains to be studied if the silken cocoon is solely produced by *P. adisi* prior to the flood event or if it generally serves as a refuge when parajapygids molt or their females lay eggs.

Many terricolous invertebrates inhabiting blackwater inundation forests in the Rio Negro valley near Manaus are endemic (Adis 1997, 2001). This seems to be the case for *P. adisi* as well. A preliminary taxonomic examination of diplurans sampled from the soils of the adjacent upland forest showed that Parajapygidae represented a closely related but taxonomically different species. However, in a mixedwater forest located between the Rio Negro and the Rio Solimões-Amazonas, diplurans from the soil (Morais 1995) were represented by the same two terricolous species found in the blackwater forest: *P. adisi* and an undescribed genus of the Japygidae (see above). The latter also passed the aquatic phase in a cocoon (Adis unpubl.). No diplurans have yet been detected in whitewater floodplains along the Rio Solimões-Amazonas near Manaus (*cf.* Adis 1981, 1997).

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