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Population Structure and Biomass Allocation of the Naturalized Shrub *Lonicera maackii* (Rupr.) Maxim. in Forest and Open Habitats

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ABSTRACT: Open-grown populations of *Lonicera maackii* (Rupr.) Maxim. in northern Kentucky had significantly ($P \leq 0.05$) higher aboveground net primary production (NPP) per stem and per shrub, and a significantly ($P \leq 0.05$) higher percentage of aboveground biomass in leaves than forest-grown populations. The contribution of current (young-of-the-year) stems to aboveground NPP was significantly ($P \leq 0.05$) higher in forest-grown populations.

Stem demography was habitat-specific. Open-grown populations were characterized by unimodal age- and size-class distributions, low stem recruitment and low stem mortality. Forest-grown populations were characterized by right-skewed, bimodal, unimodal and random age- and size-class distributions, high stem recruitment and high mortality of small stems.

In open-grown populations, intragenet regulation of basal stem sprouting after 3-5 years assures that future NPP will be allocated primarily to residual (> 1 year old) stems. In forest-grown populations, continued production of current basal stems means that the subcanopy environment is annually tested for changes in resource availability. The results suggest that future NPP in forest-grown populations will be allocated to a mixture of current and residual basal stems.

INTRODUCTION

Because shrubs are long-lived and may show clonal growth, demographic studies encompassing the entire life cycle are difficult to carry out (Harper, 1977). However, when analyses of population structure at one time are coupled with growth measurements, a clear picture of shrub life history emerges (Chew and Chew, 1965; Schlesinger and Gill, 1980; Gray, 1982; Huenneke, 1987).

This research concerns the naturalized deciduous shrub *Lonicera maackii* (Rupr.) Maxim. growing in Northern Kentucky. A native of northeastern Asia, *L. maackii* was introduced to North America in the late 1850s for landscaping purposes (Dirr, 1983). Since that time, it has spread and become established in isolated parts of the eastern United States and southeastern Canada (Pringle, 1973). Braun (1916) did not mention *L. maackii* in her ecological survey of the Cincinnati region and Northern Kentucky. She later noted that *L. maackii* was restricted to Hamilton County, Ohio, where it was spreading into pastures and forests (Braun, 1961). Pringle (1973) also observed that *L. maackii* invaded open sites and forests in Ontario.

Each *Lonicera maackii* shrub produces a stout base from which grow several elongate stems. ("Shrub" will hereafter be used in reference to an individual plant (*i.e.*, genet), whereas "stem" will be used in reference to a structure arising from an adventitious bud on the shrub base (*i.e.*, ramet)). The red fruits of *L. maackii* are eaten by birds; thus the seeds are widely dispersed (U.S. Forest Service, 1974; Ingold and Craycraft, 1983.)

Tree canopy openings have been linked to increases in cover of several species of understory shrubs (Auclair and Cottam, 1971; Good and Good, 1972; Ehrenfeld, 1980; Huenneke, 1983; Sakai and Sulak, 1985; Dunn, 1986). However, few data are available on the effects of environment on growth and biomass allocation in shrubs (Whittaker, 1962). Variable allocation patterns in shrub species may allow them to persist in a variety of habitats and may also facilitate rapid growth responses to changing environments. Since *Lonicera maackii* successfully dominates both forest and open habitats, I hypothesized that *L. maackii* possesses a high degree of plasticity so that both biomass allocation and stem demography are habitat specific.

STUDY AREA AND METHODS

I sampled five open-grown *Lonicera maackii* populations located on roadsides in Campbell Co., Kentucky, near the Northern Kentucky University (NKU) campus (39° 5'N). Sites showing evidence of previous cutting or spraying were avoided. I also sampled six forest-grown populations of *L. maackii* located in isolated forest stands on the NKU campus. The forest isolates were dominated by black locust (*Robinia pseudoacacia*), slippery elm (*Ulmus rubra*), sugar maple (*Acer saccharum*) and white ash (*Fraxinus americana*).

Population structure.—Populations of *Lonicera maackii* were sampled during mid-July 1986. All forest-grown populations and three open-grown populations were sampled within 3 x 6 m rectangular plots. Two low-density open grown populations were sampled within 4 x 6 m and 12 x 10 m rectangular plots. A single plot was subjectively positioned in each population to avoid edge effects, trees, and to sample those areas where *Lonicera maackii* was the dominant shrub. Net primary production and biomass estimates may have been biased by this method of plot placement, but such a sampling technique was necessary in these highly fragmented plant communities.

In each plot, all living and dead stems were clipped or sawed 10 cm above their bases. Diameter and length were measured and living stems were sanded, stained and aged by counting annual rings. Lengths and widths of the cut shrub base surfaces were measured. All dead stems could not be accurately aged because of differences in wood quality; thus, they were not included in age-class distributions, although they were included in size-class distributions.

Populations and individual shrubs were aged by assuming the oldest stem in a population or on a shrub represented maximum age. This assumption may not be valid (Harper, 1977), especially among resprouting species experiencing frequent fires. However, there was no evidence of recent fire or disturbance in these study sites. This fact, together with the absence of large dead stems, the absence of completely dead shrubs and the inability of the shrubs to spread by underground structures support the preceding assumption.

Biomass and NPP.—Dimension analysis techniques described by Whittaker and Marks (1975), with slight modifications, were used to estimate biomass and NPP of residual stems older than 1 year. Regressions for estimating biomass and NPP were derived from 16 forest-grown and 15 open-grown stems that were sampled during late July and early August 1986. Stems were sampled in close proximity to the population study plots and at least two stems were sampled near each plot. Diameters of destructively sampled stems spanned the range of stem diameters found in the study plots.

Foliage, twigs and branches were removed from each stem. Fruit production was low and highly variable from stem to stem; thus fruits were included in the foliage estimates. Little herbivory or litterfall was evident at the time of sampling; therefore, no corrections were applied. Biomass was determined by weighing material either in the laboratory or the field and then subsampling to correct for moisture content (70 C dry weight basis).

Net primary production in the form of secondary wood and bark growth was estimated on stems and their branches. On stems and branches > 3 years old, wood growth was estimated by measuring length, annual ring widths and wood density. Bark growth was estimated from wood/bark ratios. Secondary wood and bark growth of stems and branches ≤ 3 years old were estimated by dividing dry weight by age.

Regressions for estimating belowground biomass were derived from 10 excavated shrub bases and their attached roots. Five shrub bases were sampled from forest-grown populations and five were sampled from open-grown populations. Attached roots were severed 50 cm from the shrub bases in an effort to maintain connections between roots and stem bases during excavation. This estimate of root biomass was probably an underestimate of the coarse root fraction and did not include fine roots.

Double log arithmetic regressions were calculated to predict various components of

Aboveground NPP ranged from 159.1-553.3 $\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ in forest-grown populations and from 141.2-1350.1 $\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ in open-grown populations (Fig. 1). Open-grown populations had significantly ($P \leq 0.05$) higher NPP per stem and per shrub than forest-grown populations, while the allocation of NPP to stem and leaf tissue did not differ between the two habitats (Table 3). Current stems in forest-grown populations contributed a significantly ($P \leq 0.05$) higher share of residual stem NPP than did current stems in open-grown populations (Table 3). Lastly, in forest-grown populations the ratio of aboveground biomass/aboveground NPP was significantly ($P \leq 0.05$) higher than in open-grown populations (Table 3).

Shrub and stem demography.—Stem mortality was higher in forest-grown populations as indicated by greater dry mass of standing dead stems (43.8-115.9 g/m^2 forest vs. 0-1.4 g/m^2 open) as well as a significantly ($P \leq 0.01$) higher number of dead stems per shrub (Table 4). Open-grown populations had significantly ($P \leq 0.05$) more residual stems per shrub (Table 4). A significantly ($P \leq 0.01$) higher rate of stem recruitment in forest-grown populations was indicated by the higher ratio of current stems/residual stems (Table 4).

Age and size structure.—Forest-grown populations (mean maximum age = 11.8 years, $\text{SE} = 0.6$) were significantly ($P \leq 0.05$) older than open-grown populations (mean maximum age = 7.2 years, $\text{SE} = 0.4$). Forest-grown populations varied more in stem age-class distribution than open-grown populations (Fig. 2). However, direct comparison of age-

TABLE 2.—Biomass allocation ratios for forest- and open-grown populations of *Lonicera maackii*. All values are means \pm SE with $n = 6$ and $n = 5$ for forest- and open-grown populations, respectively

Ratio	Forest	Open	t value	$P \leq$
Stem + leaf biomass/stem density	271.83 \pm 114.40	377.31 \pm 76.72	0.73	ns
Above + belowground biomass/shrub density	1596.76 \pm 516.23	2265.20 \pm 584.64	0.86	ns
Root biomass/total aboveground biomass	0.11 \pm 0.02	0.16 \pm 0.03	1.56	ns
Leaf biomass/total aboveground biomass	0.15 \pm 0.02	0.23 \pm 0.01	3.52	0.01
Stem wood biomass/total aboveground biomass	0.85 \pm 0.02	0.77 \pm 0.01	3.54	0.01

ns=no significant difference between forest- and open-grown populations at $P > 0.05$

TABLE 3.—Net primary production allocation ratios for forest- and open-grown populations of *Lonicera maackii*. All values are means \pm SE with $n = 6$ and $n = 5$ for forest- and open-grown populations, respectively

Ratio	Forest	Open	t value	$P \leq$
Total aboveground NPP/stem density	79.37 \pm 23.71	199.06 \pm 36.71	2.83	0.05
Total aboveground NPP/shrub density	345.07 \pm 88.89	945.04 \pm 232.84	2.56	0.05
Leaf NPP/total aboveground NPP	0.42 \pm 0.01	0.42 \pm 0.01	0.27	ns
Stem wood NPP/total aboveground NPP	0.58 \pm 0.01	0.57 \pm 0.01	0.36	ns
Total current stem NPP/total residual stem NPP	0.09 \pm 0.01	0.02 \pm 0.01	2.92	0.05
Total aboveground biomass/total aboveground NPP	2.96 \pm 0.32	1.84 \pm 0.08	3.12	0.05

ns=no significant difference between forest- and open-grown populations at $P > 0.05$

TABLE 4.—Stem distribution ratios for forest- and open-grown populations of *Lonicera maackii*. All values are means \pm SE with $n = 6$ and $n = 5$ for forest- and open-grown populations respectively

Ratio	Forest	Open	t value	$P \leq$
Dead stem density/shrub density	4.05 \pm 0.90	0.16 \pm 0.11	3.89	0.01
Residual stem density/shrub density	3.37 \pm 0.26	4.43 \pm 0.33	2.50	0.05
Current stem density/residual stem density	0.32 \pm 0.04	0.10 \pm 0.03	3.83	0.01
Current stem density/shrub density	1.12 \pm 0.25	0.48 \pm 0.16	2.09	ns

ns=no significant difference between forest- and open-grown populations at $P > 0.05$

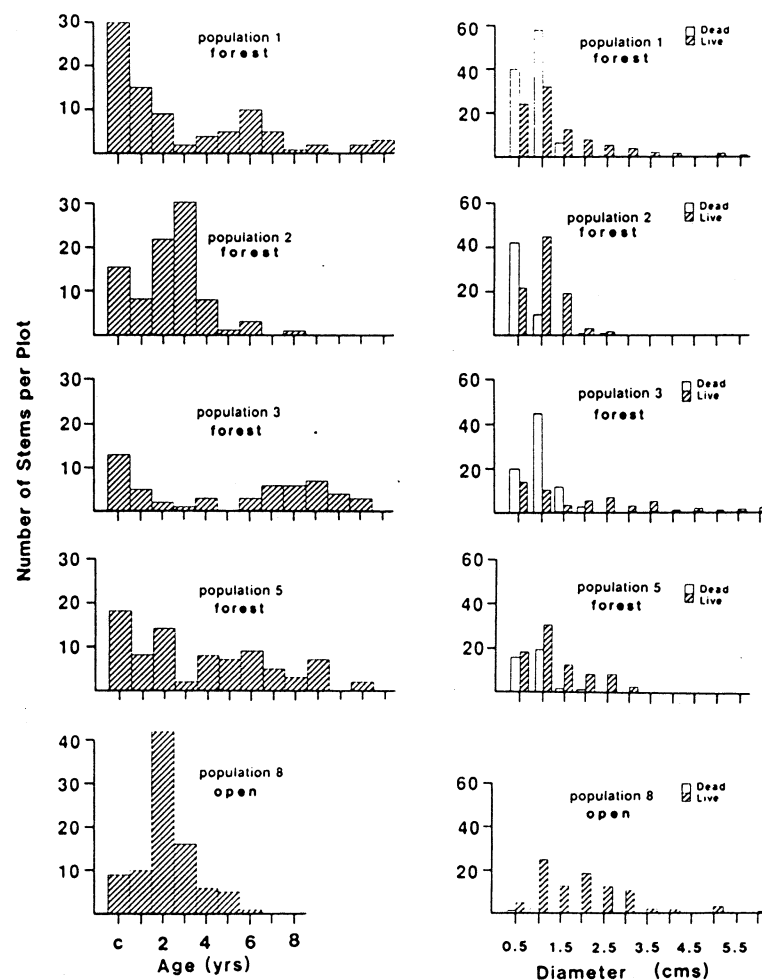


Fig. 2.—Age- and diameter-frequencies for the stems of selected forest- and open-grown *Lonicera maackii* populations. Age-frequencies include living stems only. Plot size was 18 m^2 for the populations presented. C = current year (1986) basal stem sprouts. Populations 1, 2, 3 and 5 are forest-grown; population 8 is open-grown

To what extent resource availability controls allocation between existing stems and new stems in this shrub species is unknown. It is also not known whether population-level differences are due to genetic or environmental factors. Regardless, it is clear that populations of *Lonicera maackii* can respond to closed and open environments through changes in demography and biomass allocation. Future NPP in open-grown populations will be allocated primarily to existing stems, while future NPP in forest-grown populations will be allocated to new and existing basal stems. Such flexibility may be an important characteristic allowing this introduced plant species to dominate a variety of habitats.

Acknowledgments.—Early drafts of this manuscript were improved by the comments of W. H. Schlesinger, J. L. Vankat and several anonymous reviewers. Support was provided by an NKU Faculty Project Grant.

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SUBMITTED 19 JANUARY 1987

ACCEPTED 8 SEPTEMBER 1987