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The Ecology and Biology of Panax quinquefolium L. (Araliaceae) in Illinois

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ABSTRACT.—A statewide study of *Panax quinquefolium* L. (American ginseng), a herb commonly collected for commercial sale, was conducted on 33 protected and unprotected forested sites in the northern, central and southern sections of Illinois. Within these sites, data on the tree, sapling, seedling, shrub and herbaceous strata, and on soil texture and nutrients were collected from a 0.05-ha circular plot in each site. Additional recorded site data included aspect, slope position, steepness and exposure, and disturbance from grazing or timber harvesting.

Populations of *Panax quinquefolium* were found in stands dominated by *Acer saccharum, Quercus alba* or *Q. rubra* and with a variety of other herbaceous species common to cool, moist site conditions; 84% of the sites were located on NW-, N- and NE-facing slopes and 80% were in mid- to low-slope positions.

Phenological events began in early May and progressed from S–N; plants were dormant by mid-October. Seeds from individuals growing on several sites within each region were planted at the time of leaf senescence. Seedlings did not appear until the 2nd spring; 66% of the seeds produced seedlings.

An anatomical and morphological study of 30 whole field-collected plants indicated that plant age could be accurately determined by counting bud scale scars on the rhizome. These data were used to develop a multiple regression model to predict rhizome age from stem height and number of leaflets. For 30 field-collected and 65 forest-cultivated roots, average weight increased linearly up to age 20, the age of the oldest roots.

Population age structure and fruit production on protected sites were compared with that of sites where roots had been removed by collectors. We found fewer plants of all ages on unprotected sites. Fruit production was lower on unprotected sites because fewer 5- to 11-yr-old plants limit fruit production and rate of population recovery after harvesting.

INTRODUCTION

Panax quinquefolium L. (American ginseng) is a forest herb whose range extends from Quebec and Manitoba S to northern Florida, Alabama, Louisiana, Arkansas and Oklahoma (Gleason, 1963; Anderson *et al.*, 1984). *Panax quinquefolium* and a related species, *P. ginseng* C. A. Meyer (Asian ginseng), are widely used as medicinal herbs (Court, 1975; Dubrick, 1983; Shim *et al.*, 1987), and roots of both wild and cultivated plants are commercially important.

Numerous studies of one or both species have examined various ecological relationships (Lewis and Zenger, 1982; Lewis, 1984; Anderson *et al.*, 1984; Stathers and Bailey, 1986), reproductive biology (Carpenter and Cottam, 1982; Lewis and Zenger, 1982; Schlessman, 1985, 1987), chemical composition (Shim *et al.,* 1983; Tomoda *et al.,* 1985; Hansen and Boll, 1986; Hikino *et al.,* 1986; Oshima *et al.,* 1987), medicinal properties (Hu, 1976; Carlson, 1986; Dubrick, 1983) and growth, yield and rates of photosynthesis, respiration and transpiration under varied solar radiation and/or temperature conditions (Hu, 1976; Lee *et al.,* 1980; Konsler, 1986; Proctor and Tsujita, 1986; Stoltz, 1982; Strick and Proctor, 1985).

The anatomy and morphology of *Panax quinquefolium* have received limited study and few illustrations of the plant in either the popular or pharmacological literature are accurately detailed. Most studies do not indicate that the plant has a rhizome as well as a root system. The life span of *P. quinquefolium* plants has been reported to range from 50+ yr (Lewis and Zenger, 1982) to an unlikely 400 yr (Heffern, 1976). Although methods used to age plants range from counting rings of wrinkles on the root to stem scars on the rhizome (Carpenter and Cottam, 1982), no morphological study has confirmed the accuracy of these techniques. There is little information on environment, tolerances or plant associates of *P. quinquefolium* populations.

The purpose of the research reported here was to obtain information on the ecology and biology of *Panax quinquefolium* individuals and populations in Illinois that could be used to develop management recommendations for this intensively collected herb. Specific objectives were to (1) determine site conditions and forest community composition of natural populations; (2) examine phenology and reproductive biology; (3) describe stem and rhizome morphology and anatomy; and (4) develop a method for aging individuals from rhizome characteristics in order to study root growth, as well as population age structure and fruit production on protected and unprotected sites where roots have been collected.

Distribution and Sites in Illinois

Herbarium records and reported sightings indicate that *Panax quinquefolium* is found in 84 of 102 Illinois counties, although it probably occurs throughout the state. It has been most commonly seen and/or collected in the heavily forested counties along the Ohio and Mississippi rivers of unglaciated southern Illinois, but the species also occurs in the northern two-thirds of Illinois where prairie and savanna were the dominant presettlement vegetation types (Anderson *et al.,* 1984). Here, it is found in forest communities restricted to waterways and areas of dissected topography associated with glacial deposits.

The state was divided into three approximately equal sections and a total of 33 *Panax quinquefolium* populations (16 N, seven central and 10 S) were located at 16 protected and 17 unprotected sites. Unprotected sites were areas where frequent collecting of ginseng was likely to have occurred (*i.e.,* private property and state or national forests); protected sites were located primarily in Illinois Nature Preserves. In central and northern Illinois, 15 of 23 study sites were unprotected. In the southern part of the state, nine study areas occurred on unprotected sites and only one site (Beall Woods) was protected; roots were removed from the majority of unprotected sites during the research. Approximately 721 plants were included in the study.

Methods

Community composition and environment.—A 0.05-ha circular quadrat was positioned to enclose one or two separate *Panax quinquefolium* populations at each site. Within each quadrat, all trees >4.9 cm in diam at a height of 1.3 m (DBH) were measured to the nearest 0.1 cm and recorded by species. Species importance values (IV) [(relative basal area + relative density)/2] were calculated separately for stems 5–9 cm (mid-canopy) and >9 cm DBH (overstory). A list of all shrubs, vines, ferns and herbaceous plants on the plot was compiled. The number of *P. quinquefolium* plants within each quadrat was recorded.

A probe was used to obtain five soil samples (one at plot center and one in each plot quadrant) from the A horizon (0–15 cm depth). Samples from each plot were placed in a plastic bag, thoroughly mixed and air-dried in the laboratory. Sample texture was obtained using the Bouyoucos hydrometer method following the procedure of Wilde *et al.* (1979). Calcium, magnesium, phosphorus and potassium levels and pH were determined at the Wisconsin State Soil Testing Laboratory, Madison.

Phenology.—Phenological study sites were established in northern Illinois at Kankakee River State Park Nature Preserve (Kankakee County), in central Illinois at Breens Woods (McLean County) and in southern Illinois at Ozark Hills Nature Preserve (Union County). Data collection began on 26 June and 26 July 1981, at the central and northern sites, respectively. It continued at the northern site until senescence in October 1982, and at the central site until June 1983. Data at the southern site were collected only during the 1982 growing season.

At each study site, 4–12 plants of various sizes were marked for study; about one-half of the plants were flowering. At approximately 1-wk intervals, stem height, peduncle length, leaflet length and width, number of leaves, leaflets/leaf, flower buds, open flowers, and immature (green) and mature (red) fruits for each plant were recorded. Leaf and leaflet abscission dates also were recorded. The length and width of leaflets were measured until full expansion.

Leaflet area was determined by tracing leaflets of various sizes and measuring their area with a planimeter. A regression model was developed to estimate leaflet area from length and width. Total leaf area for each of the phenology study plants was determined by summing the estimated leaflet areas at each measurement date. Total leaf area estimated for each observation was expressed as a percent of the leaf area at full expansion. For each plant, the percentage of eaten, chlorotic or abscissed areas of each leaflet was estimated and the percent lost summed for each plant, site and measurement date. For each section of the state, shoot development and senescence were examined by plotting the percent of the maximum leaf area over time.

Seedling establishment.—Seed germination and seedling establishment under field conditions were studied at each of the three phenological study sites. Fruit was collected in early to mid-September 1981. The fleshy pericarp was removed, and 20 or 25 seeds were planted ca. 10 cm apart and 1.25 cm below the soil surface. Seed locations were marked and the number of new seedlings that appeared during the following 2 growing seasons was recorded.

Plant age and growth.—Thirty whole *Panax quinquefolium* plants were collected from two sites in E-central Illinois, oven-dried at 80 C for 48 h and weight obtained for the shoot, root, reproductive parts and whole plant. Rhizomes of these 30 plants and eight others uncovered in situ were examined using a binocular microscope to identify morphological features and determine plant age. Age was recorded by counting the number of bud scale scars on the rhizome. Recently germinated seedlings in their 1st growing season were recorded as 1 yr old, plants in their second growing season were recorded as 2 yr old, etc.

Other morphological data obtained from these 38 plants included number of leaves and leaflets, stem height from the ground and from the rhizome, total number of red and green fruits, peduncle length and leaf area in cm^2. Morphological variables were related to rhizome age using simple linear regression analysis. A multiple regression model was developed to predict age from morphological characteristics.

Age, weight and number of leaves and leaflets were obtained from an additional 65 forest-cultivated roots and attached rhizomes purchased from a grower. The roots and rhizomes were dried for 48 h at 80 C before weighing. The number of leaves and leaflets was determined by dissecting the terminal bud and counting leaf and leaflet primordia. Average root weight for each age was calculated from data for the 30 field-collected plants and 65 forest-cultivated roots.

Age structure and fruit production.—The relationship between plant age and fruit production was determined from plants used in the phenology study and from plants aged at four additional sites, two each in central and southern Illinois. The number of mature red fruits produced was counted for the phenology study plants. For study plants which were not visited weekly, the number of mature red and green (*i.e.*, those which were nearly full size) fruit was tabulated. Because these plants were sampled late in the summer, the number of green and red fruit provided a reasonable estimate of total fruit production. A linear regression equation was developed to predict the average number of fruit produced by plants of various ages. For plants that were not aged, age was predicted from the multiple regression model. Using these models, age and number of fruit were predicted for each plant within the 0.05-ha plots and the number of fruit by 1-yr age intervals determined for each plot. The average number of fruit/age interval/plot and the total number of fruit/plot were calculated separately for protected and unprotected sites.

RESULTS

Community composition and environment.—In the overstory, *Acer saccharum* had the highest average IV because of its strong dominance in the northern and southern regions (Table 1). It was the leading dominant on 11 study sites. *Quercus alba* had the second highest average IV and was the leading dominant in the central region. *Quercus rubra* was the third leading dominant with a relatively consistent IV across the three regions. Other species had substantially lower IVs except for *Tilia americana* in the N and *Liriodendron tulipifera* in the S. A total of 36 tree species (N, 17; central, 21; S, 29) were recorded.

In the mid-canopy, *Acer saccharum* was the leading dominant, particularly in the central region, but other important species were *Ostrya virginiana, Ulmus rubra, Sassafras albidum* and *Tilia americana*; 15 tree species were recorded for the mid-canopy stratum. Basal area of the overstory and mid-canopy combined was relatively high (>25 m^2/ha).

A total of 49 herbs, six ferns, nine shrubs and 11 vines were found on the study sites. *Ribes missouriensis* was the most common shrub (14 sites); *Parthenocissis quinquefolia* was found on 31 of the 32 sites. The most commonly encountered herbs listed by decreasing number of sites were *Smilacina racemosa* (26 sites), *Arisaema triphyllum, Sanicula marilandica, Phryma leptostachya, Podophyllum peltatum, Circaea quadrisulcata, Sanguinaria canadensis, Galium circaezaens, Geranium maculatum* and *Osmorhiza claytonia* (13 sites). Common ferns included *Botrychium virginianum* (22 sites), *Cystopteris fragilis* (14 sites) and *Polystichum acrostichoides* (all southern sites). A complete listing of species is reported in Anderson *et al.* (1984).

Panax quinquefolium occurred on a wide range of soils which varied in texture from high sand (88%) to high silt (76%) to moderately high clay (34%) in the A horizon (Table 1). Only two study populations were on coarse-textured (loamy sand) soil, and three populations occurred on fine-textured (clay loam, silty clay loam, silty clay) soil. The remaining populations were on medium-textured (sandy loam, loam, silt loam) soil of moderate to high available water-holding capacity (6–9 cm H_2O/30 cm soil depth). Soil pH ranged from moderately acid (pH = 4.4) to near neutral (pH = 7.3).

In the northern section, *Panax quinquefolium* study populations were about equally divided among high-, mid- and low-slope positions. On the gently rolling topography of the central section, five populations were found on high slopes, ridges and level topography, only two

TABLE 1.—Species importance values and soil data for 16 northern, seven central and 10 southern Illinois forest communities in which *Panax quinquefolium* populations were studied. Average importance values [(relative density + relative basal area)/2] are for overstory (DBH >9.0 cm) and mid-canopy (DBH 5–9 cm) species with importance values >10.0. Density and basal area data are summed from overstory and mid-canopy values. Soil data are from the top 15 cm

	North	Central	South	Range/average
	Overstory species importance values			
Species				
Acer saccharum	34.6	9.0	20.0	21.2
Quercus alba	13.4	35.2	11.3	20.0
Q. rubra	12.2	10.9	12.3	11.8
Tilia americana	12.1	1.3	0.0	4.5
Other species	27.7	43.6	20.1	42.5
	Mid-canopy species importance values			
Species				
Acer saccharum	19.7	40.0	17.4	25.7
Ostrya virginiana	28.7	17.2	15.0	20.3
Ulmus rubra	5.1	17.3	3.2	8.5
Sassafras albidum	6.7	5.8	13.8	6.7
Tilia americana	15.7	1.0	0.0	5.5
Other species	24.1	18.7	50.6	33.3
	Community characteristics			
Basal area (m^2/ha)	26	26	30	27.1
Density (stems/ha)	355	371	422	377
	Soil texture (%)			
Variable				
Sand	41.5	34.3	15.6	6–88
Silt	38.0	45.7	67.4	10–76
Clay	20.5	20.0	17.0	2–34
	Soil nutrients (kg/ha)			
Phosphorus	63	53	45	14–152
Potassium	204	156	218	135–270
Calcium	4011	2992	1764	1011–8928
Magnesium	697	573	435	191–1179
pH Range	4.9–7.3	5.3–6.9	4.4–6.0	

populations on mid and low slopes. However, on the steeper topography of the southern section, all populations occurred on mid and low slopes and level stream terraces.

Statewide, for sites on slopes, 85% had a NW, N or NE aspect (azimuth = 270 to 360° and 0 to 90°); 44% were on slopes with an azimuth of 0–45°. Only 15% had a SE, S and SW aspect. Approximately 50% of the populations were on slopes of <20%, and 6% on slopes of >60%. Most of the study populations (70%) were moderately protected from wind while 21% were well protected.

Panax quinquefolium generally occurred in stands with little or no disturbance. Within the lifetime of the overstory trees, 58% of the study sites had not been cut, 21% were lightly cut and only 15% heavily cut. Approximatey 91% of the sites had light to no grazing; no site was grazed at the time of sampling.

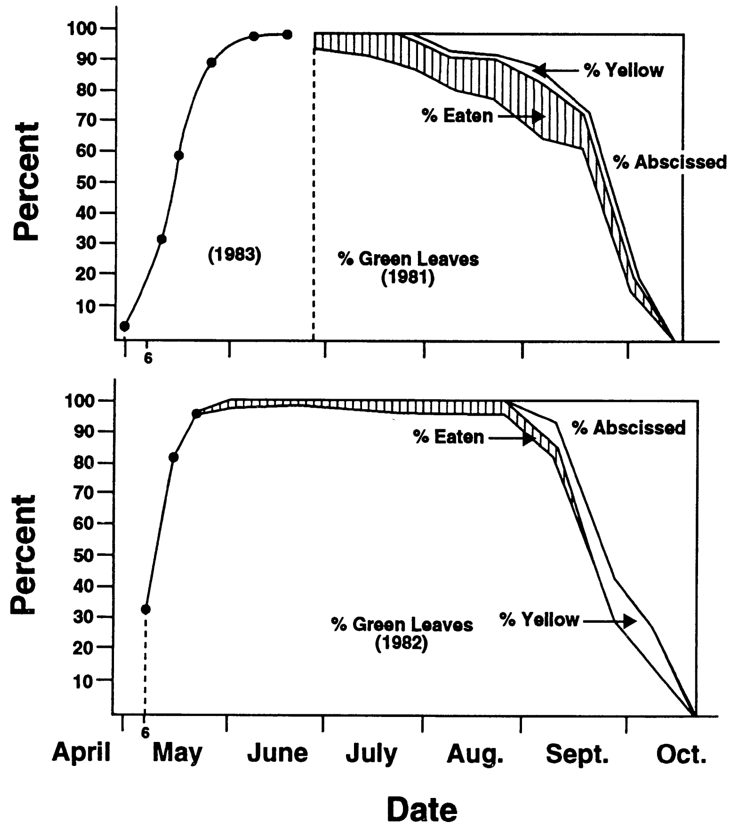

FIG. 1.—Shoot phenology for *Panax quinquefolium* in central Illinois

Vegetative phenology.—In central Illinois, shoot growth was initiated between 30 April and 7 May (Fig. 1). Full leaf expansion occurred by late May in 1982 and probably also in 1981 but was delayed until late June in 1983. While there was some variation in the timing of full shoot development between sections of the state probably because of the effect of different site conditions (*e.g.*, high sites in the N vs. low sites in the S) and the time interval between measurements, plant development appeared to begin in the S and progress northward.

Immediately after full leaf expansion, some insect herbivory occurred mostly in the form of small holes; leaf area loss was ca. 5% and 10% in northern and central Illinois, respectively. There was more insect damage in southern Illinois during 1982 than at the other study sites; maximum amount eaten was ca. 42–43% at one site and 15% at the other.

Throughout the state, a few leaflets dropped by late August and nearly all leaves began to yellow by mid-September. At the southern sites, shoots were leafless by 7 October 1982. At the central site, leaves were down by 18 and 21 October in 1981 and 1982, and at the northern site, by 25 October and 6 November in 1981 and 1982, respectively.

Reproductive phenology.—Phenological events generally began earliest at the southern sites and latest at the northern sites. In flowering plants, a single peduncle supporting a terminal umbellate inflorescence began to develop shortly after leaf expansion was initiated. However, because of the time interval between observations, flower initiation was recorded

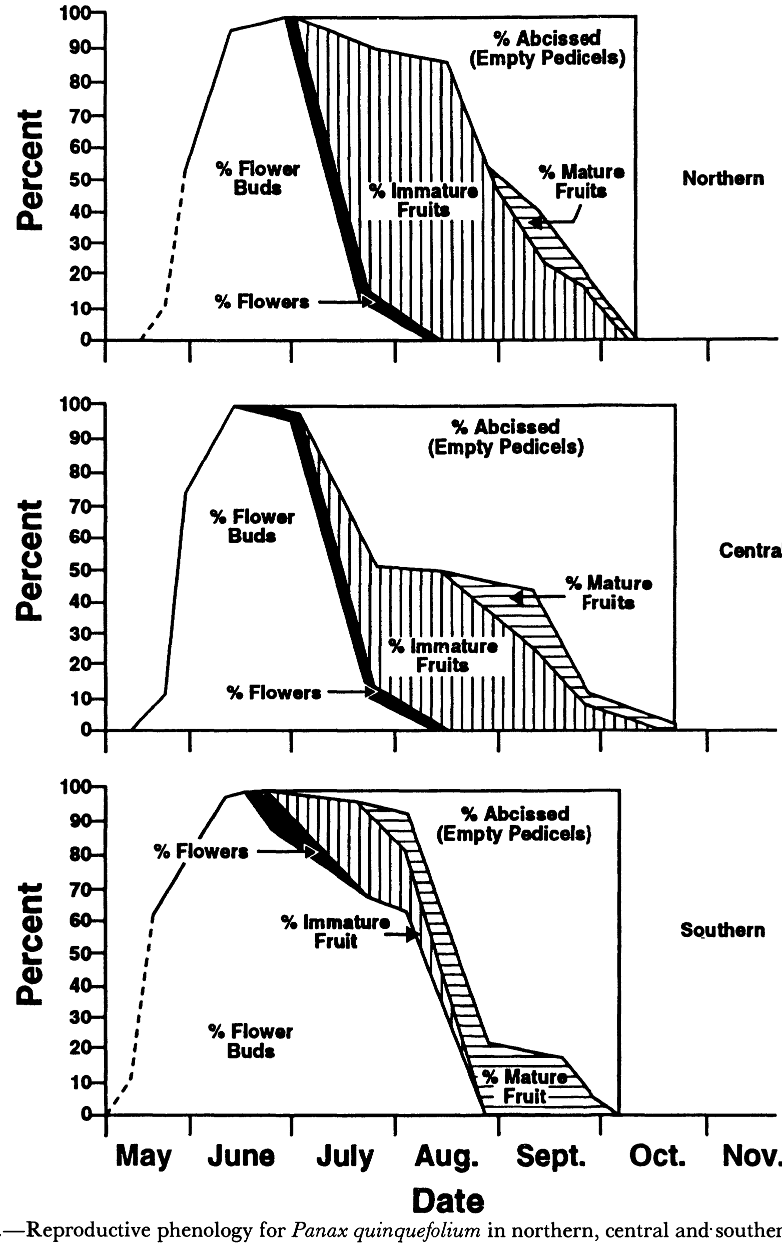

FIG. 2.—Reproductive phenology for *Panax quinquefolium* in northern, central and southern Illinois. The percentage of pedicels bearing flower buds, flowers, immature or mature fruits, or that were empty is plotted over the date of observation

in early, mid- and late May at the central, southern and northern phenological sites, respectively (Fig. 2). Inflorescences contained as many as 70 flowers but because of the continuous nature of flowering, there were few open flowers on any given day.

Immature (green) fruits were present by mid- to late June at the southern sites, and at the central and northern sites by the end of June. Mature (red) fruits appeared first on ca. 21 July at the southern sites and on ca. 12 and 16 August at the central and northern sites, respectively. The maximum number of fruit was present on the plants on 28 August and 9 and 12 September for southern, central and northern sites, respectively.

In early August, a second peduncle bearing a small cluster of flower buds occasionally developed near the base of the primary inflorescence which already had immature fruit. This second peduncle seldom exceeded 1.0 cm in length and only rarely did it produce fruit.

Complete data on fruit phenology for 1981 were available only from central Illinois (Breen's Woods) as plants at the northern site were removed by collectors before the end of the growing season. At the central site, mature fruit first appeared on 6 August in 1981 and on 12 August in 1982, about a 1-wk difference. However, there was ca. a 2-wk difference in mature fruit fall which occurred about 5 October 1981, and 21 October 1982.

Fruits were dispersed by the middle of October. Based on the tight clustering of plants in the study populations and the location of fruit on the ground, dispersal distance appeared to be limited to <1.0 m.

No seedlings were found during the 1st growing season after planting (1982); however, in 1983, new seedlings occurred at all sites. The seedling consisted of a primary root and a single trifoliate leaf with small unbranched hairs on the veins of the upper surface. At the central and southern sites, most of the seedlings emerged from 1–10 May, and all emerged within a period of 2 wk. Emergence at the northern sites occurred later, ca. 10–24 May. At the northern, central and southern sites, 80, 70 and 48% of the planted seeds produced seedlings, respectively. Average germination was 66%.

Shoot morphology and anatomy.—No hypocotyl elongation occurred immediately after germination, so the first true leaf developed at the cotyledonary node or root collar. The two cotyledons were shed early but a bud formed in the axil of each cotyledon. During the 1st growing season, the larger bud formed a single determinate shoot (a sympodium), which also contained two bud primordia. The sympodium included the aerial shoot and a portion of the rhizome. The next year, two branch buds developed from the primorida, but again only the larger upper bud produced the next sympodium. The smaller bud apparently remains dormant unless the larger bud is damaged.

Each successive dormant bud and aerial shoot bud is rotated on the shoot axis almost 90° clockwise or counter-clockwise from the previous one. This rotation occurs because the plane of the distichous aerial shoot bud scales is 180° from the plane of the bud scale in whose axil it formed (Fig. 3a). Thus, successive sympodia are oriented 90° apart. Based on the morphology of the rhizomes examined, yearly growth seems to have an equal chance of being oriented 90° clockwise or counter-clockwise from the previous year. This pattern is consistent for plants that have erect rhizomes. No branched rhizomes (*i.e.*, rhizomes bearing two or more aerial shoots) were observed.

The morphology of the uppermost bud, the aerial shoot bud, showed little variability (Fig. 3b). In late summer and autumn, this bud had three large distichous bud scales that surrounded the shoot and leaf primordia. The number of leaves, leaflets and an inflorescence with floral primordia were observed during dissection. Bud primordia with two differentiated bud scales were present in the axils of the upper two bud scales of the aerial shoot bud.

At maturity, the nonreproductive aerial shoot terminated in a whorl of one to five 3–5-foliate leaves. Reproductive shoots terminated in a single umbellate inflorescence above the whorl of leaves.

The primary root becomes a fleshy storage root. Adventitious roots form from several nodes on the rhizome, and it appears that within 3 or 4 yr, at least one adventitious root becomes a fleshy storage organ in addition to the primary root. In older plants, as many as

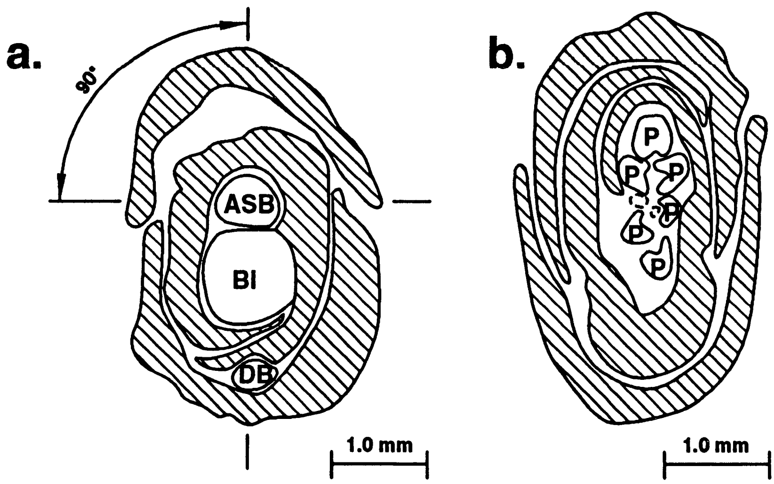

FIG. 3.—(a) Camera lucida tracing of a base cross-section of a *Panax quinquefolium* aerial shoot bud. The three bud scales are cross-hatched. The basal internode (BI) of the rhizome will develop during the next growing season. The aerial shoot bud (ASB) that will develop the following year is in the axil of the innermost bud scale, and a dormant bud (DB) is in the axil of the second bud scale. The aerial shoot bud primordium (horizontal line) is oriented perpendicular to the plane of bud scales (vertical line). (b) Camera lucida tracings of a cross-section of the central portion of a *Panax quinquefolium* aerial shoot bud showing three distichous (two-ranked) bud scales (cross-hatched) and two leaf primordia, bearing five and three leaflets (P), respectively. The lower leaflets (dotted outlines) of the upper leaf are below the plane of this section

three adventitious roots were as large as or larger than the primary root. Contractile activity of the adventitious roots apparently produced irregular wrinkles below the root collar (cotyledonary node) while pulling the slowly elongating rhizome into a nearly horizontal position.

Internal secondary growth of the rhizome and the root had no annual features that could be used to determine the plant age. Although cambial activity in the rhizome produced secondary xylem and phloem annually, there was little increase in diameter. Both the xylem and phloem had few, if any, fibrous elements and were largely parenchymatous. Newly formed tissues crushed and obliterated older vascular tissue, the pith and cortical parenchyma.

Each year an internode is added to the rhizome (Fig. 4a). First-year growth was marked by a dormant bud at the cotyledonary node where the rhizome joins the root collar. In each subsequent year, growth was marked by a circle of one or two bud scale scars. Following abscission of the aerial shoot, a dormant bud persisted above the second bud scale scar. However, because of the short internode distance between bud scales and the distichous arrangement of the scales, the dormant bud appeared to be above the circle of bud scale scars. Adjacent to each small dormant bud was a shelf-like aerial shoot abscission scar which was nearly overgrown and obliterated by the enlargement of the adjacent aerial shoot.

Plant age was determined by using the point at which the rhizome joins the root collar to identify 1st-yr growth. In subsequent years, growth was marked by a circle of bud scale scars and a dormant bud. In all study plants, there was an easily identifiable primary root, even in forest-cultivated roots up to 20 yr old. Dormant buds may differentiate to form a new aerial shot if the rhizome above the bud or the uppermost bud is destroyed (Fig. 4b).

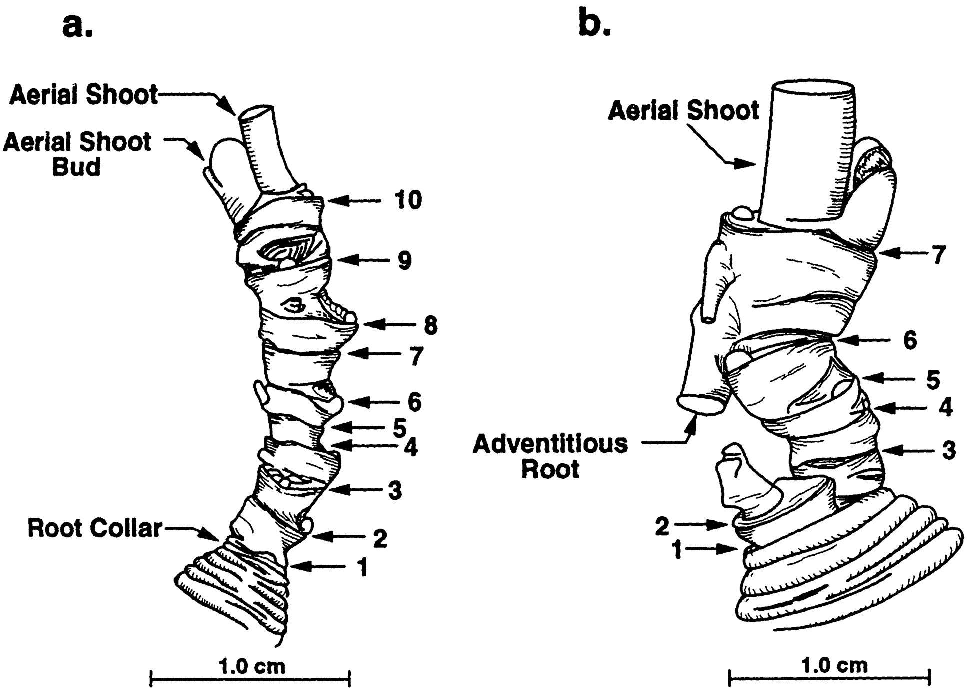

FIG. 4.—(a) Camera lucida drawing of a 10-yr-old *Panax quinquefolium* rhizome. The arrows indicate the top of the basal internode developed each year. A portion of the aerial shoot produced during the current year is attached. Note the size difference between next season's aerial shoot bud and the dormant bud on the opposite side of the aerial shoot. (b) Camera lucida drawing of a 7-yr-old *Panax quinquefolium* rhizome. Arrows show 2-yr growth of the original rhizome; the 3rd season aerial shoot bud aborted. Beginning the 3rd yr, the dormant bud located at the root collar developed a new rhizome which continued growth

Population size and age.—Protected sites had a substantially larger number of plants of all ages compared to unprotected sites. The 16 protected sites averaged 35.7 plants/0.05-ha plot (SE = 10.6) and the 17 unprotected sites 12.0 plants/0.05-ha plot (SE = 1.9). In both protected and unprotected populations, the largest average number of plants was in the 2-yr-old category rather than the 1-yr-old category (Fig. 5). There appears to be high mortality between ages 3 and 4 and after 7 yr. No plants were older than 11 yr.

Age and morphological relationships.—Rhizome age in field-collected plants was most strongly correlated with stem height from ground level [HT (cm) = 2.29 + 2.04(yr); r = 0.76], leaf area [Leaf Area (cm) = −35.2 + 45.6(yr); r = 0.74], number of leaflets [No. Leaflets = 3.88 + 1.28(yr); r = 0.73], number of leaves [No. Leaves = 1.09 + 0.23(yr); r = 0.70] and root dry weight [Root Wt. (g) = −0.6 + 0.3(yr), r = 0.63] (Table 2). Correlation coefficients between age and stem height from rhizome, root fresh weight, shoot dry weight, dry weight of fruits, peduncles and pedicels, whole plant dry weight and total number of fruit ranged from 0.44 to 0.75 ($P < 0.01$; n = 30).

The regression model for estimating leaflet area for leaf area determination (Table 2) was: Leaflet Area = 0.509 + 0.618(Leaflet Width × Length); r = 0.97, $P < 0.0001$ and n = 40.

The multiple regression model for predicting plant age was: Age = 0.720 + 0.185(Stem Height from Ground Level) + 0.204(Number of Leaves); r = 0.79, $P < 0.001$ and n = 38.

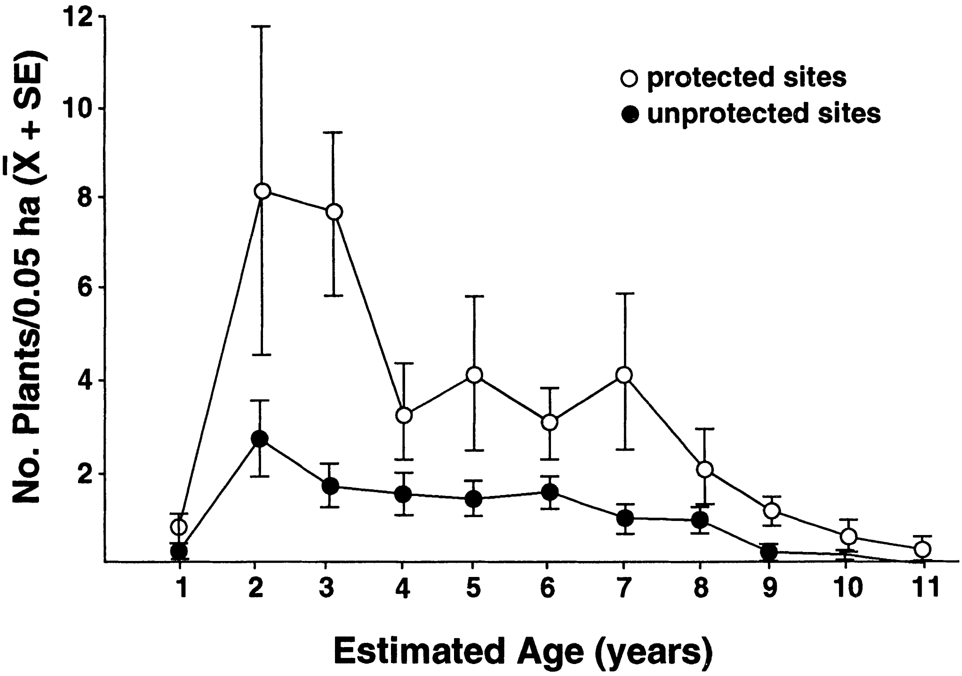

FIG. 5.—Number of *Panax quinquefolium* plants/0.05 ha by 1-yr age classes on protected and unprotected study sites. Plant age was estimated using a regression model based on morphological characteristics

Fruit production.—Fruit production increased with plant age. Data from the phenological study plants were used to develop a predictive model: Number of Fruit = −6.88 + 1.78 ×(Plant Age); r = 0.59, P < 0.01 and n = 94. Plant age was determined from the age regression model. The estimated mean number of fruit/plant produced by plants ranging in age from 4–11 yr is shown in Table 2. No plants younger than 4 yr produced mature fruit. From age 4, annual fruit production/plant increased arithmetically with 11-yr-old plants producing an average of 13 berries.

On protected sites, the greatest number of fruit/0.05-ha plot was produced by 7-yr-old plants (Fig. 6). Fruit production/0.05 ha progressively decreased in age classes 8–11 as *Panax quinquefolium* density decreased although the difference in fruit/0.05 ha between protected and unprotected sites continued to increase. Collectively, 4-, 5- and 6-yr-old plants produced 32.2 fruit/0.05 ha on protected sites and 13.7 fruit/0.05 ha on unprotected sites. Plants >6 yr old collectively produced 69.3 fruit/0.05 ha on protected sites and only 18.9 fruit/0.05 ha on unprotected sites. The estimated total number of fruit produced/0.05 ha was 101.6 on protected sites but only 32.5 on unprotected areas because of fewer plants.

Of 77 fruit collected from the northern and central sites, 55 contained two seeds (66.2%) and 26 contained one seed (33.8%).

Root weight.—When root dry weight was regressed against plant age using combined data from the 30 field-collected plants and 65 forest-cultivated plants, the correlation coefficient remained nearly the same (r = 0.64) as for the field plants alone. For the 95 plants, root dry weight linearly increased with age (Table 2). However, since the increase in average weight from year to year varied somewhat with 4- and 9-yr-old plants weighing more than

TABLE 2.—Mean size of stem structures and roots for mature *Panax quinquefolium* plants at different ages. Data on stem height, number of leaves, leaflet and fruit and leaf area are from regression equations developed from 30 field-collected plants which had a maximum age of 11 yr. Regression of mean root weight by age class was calculated using a regression equation developed from root data of 30 field-collected plants and 65 forest-cultivated plants whose maximum age was 20 yr. Age was determined by counting bud scale scars on the rhizome

Number of sample plants = 30						Number of sample plants = 95		
Age (yr)	Stem ht. (cm)	Number of leaves/ plant	Number of leaflets/ plant	Leaf area/ plant (cm^2)	Number of fruit/ plant	Number of plants (n)	Arithmetic mean root dry wt. (g)	Regression mean root dry wt. (g)
1	4.3	2.0	3.0	10	0.0	2	0.03	0.09
2	6.3	1.5	6.4	60	0.0	6	0.14	0.13
3	8.4	1.8	10.7	102	0.0	10	0.34	0.42
4	10.5	2.0	9.0	147	0.3	8	0.76	0.70
5	12.5	2.2	10.3	193	2.0	9	0.69	1.00
6	14.5	2.5	11.5	238	3.8	12	0.88	1.30
7	16.6	2.7	12.8	284	5.6	8	1.24	1.60
8	18.6	2.9	14.1	330	7.4	11	1.62	1.90
9	20.7	3.1	15.4	375	9.2	6	2.98	2.15
10	22.7	3.4	16.6	421	11.0	10	2.48	2.43
11	24.8	3.6	17.9	466	12.7	7	2.66	2.72*
14–17						3	3.88	
18–20						3	4.89	

* Weight data on 12- to 20-yr-old roots (Age/root weight in g): 12/3.01; 13/3.30; 14/3.60; 15/3.88; 16/4.17; 17/4.46; 18/4.74; 19/5.03; 20/5.32

5- and 10-yr-old plants, respectively, and since only six roots were found to be between 11 and 20 yr old, regression line averages may provide a better estimate of root dry weight at each age.

Root dry weight was strongly correlated with dry weight of shoots ($r = 0.98$), stem height from rhizome ($r = 0.92$), total number of fruit ($r = 0.92$), height from ground level ($r = 0.90$) and leaf area ($r = 0.88$). However, root dry weight had a weaker correlation with age ($r = 0.63$) and number of leaves ($r = 0.62$) ($P < 0.01$).

DISCUSSION

Environment.—All identified *Panax quinquefolium* populations were included in the study; thus the study sites are a representative sample of forest communities and environmental conditions where the species is found in Illinois. Because of the diversity of conditions where *P. quinquefolium* grows, biological information reported here probably has application in other states.

While *Panax quinquefolium* can grow on a wide range of soil textures and topographic conditions, it requires moist soils and sites of low evapotranspiration loss and is only infrequently found on droughty sand. The shift to a lower slope position in southern Illinois compared to more northern regions may reflect the warmer regional climate and more rocky, drier and higher slopes which characterize the Shawnee and Ozark Hills regions.

Soil nutrient levels for P and Ca in the A horizon generally were near the values (66 and 2200 kg/ha for P and Ca, respectively) considered by Wilde (1958) as suitable for

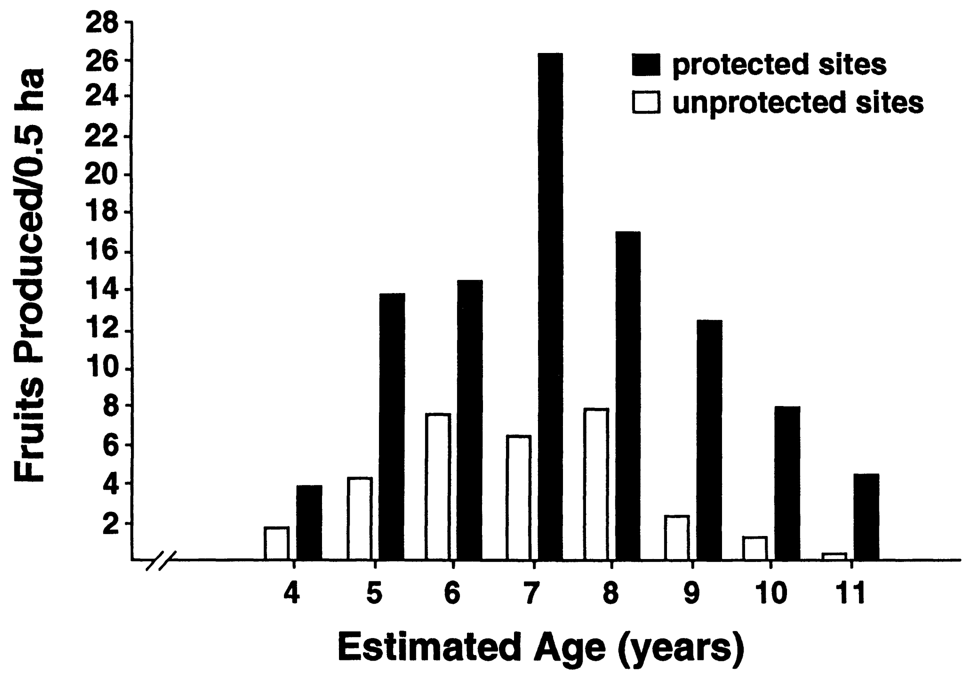

FIG. 6.—Estimated fruit production on protected and unprotected study sites. Protected sites have a greater plant density resulting in increased total fruit production in all age classes. Plant age was estimated using a regression model based on morphological characteristics

forest growth. However, all values for K were generally below an acceptable level of 275 kg/ha and several sites had exceptionally low values. *Panax quinquefolium* forms vesicular-arbuscular mycorrhizae (Seo and Anderson, 1990) which may increase plant survival when soil inorganic nutrients are not readily available (Allen, 1991).

The continued existence of *Panax quinquefolium* on cool, moist sites and in communities that have a high tree density or basal area and a heavy cover of shrubs and herbs follows the pattern of shade-tolerant species (Fralish, 1988). Proctor (1980) reported that light saturation for *P. quinquefolium* occurs at 10% of full sunlight while maximum growth occurs between 8 to 30% (Park, 1980; Proctor, 1980). Moderate to severe disturbance from timber harvesting and grazing appear to be detrimental to population maintenance.

Biology.—A generalized growth and development model for *Panax quinquefolium* developed for Illinois (Fig. 7) probably is applicable to the central hardwood forest region. The morphological development of the plant depicted as a function of age is taken largely from linear regression relationships. Seedlings consist of a single trifoliate leaf which emerges in early to mid-May. After germination, contractile roots pull the rhizome into the soil (Grushvitzky, 1952). Suppression of the dormant bud prevents the single rhizome from branching and forming a clonal cluster similar to many rhizomatous perennials.

During the 2nd growing season, *Panax quinquefolium* usually has a single leaf with 3–5 leaflets. In subsequent years, leaves and leaflets are added with 8- to 10-yr-old plants having as many as 4–5 leaves and 15–20 leaflets. Leaflet and leaf area increase concurrently with age. Our equation for leaflet area is similar to the equation of Hughes and Proctor (1981) which was based on leaflets from 3-yr-old roots.

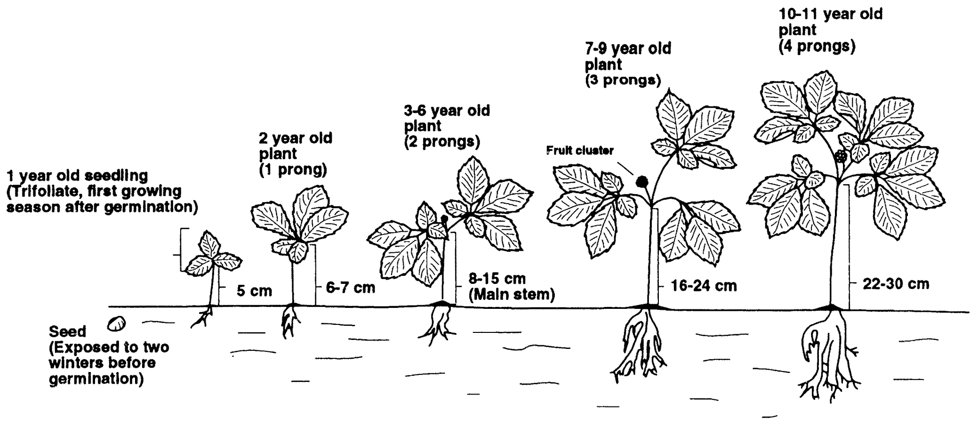

FIG. 7.—The life cycle of *Panax quinquefolium* in Illinois

Under natural forest conditions, relatively few plants grow to more than 10 or 11 yr old, while forest-cultivated plants may grow to be 20 yr old. These data agree with those of Lewis and Zenger (1982) who found that *Panax quinquefolium* plants older than 13 yr are uncommon among field populations. However, Carpenter and Cottam (1982) found plants as old as 23 yr in Wisconsin field populations, but most (73 out of 80) plants were less than 13 yr old. We estimate maximum age to be 25–30 yr. Rhizome damage could make the plant appear younger than its actual age, but growth probably would continue with adventitious roots assuming the storage and absorption functions.

Stem height, root weight, and the number of leaves and leaflets increase with and are good predictors of age. In addition, our work, as well as that of others (Carpenter and Cottam, 1982; Lewis and Zenger, 1982), has shown that fruit production is correlated with plant size. However, no fruit is produced until the beginning of the 4th growing season and not all 4-yr-old plants produce fruit. In contrast, Wisconsin populations did not produce fruit until they were at least 8 yr old (Carpenter and Cottam, 1982).

The perfect flowers of *Panax quinquefolium* can be weakly to strongly protandrous, a character that varies geographically (Lewis and Zenger, 1983). The breeding system can be xenogamy, geitonogamy or autogamy. The common pollinators are generalists and include small bees (Halictidae) (Carpenter and Cottam, 1982; Lewis and Zenger, 1983). Although the bright red color suggests animal dispersal, most fruit are passively disseminated (Lewis and Zenger, 1982).

The percentage of one-seeded (33.8%) and two-seeded fruit (66.2%) in our sample somewhat varies from the findings of Stoltz and Garland (1980) who examined 10,499 fruit and found that 16.3% were one-seeded and 77.0% were two-seeded. Their sample also contained a small number of three- and four-seeded fruit, 6.5 and 0.2%, respectively. Schlessman (1985) reported that flowers containing one, two and three ovaries produce one-, two- and three-seeded fruit, respectively, and the ratio of two- to one-ovuled flowers increases with plant size (age).

Our observation that planted seed required exposure to the chilling temperatures of 2 winters before germination is consistent with Lewis and Zenger (1982). They reported that most *Panax quinquefolium* seed require an after-ripening period of 18–22 mo for germination, although some seed may germinate after 8 mo (Baranov, 1966).

Collectors reduce populations by removing the largest plants which produce the most seed. Generally, plants 7–10 yr old have an average of three leaves, and it has been our experience that collectors will dig only plants with three or more leaves. On unprotected sites, an average of only 2.4 three-leaf plants/0.05 ha were found. If all 7- to 11-yr-old plants were removed from a site, approximately 69 fruit or 68% of the fruit produced on protected sites (101 fruit) would be lost. Differences in fruit production between protected and unprotected sites remain pronounced if only 9- to 11-yr-old plants are considered. On unprotected sites, these plants produce 4.5 fruits/0.05 ha (13.7% of the total), whereas on protected sites, plants >8 yr old produce 24.6 fruits/0.05 ha (24.3% of the total). Compared to protected sites, reduced seed production on unprotected sites results in a lower population density at all ages. These differences are a direct result of collecting.

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