

Growth rates, survivorship, and sex ratios of *Juniperus virginiana* on the New Jersey Piedmont from 1963 to 2000

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QUINN, J. A. (Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ 08901-1582) and S. J. Meiners (Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920-3099). Growth rates, survivorship, and sex ratios of *Juniperus virginiana* on the New Jersey Piedmont from 1963 to 2000. *J. Torrey Bot. Soc.* 131: 187–194. 2004.—Studies of the growth, survival, and sex ratios of dioecious species have been predominantly short-term. This research investigated growth rates, survivorship, and sex ratios among cohorts of *Juniperus virginiana* L. from 1963 through 2000. Males (M) and females (F) in six old-fields of different ages on the New Jersey Piedmont were analyzed, starting with the initial data on height and sex expression collected by John Small on labeled recruits from 1963 through 1976. These plants were relocated and censused during the summer and fall of 2000. No changes in sex expression were recorded between 1976 and 2000. The overall sex ratio was almost 1:1 (333 M, 332 F); only one of the fields showed a significant departure from 1:1. Males grew slightly, but significantly, faster in height than females, but relative growth rates dropped by approximately 50% for both males and females once they became reproductive. Female trees were on average 23 cm taller (and older) than males at first reproduction. Heights in those males and females surviving to 2000 were not significantly different. There was no effect of an individual's sex on its likelihood of dying, but plants that became established later were shorter, often non-reproductive, and had an increased risk of mortality. These long-term results strongly support genetically-determined sex ratios and a lack of major differences between males and females in growth rates and survival, which had been suggested by single-year studies elsewhere in the species' range.

Key words: Dioecy, *Juniperus virginiana*, New Jersey, reproductive biology, secondary succession, sex ratios, survivorship.

Lloyd and Webb (1977) suggested that if females of dioecious species allocated a greater proportion of their available energy to reproduction than males, then females should be slower growing and have lower survival rates. Females of woody species have been reported to show reduced growth and/or survivorship (e.g., Armstrong and Irvine 1989, Obeso et al. 1998, Rochelleau and Houle 2001, Espírito-Santo et al. 2003). However, the existence of these detrimental effects often appear to depend on the amount of reproductive investment of energy and/or nutrients relative to that available (e.g., Popp and Reinartz 1988, Vasiliauskas and Aarssen 1992), to exist at the branch level or ramet level (e.g., Luken 1987, Obeso 1997), or to affect reproductive frequency rather than annual

growth or survivorship (e.g., Abe 2002). Indeed, females of woody species sometimes show growth rates and survivorship equal to or greater than males (e.g., Grant and Mitton 1979, Willson 1986, Alliende and Harper 1989, Davidson and Remphrey 1990, Nicotra et al. 2003).

A major shortcoming of prior studies on growth rates, survivorship, and sex ratios of woody dioecious species is the lack of information on identified individuals over their lifespan. This is particularly critical when population data at a point in time are used to infer recruitment, survivorship, constancy of sex expression, and sex ratios. This paper utilizes long-term observations on labeled individuals of *Juniperus virginiana* L. to overcome these difficulties.

There are 13 dioecious species of *Juniperus* (Cupressaceae) native to North America, and two of the most widespread are *J. communis* and *J. virginiana* (Elias 1989). Females of *J. communis* do not show reduced growth rates and survivorship (Marion and Houle 1996), even when allocating significantly more resources to reproduction (Ortiz et al. 2002). Single-year studies of *J. virginiana* in Ontario (Vasiliauskas

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and Aarssen 1992) and in Alabama (Lawton and Cothran 2000) have shown a lack of major differences between males and females in growth rates and survival, and suggested that the genetically-determined sex ratio was 1:1. However, it was not possible in those studies to determine the long-term survivorship of marked individuals and the effect that it may have had on the observed sex ratio. There have been frequent reports of inconstant sex expression in *Juniperus* species (Vasek 1966, Freeman et al. 1981, Lloyd and Bawa 1984, Jordano 1991), but there have been no long-term observations on the sex expression of *J. virginiana* individuals in natural populations.

The objective of this research was to utilize long-term observations (1963–2000) on cohorts of labeled individuals of *J. virginiana* to directly determine growth rates and survivorship of individual males and females, constancy of sex expression, and resulting sex ratios.

Materials and Methods. **STUDY SPECIES, SITE DESCRIPTION, AND DATA COLLECTION.** *Juniperus virginiana* L. (eastern redcedar) grows throughout the eastern half of the United States, southern Ontario, and the southern tip of Quebec, and is the most widely distributed conifer of tree size in the eastern United States (Elias 1989, Lawson 1990). The species has an ability to grow under varying climatic conditions (annual precipitation ranging from 38 to 152 cm and growing seasons from 120 to 250 days) (Lawson 1990) and on a variety of soils ranging from swampy areas to dry rocky outcrops with thin soils (Elias 1989, Lawson 1990). *Juniperus virginiana* is intolerant to shade, and hardwoods usually replace it on better sites (Arend 1950, Bard 1952). However, once established, *J. virginiana* may persist under shade for long periods (Lassoie et al. 1983). On the New Jersey Piedmont it is the pioneer native woody species that invades cleared areas and abandoned fields and pastures, entering primarily through bird ingestion and excretion the first 6 yr after abandonment (Bard 1952, Holthuijzen and Sharik 1985).

The study sites were located at the Hutcheson Memorial Forest Center (HMFC) near East Millstone (Somerset County), New Jersey (40°30'N, 74°34'W). HMFC experiences a continental temperate climate with 113 cm of precipitation annually and a mean annual temperature of 11.7 C (Collins and Anderson 1994). The soils have developed from the Triassic red shales of the Brunswick formation of the Piedmont (Kummel

1940) and are moderately well-drained silt loams (~ pH 5.0) of 46 to 61 cm in depth (Ugolini 1964).

Six old-fields in a long-term successional study (Small et al. 1971) were utilized—two of these fields were abandoned from cultivation in each of 1957, 1959, and 1961, and were rectangular, ranging in size from 0.25 to 1.0 ha. From 1963 through 1976, as *Juniperus virginiana* seedlings appeared in these old-fields, John Small and coworkers attached aluminum labels and recorded their location (compass direction and distance from permanent grid markers) (Helen Buell, personal comm.); each year they also recorded height and sex expression, or mortality, of these labeled seedlings. These observations and measurements were made in the fall and winter when the seedlings, and their male or female cones if any, were most visible. In the summer and fall of 2000, we relocated the surviving individuals, recording their height, degree of overtopping by hardwoods, and sex expression. Heights were estimated with a telescopic measuring rod. Overtopping in 1963–76 and in 2000 was a qualitative ocular assessment. We used the early years of data collected by John Small and our data in 2000 to determine growth rates and heights, survivorship, and sex ratios. Plants were designated as non-reproductive when they showed no sex expression in both the initial surveys by John Small and in our census in 2000.

DATA ANALYSES. Analysis of initial height, height at first reproduction, and final height was done with ANOVA (Proc GLM) (SAS Institute 1989) including sex (male, female, non-reproductive), field, and the sex × field interaction. Height at first reproduction included reproductive individuals only. To determine the effects of sex and reproductive status on growth rates, the relative growth rate (RGR) of each tree was calculated for the 3-yr period immediately before and immediately after the first reproductive event. Relative growth rate was calculated as $[\ln(\text{height } t_2) - \ln(\text{height } t_1)] / (t_2 - t_1)$ (Reiling and Davison 1993). Where data were missing, RGR was calculated over the time span available. Missing data resulted from juveniles being followed less than 3 yr before reproducing (18.9% of all cases) or from being followed for less than 3 yr after becoming reproductive (13.5% of all cases). Analysis of pre-reproductive and reproductive RGRs were conducted for individuals which became reproductive during the study using 2-way ANOVA including field identity and

sex. To conform to the normality assumptions of ANOVA, RGR data were log-transformed prior to analysis.

To determine the impacts of sex on time from first census to reproductive maturity, an ANCOVA was conducted on all individuals that became reproductive before 2000. The analysis included sex and field identity and their interaction while controlling for the height of individuals at their initial measurement.

Cox regression (Proc PHREG) (SAS Institute 1989) was used to assess seedling mortality and to account for variation in time of entry into the data set. Mortality of *Juniperus* during the entire period of sampling was related to time of entry into the data set (a surrogate for time of establishment) and to field identity. To standardize across fields, time since abandonment was used to relate field age to likelihood of *Juniperus* mortality. To account for variation among fields in risk of mortality, the analysis of time of entry was stratified by field. Relative risk of mortality was calculated as the exponential transformation of the regression coefficients from the Cox regression.

A more detailed analysis of mortality patterns was conducted using a subset of the data. Only the two oldest fields, C3 and D1, were used in this analysis because they contained the majority (80%) of individuals of known sex that died during this study. The low sample size of dead individuals in each of the remaining four fields and variation in growth rates among these sites would bias mortality estimates in the Cox regression and were therefore omitted from the analysis. Mortality in the period from 1975 to 2000 was related to field identity, plant reproductive status (reproductive, non-reproductive), plant height in 1975, and RGR (from 1973 to 1975) using multiple logistic regression (Proc LOGISTIC) (SAS Institute 1989). This time period was chosen because most of the deceased individuals of known sex died during this interval. Forward model selection was used with a $P = 0.05$ criteria for model entry. This analysis was repeated using reproductive individuals only to determine sex-based differences in mortality.

Results. GROWTH RATES AND HEIGHTS. Growth rates varied significantly among fields both before and after individuals became reproductive (Fig. 1; Pre-reproductive: $F_{5,570} = 26.59$, $P < 0.0001$; Reproductive: $F_{5,571} = 15.05$, $P < 0.0001$). Pre-reproductive males grew slightly,

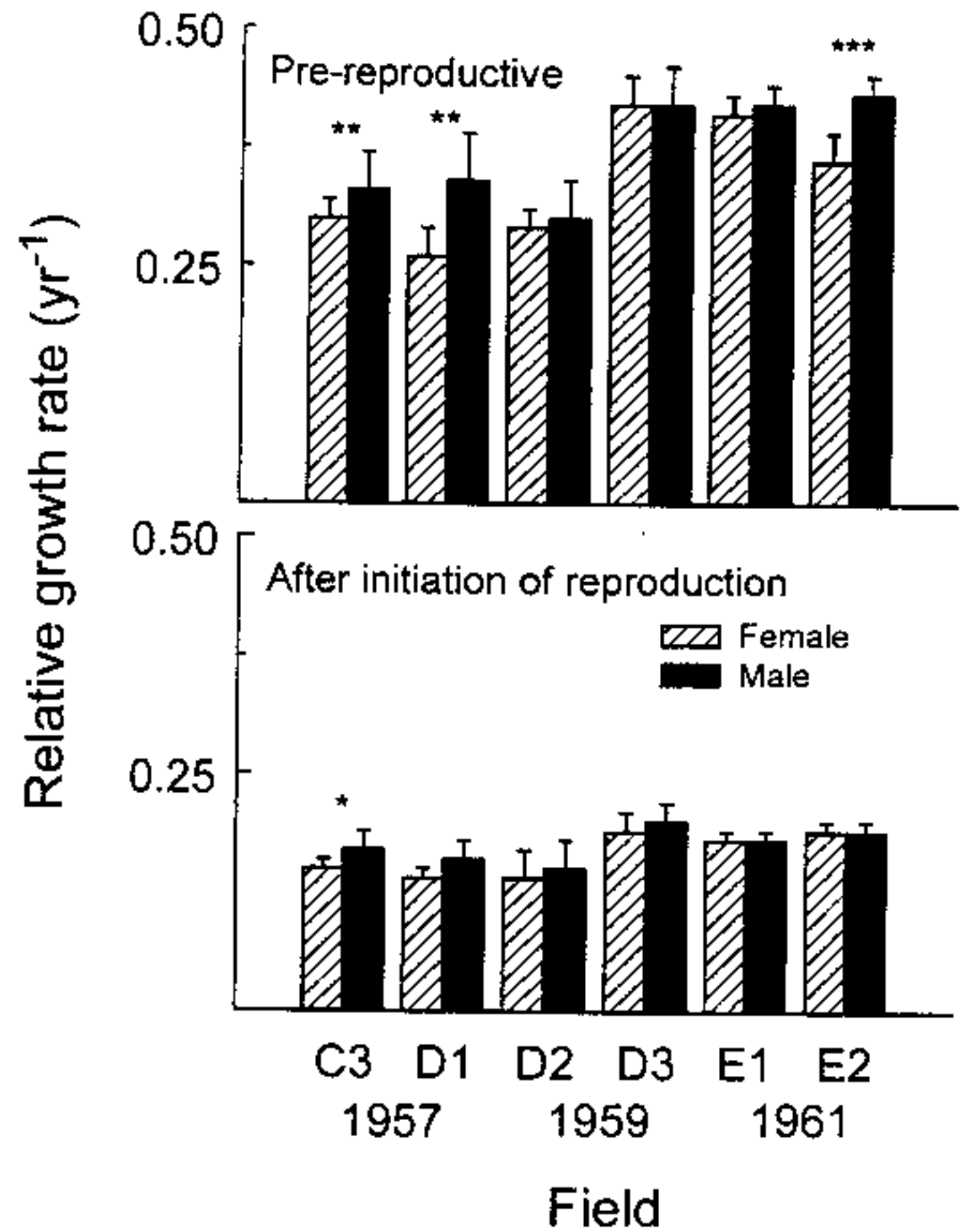


FIG. 1. Back-transformed means and standard errors of pre- and post-initial reproduction RGRs for females and males of *Juniperus virginiana* in the successional fields at the Hutcheson Memorial Forest Center. Year of abandonment from cultivation is shown below each field designation, and significant differences between the females and males in a field are indicated by * ($P < 0.05$), ** ($P < 0.01$), or *** ($P < 0.001$).

but significantly ($F_{1,570} = 12.88$, $P = 0.0004$), faster in height than pre-reproductive females (male RGR 0.409 ± 0.008 ; female RGR 0.365 ± 0.006). However, relative growth rates dropped by approximately 50% for both males and females once they became reproductive (Fig. 1). These trends were shown in each of the fields. After initiation of reproduction, males continued to grow at a faster rate than females ($F_{1,571} = 7.84$, $P = 0.0053$), but the differences were much less with an overall average growth rate of 0.175 yr^{-1} (± 0.003) for females and 0.188 yr^{-1} (± 0.003) for males.

Females were taller than males at time of first reproduction in all fields (Fig. 2). They were significantly taller than males in four of the fields and in all fields combined ($F_{1,613} = 20.00$, $P < 0.0001$). Females were on average 23 cm taller (and older, as indicated by RGRs) than males at first reproduction. After accounting for field identity and initial height, an ANCOVA verified that females took longer to reach reproductive maturity ($F_{1,612} = 11.19$, $P < 0.001$). Initial and

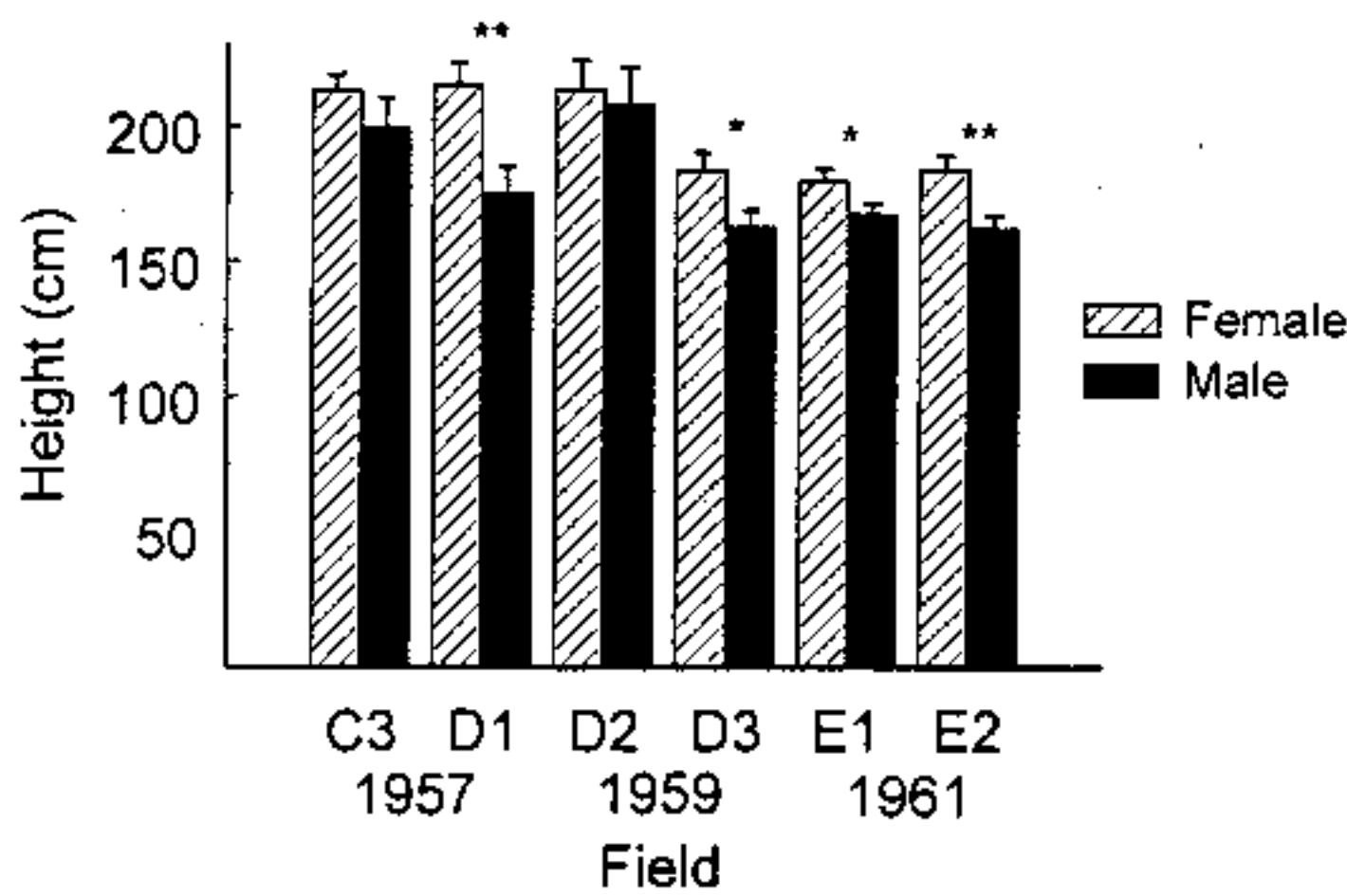


FIG. 2. Height (mean and SE) at first reproduction for females and males of *Juniperus virginiana* in the successional fields at the Hutcheson Memorial Forest Center (* = $P < 0.05$; ** = $P < 0.01$).

final heights for those females and males surviving to 2000 were not significantly different, although non-reproductives were significantly shorter (Fig. 3). The percentage of individuals in a field observed by Small and the authors to be suppressed or overtopped by hardwoods ranged from 3.5 to 41.9% (Table 1).

SURVIVORSHIP. Of the 818 individuals initially measured and labeled in the six fields, 81.8% survived to 2000 (Table 1). Risk of mortality varied significantly among fields (Fig. 4; Wald $\chi^2 = 110.85$, $df = 5$, $P < 0.0001$), but there was no effect of an individual's sex on its likelihood of dying (4.8% and 7.2% mortality for females and males, respectively) (Table 1). However, non-reproductives (usually later in establishment and shorter in height) had a mortality of 72.0% (Table 1).

A detailed analysis of mortality patterns was conducted only in the two oldest fields, C3 and D1, because they contained the majority of the individuals of known sex that died in this study

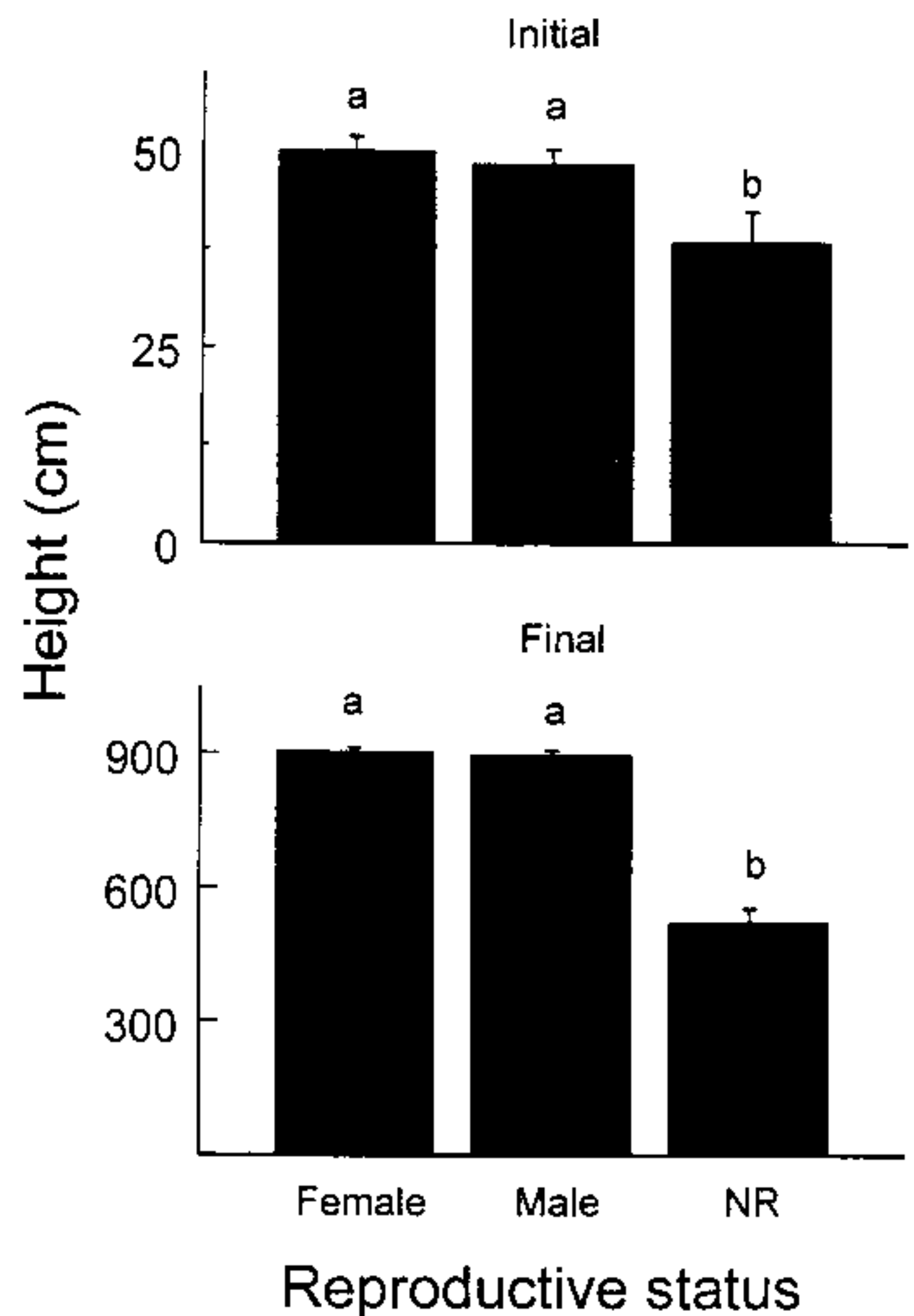


FIG. 3. Heights (mean and SE) at time of initial measurement and at final measurement in 2000 for females, males, and non-reproductives of *Juniperus virginiana* in successional fields at the Hutcheson Memorial Forest Center.

(Table 1). Using multiple logistic regression (Proc LOGISTIC) (SAS Institute 1989), mortality was related to sex, time of establishment, height in 1975, RGR from 1973 to 1975, and reproductive status (reproductive, non-reproductive). Individuals that became established later were more likely to die with risk of mortality increasing 36.5% with each year after abandon-

Table 1. Numbers of female, male, monoecious, and non-reproductive individuals of *Juniperus virginiana* initially measured and labeled, degree of overtopping, and their survivorship to 2000, in the successional fields at the Hutcheson Memorial Forest Center.

Field and Year	Number of each with dead in parentheses				% Overtopped ^a	Total Individuals	Total Deaths	% Survivorship
	Female	Male	Monoecious	Non-repro.				
C3/1957	63 (5)**	36 (6)	0	48 (40)	22.4	147	51	65.3
D1/1957	41 (9)	42 (13)	0	55 (49)	27.5	138	71	48.6
D2/1959	19 (1)	17 (2)	0	7 (4)	41.9	43	7	83.7
D3/1959	63 (0)	64 (0)	1 (1)	16 (1)	19.4	144	2	98.6
E1/1961	76 (1)	85 (1)	1 (0)	12 (5)	4.6	174	7	96.0
E2/1961	70 (0)	89 (2)	1 (0)	12 (9)	3.5	172	11	93.6
ALL FIELDS	332 (16)	333 (24)	3 (1)	150 (108)	16.0	818	149	81.8

** Significantly different from a 1:1 expectation at the 0.01 level.

^a Percentage of individuals recorded by Small and/or by the authors as suppressed or overtopped by hardwoods.

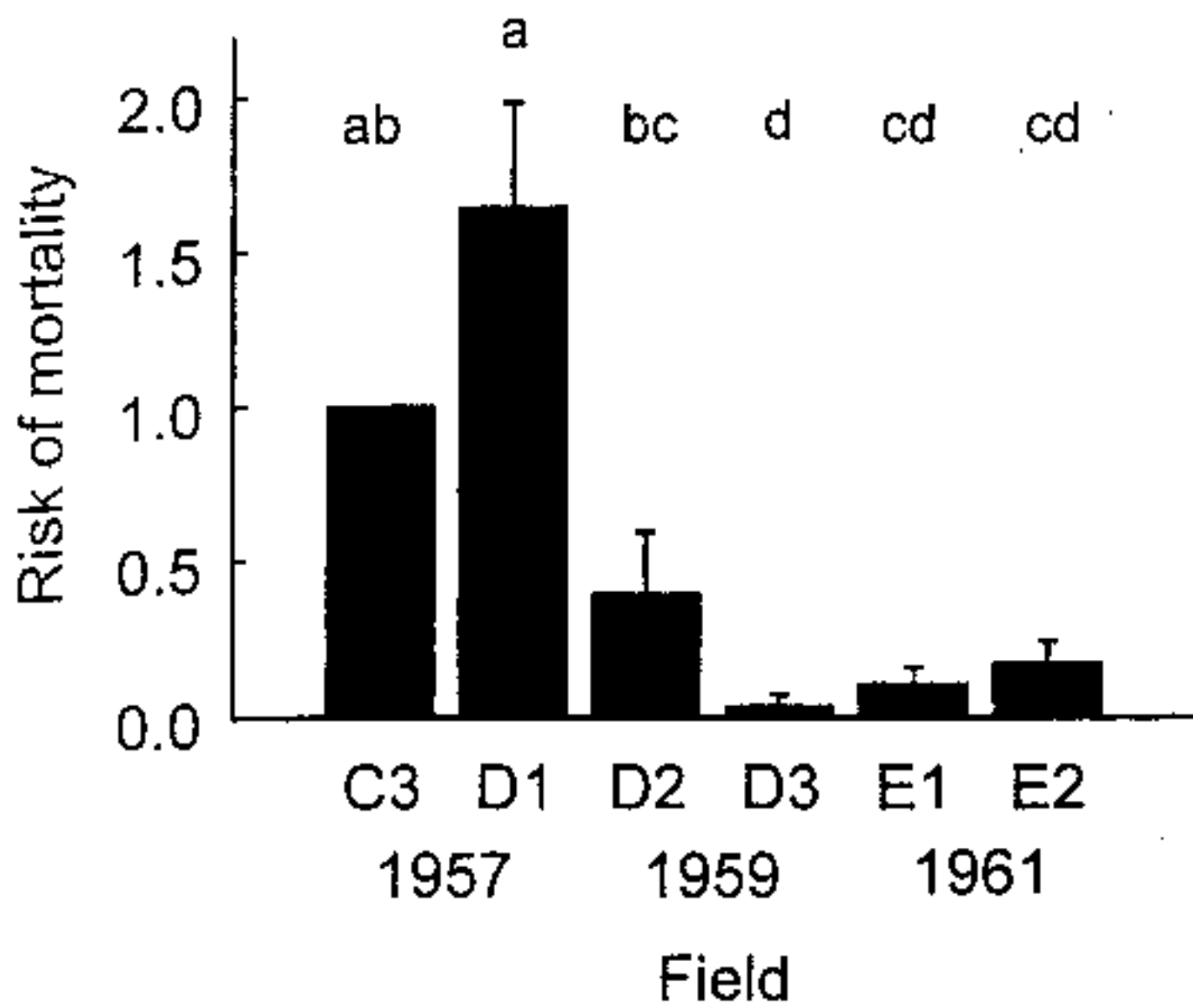


FIG. 4. Proportional risk of mortality from Cox regression for individuals within each of the fields reported as the mean risk (± 1 SE). Risk of mortality is calculated relative to field C3, which is for that reason set to a risk of 1.0. Fields with the same letter are not significantly different at the 0.05 level.

ment (Wald $\chi^2 = 82.09$, $df = 1$, $P < 0.0001$). Just as for the entire data set, when we separated out the reproductive individuals there was no effect of sex on the likelihood of dying ($P > 0.05$). For this reason we classified individuals as reproductive or non-reproductive only. The multiple logistic regression retained three variables as significantly affecting the likelihood of mortality in *J. virginiana* (model Wald $\chi^2 = 68.87$, $df = 3$, $P < 0.0001$). For each 25 cm less in height in 1975, individuals were 1.39 times more likely to die (Wald $\chi^2 = 42.09$, $df = 1$, $P < 0.0001$), for each decrease of 0.01 in RGR, individuals were 1.25 times more likely to die (Wald $\chi^2 = 22.59$, $df = 1$, $P < 0.0001$), and non-reproductives were 4.61 times more likely to die than reproductive individuals (Wald $\chi^2 = 10.46$, $df = 1$, $P = 0.0012$). All interactions and field identity (C3 vs D1) were non-significant and dropped from the model. The overall model fit was adequate as tested by a Homer and Lemeshow goodness of fit test ($\chi^2 = 11.98$, $df = 8$, $P = 0.1523$) (SAS Institute 1989).

SEX EXPRESSION AND SEX RATIOS. No changes in sex expression were recorded between 1976 and 2000. The overall sex ratio was almost 1:1 (333 M, 332 F, and 3 monoecious); only one of the fields (C3) showed a significant departure (female bias) from a 1:1 expectation (Table 1). E1 and E2 both had a non-significant greater number of males.

Discussion. Our 1963–2000 results from labeled *J. virginiana* in central New Jersey strongly support a lack of major differences between males and females in growth rates and survival, and a genetically-determined sex ratio of 1:1, which had been suggested by the prior single-year studies in Ontario (Vasiliauskas and Aarssen 1992) and in Alabama (Lawton and Cothran 2000).

GROWTH RATES AND HEIGHTS. We found that pre-reproductive males grew significantly faster in height than pre-reproductive females (Fig. 1). Because males initiate cone development earlier than females (4 vs 10 years in age, Van Haverbeke and Read 1976), this early height growth may lead to crowns that extend above the dense herbaceous canopy of early-successional environments, facilitating wider pollen dispersal. In addition, since pollen transfer is passively mediated by wind, increased height would increase distance of transport. Because of their later production of cones, females were significantly taller at the time of first reproduction (Fig. 2).

Relative growth rates dropped by approximately 50% for both males and females once they became reproductive (Fig. 1), but this occurred significantly later for females (see ANCOVA in Results). Because of this delay in the 50% drop in RGRs for females, heights in those males and females surviving to 2000 were not significantly different (Fig. 3), even though RGRs after the initiation of reproduction were still slightly higher for males. In the Ontario study (Vasiliauskas and Aarssen 1992), males were taller than females in 3 of the 20 stands and in the pooled data; this was attributed to sexual selection for greater success as a pollen donor, especially in dense monospecific stands characteristic of this species. Adult females may compete less effectively than males in less productive habitats, such as in the Ontario populations at the northern limits for *J. virginiana* and in the mountainside population in the Alabama study (Lawton and Cothran 2000). In Alabama, radial growth and the effects of shade were similar for males and females. Thus, the three studies on sex-specific growth rates in *J. virginiana* indicate that although there may be a trend for slightly greater height growth in males, there were no major or consistent differences in growth rates and trunk diameters.

SURVIVORSHIP. We found that sex had no effect on an individual's likelihood of dying (Table 1), but the risk of mortality as assessed by Cox

regression varied significantly among fields (Fig. 4). Substratum and topography were relatively consistent from field to field (Ugolini 1964), but those fields with the greatest risk of mortality (C3, D1, and D2) were adjacent to or shared the greatest border with an upland forest where, according to the notes of John Small and our observations in 2000, a high proportion of the labeled *J. virginiana* were subjected to overtopping and shading by hardwoods (Table 1). In contrast, fields D3, E1, and E2, which either shared a border with woody vegetation along a stream or were isolated from the upland forest by intervening fields had a reduced incidence of overtopping by hardwoods and a greater frequency of open or partially open canopy (Table 1). In addition, the low rainfall of 1962 (Small et al. 1971) may have reduced hardwood seed production and seedling recruitment in E1 and E2, resulting in a high density of *J. virginiana* but few overtopping hardwoods. Although *J. virginiana* has been classed as very intolerant to the shade of hardwoods (Lawson 1990), Williamson (1957) emphasized the failure of *J. virginiana* to self-thin; thus, the greatest risk of mortality existed in those fields with a greater density of overtopping hardwoods.

Our detailed analysis of mortality in C3 and D1 using multiple logistic regression again showed that there was not a significant effect of sex on the likelihood of dying, but in regards to time of establishment, the risk of mortality increases 36.5% for each year after abandonment. For each 25 cm less in height in 1975, individuals were 1.39 times more likely to die by 2000, and for each decrease of 0.01 in RGR, individuals were 1.25 times more likely to die. Non-reproductives were 4.61 times more likely to die than reproductives. These regression results from C3 and D1 help to explain the overall mortality of non-reproductives of 72% in the six fields, in relation to a mortality of only 6% for reproductives. Relative growth rates reflect the relative health and competitive environment of individuals. Growth rates in woody species have been linked with the survivorship of seedlings and adults (Kobe et al. 1995, Kobe and Coates 1997). Individuals that are more actively growing are typically much less likely to die than individuals with reduced growth. The positive relationship between growth rate and survivorship is clearly seen in this study. Similarly, non-reproductive individuals became established later, were shorter on average, and were probably experiencing greater competition for light than

reproductive individuals. These individuals also exhibited the greatest mortality rates.

In Ontario, the sex ratios and age structures of the populations at the time of measurement provided no evidence for differential survival of the sexes (Vasiliauskas and Aarssen 1992), and in Alabama, the male-biased population on the mountainside was interpreted as due to a lower frequency of reproduction among females, since the likelihood of observing females among the reproductively active trees increased with tree size (Lawton and Cothran 2000), i.e., a size-related delay in onset of reproductive activity similar to our observations.

SEX EXPRESSION AND SEX RATIOS. By utilizing multiple-year observations on the sex expression of labeled individuals, we were able to eliminate bias in the sex ratio that would be produced by those individuals not reproducing in a single year of observation. Although we had a female bias in C3 and a non-significant excess of males in E1 and E2 (Table 1), our overall sex ratio was 1:1, with no changes in sex expression between 1976 and 2000. The authors of the prior studies had suggested that the genetically determined sex ratio was 1:1. In Ontario, 19 of 20 stands had 1:1 ratios, although the pooled data from all stands showed a slight male bias (Vasiliauskas and Aarssen 1992); it was suggested that at the northern limit of the species suppressed or young male trees might produce a few cones under conditions that would preclude cone development by females. In Alabama, a population on the fertile soil of the Tennessee Valley floor with a high proportion of reproductives had a 1:1 ratio (Lawton and Cothran 2000); however, a xeric population on the rocky slopes of the Cumberland Plateau with only 24% reproductives had a male bias, attributed by the authors to a lack of reproduction by a greater proportion of the smaller female individuals—this coincides with our results that females were taller and older than males at first reproduction.

The three studies in combination produce strong evidence for a genetically-determined 1:1 ratio, but although Vasiliauskas and Aarssen (1992) reported that male trees did not have a greater representation in the younger or older age classes, i.e., no differential survival, we have no evidence as to the primary (at fertilization) and secondary (at germination) sex ratios. Only a sex-linked DNA marker (e.g., Alstrom-Rapaport et al. 1998, Kafkas et al. 2001, Urasaki et al. 2002), not yet available for *J. virginiana*,

that could be used on seeds and seedlings would help to clarify if there are any reasons other than chance for the occasional local bias in sex ratio. Such a marker could also be used to determine the sex of non-reproductives, testing the hypothesis of the lack of reproduction by a greater proportion of the smaller female individuals under more limiting conditions.

Literature Cited

- ABE, T. 2002. Flower bud abortion influences clonal growth and sexual dimorphism in the understory dioecious shrub *Aucuba japonica* (Cornaceae). *Ann. Bot.* 89: 675–681.
- ALLIENDE, M. C., AND J. L. HARPER. 1989. Demographic studies of a dioecious tree. I. Colonization, sex and age structure of a population of *Salix cinerea*. *J. Ecol.* 77: 1029–1047.
- ALSTROM-RAPAPORT, C., M. LASCOUX, Y. C. WANG, G. ROBERTS, AND G. A. TUSKAN. 1998. Identification of a RAPD marker linked to sex determination in the basket willow (*Salix viminalis* L.). *J. Hered.* 89: 44–49.
- AREND, J. L. 1950. Influence of fire and soil on distribution of eastern redcedar in the Ozarks. *J. Forest.* 48: 129–130.
- ARMSTRONG, J. E., AND A. R. IRVINE. 1989. Flowering, sex ratios, pollen-ovule ratios, fruit set, and reproductive effort of a dioecious tree, *Myristica insipida* (Myristicaceae), in two different rain forest communities. *Amer. J. Bot.* 76: 74–85.
- BARD, G. E. 1952. Secondary succession on the Piedmont of New Jersey. *Ecol. Monogr.* 22: 195–215.
- COLLINS, B. R., AND K. H. ANDERSON. 1994. Plant communities of New Jersey: a study in landscape diversity. Rutgers University Press, New Brunswick, NJ. 287 p.
- DAVIDSON, C. G., AND W. R. REMPHREY. 1990. An analysis of the architectural parameters of male and female *Fraxinus pennsylvanica* in relation to crown shape and crown location. *Can. J. Bot.* 68: 2035–2043.
- ELIAS, T. S. 1989. Field guide to North American trees. Revised ed. Grolier Book Clubs Inc., Danbury, CT. 948 p.
- ESPIRITO-SANTO, M. M., B. G. MADEIRA, F. S. NEVES, M. L. FARIA, M. FAGUNDES, AND G. W. FERNANDES. 2003. Sexual differences in reproductive phenology and their consequences for the demography of *Baccharis dracunculifolia* (Asteraceae), a dioecious tropical shrub. *Ann. Bot.* 91: 13–19.
- FREEMAN, D. C., E. D. MCARTHUR, K. T. HARPER, AND A. C. BLAUER. 1981. Influence of environment on the floral sex ratio of monoecious plants. *Evolution* 35: 194–197.
- GRANT, M. C., AND J. B. MITTON. 1979. Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates in *Populus tremuloides* Michx. *Evolution* 33: 914–918.
- HOLTHUIZEN, A. M. A., AND T. L. SHARIK. 1985. Colonization of abandoned pastures by eastern red cedar (*Juniperus virginiana* L.). *Can. J. For. Res.* 15: 1065–1068.
- JORDANO, P. 1991. Gender variation and expression of monoecy in *Juniperus phoenicea* L. (Cupressaceae). *Bot. Gaz.* 152: 476–485.
- KAFKAS, S., S. CETINER, AND R. PERL-TREVES. 2001. Development of sex-associated RAPD markers in wild *Pistacia* species. *J. Hort. Sci. & Biotech.* 76: 242–246.
- KOBE, R. K., S. W. PACALA, J. A. SILANDER, AND C. D. CANHAM. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5: 517–532.
- KOBE, R. K., AND K. D. COATES. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can. J. For. Res.* 27: 227–236.
- KUMMEL, H. B. 1940. The geology of New Jersey. N. J. Dep. Conserv. and Devel., Geol. Ser., Bull. 50.
- LASSOIE, J. P., P. M. DOUGHERTY, P. B. REICH, T. M. HINCKLEY, C. M. METCALF, AND S. J. DINA. 1983. Ecophysiological investigations of understory eastern redcedar in central Missouri. *Ecology* 64: 1355–1366.
- LAWSON, E. R. 1990. *Juniperus virginiana* L., eastern redcedar, pages 131–140. In: R. M. Burns and B. H. Honkala [eds.], *Silvics of North America*, Vol. 1, Conifers. USDA Agriculture Handbook 654, Washington, DC.
- LAWTON, R. O., AND P. COTHRAN. 2000. Factors influencing reproductive activity of *Juniperus virginiana* in the Tennessee Valley. *J. Torrey Bot. Soc.* 127: 271–279.
- LLOYD, D. G., AND C. J. WEBB. 1977. Secondary sex characters in plants. *Bot. Rev.* 43: 177–216.
- LLOYD, D. G., AND K. S. BAWA. 1984. Modification of the gender of seed plants in varying conditions. *Evol. Biol.* 17: 255–338.
- LUKEN, J. O. 1987. Interactions between seed production and vegetative growth in staghorn sumac, *Rhus typhina* L. *Bull. Torrey Bot. Club* 114: 247–251.
- MARION, C., AND G. HOULE. 1996. No differential consequences of reproduction according to sex in *Juniperus communis* var. *depressa* (Cupressaceae). *Amer. J. Bot.* 83: 480–488.
- NICOTRA, A. B., R. L. CHAZDON, AND R. A. MONTGOMERY. 2003. Sexes show contrasting patterns of leaf and crown carbon gain in a dioecious rainforest shrub. *Amer. J. Bot.* 90: 347–355.
- OBESO, J. R. 1997. Costs of reproduction in *Ilex aquifolium*: effects at tree, branch and leaf levels. *J. Ecol.* 85: 159–166.
- OBESO, J. R., M. ALVAREZ-SANTULLANO, AND R. RETUERTO. 1998. Sex ratios, size distributions, and sexual dimorphisms in the dioecious tree *Ilex aquifolium* (Aquifoliaceae). *Amer. J. Bot.* 85: 1602–1608.
- ORTIZ, P. L., M. ARISTA, AND S. TALAVERA. 2002. Sex ratio and reproductive effort in the dioecious *Juniperus communis* subsp. *alpina* (Suter) Celak. (Cupressaceae) along an altitudinal gradient. *Ann. Bot.* 89: 205–211.
- POPP, J. W., AND J. A. REINARTZ. 1988. Sexual dimorphism in biomass allocation and clonal growth of *Xanthoxylum americanum*. *Amer. J. Bot.* 75: 1732–1741.
- REILING, K., AND A. W. DAVISON. 1993. Ozone sensitivity, pages 63–65. In: G. A. F. Hendry and J. P.

- Grime [eds.], *Methods in Comparative Plant Ecology*. Chapman and Hall, London.
- ROCHELEAU, A., AND G. HOULE. 2001. Different cost of reproduction for the males and females of the rare dioecious shrub *Corema conradii* (Empetraceae). *Amer. J. Bot.* 88: 659–666.
- SAS INSTITUTE. 1989. *SAS/STAT User's Guide*, Volumes 1 and 2, Version 6, 4th ed. SAS Institute, Inc., Cary, NC.
- SMALL, J. A., M. F. BUELL, AND H. F. BUELL. 1971. Old-field succession on the New Jersey Piedmont—the first year. *William L. Hutcheson Memorial Forest Bull.* 2(4): 26–30.
- UGOLINI, F. C. 1964. Soil development on the red beds of New Jersey. *William L. Hutcheson Memorial Forest Bull.* 2(1): 1–34.
- URASAKI, N., M. TOKUMOTO, K. TARORA, Y. BAN, T. KAYANO, H. TANAKA, H. OKU, I. CHINEN, AND R. TERAUCHI. 2002. A male and hermaphrodite specific RAPD marker for papaya (*Carica papaya* L.). *Theor. Appl. Genet.* 104: 281–285.
- VAN HAVERBEKE, D. F., AND R. A. READ. 1976. Genetics of eastern redcedar. U. S. Department of Agriculture Forest Service Research Paper WO-32.
- VASEK, F. C. 1966. The distribution and taxonomy of three western junipers. *Brittonia* 18: 350–372.
- VASILIAUSKAS, S. A., AND L. W. AARSEN. 1992. Sex ratio and neighbor effects in monospecific stands of *Juniperus virginiana*. *Ecology* 73: 622–632.
- WILLIAMSON, M. J. 1957. Silvical characteristics of eastern redcedar. U. S. Forest Service Central States Forest Experiment Station Misc. Release 15.
- WILLSON, M. F. 1986. On the costs of reproduction in plants: *Acer negundo*. *Amer. Midl. Nat.* 115: 204–207.