



Earlier plant flowering in spring as a response to global warming in the Washington, DC, area

MONES S. ABU-ASAB^{1,*}, PAUL M. PETERSON², STANWYN G. SHETLER²
and SYLVIA S. ORLI²

¹Section of Ultrastructural Pathology, Laboratory of Pathology, National Cancer Institute, Bethesda, MD 20892, USA; ²Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0166, USA; *Author for correspondence (fax: +1-301-480-9197)

Received 18 April 2000; accepted in revised form 11 May 2000

Abstract. Evidence for global warming is inferred from spring advances in first-flowering in plants. The trend of average first-flowering times per year for the study group shows a significant advance of 2.4 days over a 30-year period. When 11 species that exhibit later first-flowering times are excluded from the data set, the remaining 89 show a significant advance of 4.5 days. Significant trends for earlier-flowering species range from -3.2 to -46 days, while those for later-flowering species range from $+3.1$ to $+10.4$ days. Advances of first-flowering in these 89 species are directly correlated with local increase in minimum temperature (T_{\min}).

Key words: first-flowering, global warming, minimum temperature, spring-flowering, Washington DC

Introduction

The effects of global warming in the 20th century, perhaps caused by human activity, have been marked by a rise in the average surface temperature (about 0.6 °C), a 40% thinner arctic ice cover, and increased levels of carbon dioxide in the atmosphere (Houghton et al. 1995). These changes appear to have had a profound effect on the first-flowering times of plants in the Washington, DC, area.

Climate change is an important environmental issue affecting entire ecosystems and, in particular, the dominant plants of a given region (Melillo 1999). Other studies of the natural vegetation indicate that nocturnal global warming may be an important factor in productivity (Alward et al. 1999; Chapin et al. 1995). A study of shortgrass steppe vegetation over a 10-year period shows that the net primary production of a C₄ grass (*Bouteloua gracilis*) was lower with increasing T_{\min} , whereas native and exotic C₃ forbs increased in production and abundance (Alward et al. 1999). Long-term ecological research in the Alaskan arctic indicates that climate change, when simulated by increasing the mean daily air temperature above the vegetation by 3.5 °C, can alter plant species composition (Chapin et al. 1995). Phenological changes in plants have been found in Europe, where leaf-unfolding in spring has advanced 6 days, whereas in

autumn leaf-coloring has been delayed 4.8 days; thus lengthening the average annual growing season by 10.8 days (Menzel and Fabian 1999).

Flowering in angiosperms is an important phenological cycle. Plants in temperate areas, such as the mid-Atlantic region of North America, are adapted to an annual seasonal cycle with a winter dormancy period that is sensitive to temperature and light. Flowering time is directly related with temperature. To investigate potential changes in first-flowering times we examined the first-flowering records of 100 plant species, representing 44 families of angiosperms, for 29 years of the 30-year period 1970–1999 (1984 not recorded) in the Washington, DC, area.

Methods

From a database of first-flowering records for over 600 species, we selected the 100 species with the greatest number (19 or more) of recorded years (Table 1). First-flowering here refers to the stage at which a mono- or diclinous flower begins anthesis or is receptive to pollen. Because Washington, DC, and vicinity (35-mile radius from center of DC; 38°24' to 39°23' N lat., 76°24' to 77°42' W long.) is a large area, and there were many different observers (>125) involved in the recording, in actual practice the date of first-flowering is the observed date and not necessarily the absolute earliest (Shetler and Wiser 1987). Using average first-flowering time per year, we calculated linear trends and their significance, according to the *F*-test and confidence intervals (CI), for the 100 species, the 89 species that exhibit only an earlier flowering, and the 11 species that exhibit only later flowering (Figures 1A–D). The trends for the majority of the species (82%) are statistically significant (Tables 2 and 3).

To investigate potential correlation between flowering trends and environmental factors during the last 30 years, we have calculated linear trends and confidence intervals (CI is reported when significant) for local climate data, including average minimum temperature (T_{\min}), average precipitation (Figures 2A, B), and precipitation per month. In addition, we calculated Pearson's correlation coefficients to test for relationships between T_{\min} and average precipitation versus average first-flowering times (Figures 3A, B). Climate data were obtained from the National Oceanic and Atmospheric Administration, Climate Diagnostics Center at: <http://www.cdc.noaa.gov> (District of Columbia) and: <http://www5.ncdc.noaa.gov> (College Park, Maryland).

Results and discussion

The linear trend of average first-flowering time for all 100 species shows a significant advance of 2.4 days for the 30-year period (Figure 1A; $F = 4.26$ at $P < 0.001$; CI = 2.1 at $P = 0.05$). However, the elimination from the data set of the 11 species that exhibit the later flowering trend results in a significant advance of 4.5 days for the

Table 1. List of species in the study group, and recorded first-flowering in Julian dates from 1970 to 1999 (1984 not available). Species marked with an asterisk (*) are naturalized; all others are native. Nomenclature largely follows Kartesz (1994).

Species	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
<i>Acer negundo</i>	101	94	106		91		101	75	96	90	94
<i>A. rubrum</i>	87	72	65	71	58	56	53	62	92	78	83
<i>A. saccharinum</i>	61	54	45	61	32	18	48	56	79	66	68
* <i>Ajuga reptans</i>							92	93		105	113
<i>Achillea millefolium</i>		149				150		132			145
* <i>Alliaria petiolata</i>	108	108	107	105	90	110	103	104	119	109	104
<i>Alnus serrulata</i>		61	78	97	35	61	65	65	102		
<i>Amelanchier canadensis</i>				97				92	102		
<i>Anemone quinquefolia</i>		115	114				101		107	112	110
<i>Anemonella thalictroides</i>		108	107	84	96	92	88	93	97	98	94
* <i>Anthoxanthum odoratum</i>		122		118							103
<i>Aquilegia canadensis</i>	127	114	123	96	110		95	120	118	112	109
<i>Arisaema triphyllum</i>	117	112	110	107	110	116	119	104	119	109	110
<i>Aronia arbutifolia</i>	129	129		119							125
<i>Asarum canadense</i>	106	111	107	91	97	110	88		115	90	110
<i>Asimina triloba</i>	122	114	120	114	110	123	103	107	119	118	
* <i>Barbarea vulgaris</i>	105	108	107	97	79	110		107	110		
* <i>Capsella bursa-pastoris</i>	129	91		74			68		119	112	1
* <i>Cardamine hirsuta</i>	71	58	73	60	27	61	62	75	80	80	22
<i>Cercis canadensis</i>	122	108	110		95	112	83	88	100	98	107
* <i>Chelidonium majus</i>		115	126	119							
<i>Chionanthus virginicus</i>	127	129	133	132	131		126		119	139	131
<i>Chrysogonum virginianum</i>	127	121	132	119	110		119		119		131
* <i>Cichorium intybus</i>						150				151	145
<i>Claytonia virginica</i>		72	79	77	62	82	67	71	91	87	68
<i>Cornus florida</i>	122	114	120	112	109	114	97	102	132	101	103
<i>Corydalis flavula</i>	101	101	107	91	87	102	103	93	111	109	97
<i>Dentaria laciniata</i> (<i>Cardamine concatenata</i>)	101	81	93	77	69	82	74	78	91	87	97
<i>Dicentra cucullaria</i>	101	101	107	84	90	95	85	78	99	92	97
<i>Dirca palustris</i>				97		79			98	90	83
* <i>Duchesnea indica</i>	119	120	109	108	65			74	119	80	2
<i>Epigaea repens</i>	101	114	100	82	76		81	96	99	90	
<i>Erigenia bulbosa</i>	101	121	79	69	69	60	74	78	91	90	70
* <i>Erodium cicutarium</i>	101	94	107	91	90	82	85	86	99	90	94
<i>Euonymus americanus</i>			142				137		131		138
<i>Fragaria virginiana</i>		129	109	97		111	95	102		111	
<i>Gallium aparine</i>	122	114	120	120			119	121	119	112	
<i>Geranium maculatum</i>		111	114	105	110		110	121	109	111	125
* <i>Glechoma hederacea</i>		101	107	105	92	95	67	72	98	97	97
<i>Hepatica americana</i> (<i>Anemone americana</i>)	101	101	82	68	62	61	73	72	91	88	83
<i>Houstonia caerulea</i>	101	111	107	84	53	103	73	92	99	104	95
<i>Ilex opaca</i>	137		134	142	128				142		131
<i>Kalmia latifolia</i>		146	145	147		150	137	125			138
* <i>Lanium amplexicaule</i>	35	101	103	74	27	108	54	75	101	2	2
* <i>L. purpureum</i>	93	73	85	60	58		81	75	99	90	97
<i>Lindera benzoin</i>	101	94	93	77	83	95	67	72	91	90	97
<i>Liquidambar styraciflua</i>								111			115
<i>Liriodendron tulipifera</i>	139	133	135	125	122	141	112	118	136	132	131
<i>Lonicera japonica</i>			143	116		150	126	132		132	
<i>Maianthemum canadense</i>				119							125
* <i>Melilotus officinalis</i>		141				143	137	126			
<i>Mertensia virginica</i>	101	101	104	91	90	95	72	97	99	90	97

Table 1. Continued.

Species	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
<i>Nyssa sylvatica</i>				147	143		141		136		138
<i>Osmorhiza claytonii</i>	122	121	110	114			112	113		118	
<i>Panax trifolius</i>	106	107		91				102		112	110
* <i>Paulownia tomentosa</i>	129	121	124	114	114	128	103	109	126	126	123
<i>Phlox divaricata</i>	112	101	107	105	90		101	104	103	104	97
<i>P. subulata</i>	98	87	101	86		82	82	82	99	93	
* <i>Plantago lanceolata</i>					124		118	136			125
* <i>Poa annua</i>	117		95		24			74		80	79
<i>Podophyllum peltatum</i>	122	114	126	118	110	123	105	113	119	118	125
<i>Polygonatum biflorum</i>		148			124						131
<i>Potentilla canadensis</i>	98	114	107		110				119	112	104
<i>Prunus serotina</i>		135	133	125	121	135	103	117	137	126	126
<i>P. serrulata</i> **						110	103	101	114	106	118
<i>P. × yedoensis</i> **	107	99	102	102	94	94	83	86	103	93	97
<i>Ranunculus abortivus</i>	106	101	107	91	90	102	81	78	105	97	97
* <i>Ranunculus bulbosus</i>	129	113	101	86	107	120	103				
<i>Rhododendron periclymenoides</i>		117	134	114	130		112	109	122		125
<i>Robinia pseudoacacia</i>		135	130	125	122	135		109	135	126	126
* <i>Rumex acetosella</i>			109	119		142		115			131
* <i>R. crispus</i>		150				147		124			131
<i>Salvia lyrata</i>	129	134					119			148	125
<i>Sanguinaria canadensis</i>		94	86	77	76	92	73	82	91	87	83
<i>Sassafras albidum</i>		114	106	97	95	103	85	92	109	102	103
<i>Saxifraga virginiana</i>	101	94	100	84	83	96	67	86	101	90	106
<i>Sedum ternatum</i>		115	121	119	124	123		120	119		125
<i>Senecio aureus</i>	106	108	107	105	69		85	104	109	112	97
<i>Smilacina racemosa</i>		135	142	125	124		126	120	133		131
* <i>Solanum dulcamara</i>		129			116	141					131
<i>Staphylea trifolia</i>		115	121	125	110		105		119		110
* <i>Stellaria media</i>	40	50	58	1	23	1		43	82	2	2
<i>S. pubera</i>	106	101	107	91	83		101	104	103	90	
* <i>Taraxacum officinale</i>	32	59	74	1	22	4	1	62	34	80	1
<i>Toxicodendron radicans</i>		150	142				126				138
* <i>Trifolium pratense</i>		130			122			124		125	125
<i>Trillium sessile</i>	101	101	101	97	97		101	93	99	92	96
* <i>Tussilago farfara</i>		94	79	55	55	82	73	65	103	76	83
<i>Ulmus americana</i>	66	63	61	61	32	55	48	63	81	67	72
<i>Uvularia perfoliata</i>		121	126	111	130		115		119		
<i>Vaccinium corymbosum</i>			134				101				
<i>V. stamineum</i>		115	133	119	116		114	125	133		147
* <i>Veronica hederifolia</i>	101	72	85	69	62	61	73	54	95	90	87
<i>Viburnum acerifolium</i>		136	142								
<i>V. prunifolium</i>	124	114	121	114	110		102	107	119	118	117
<i>Viola bicolor (V. rafinesquei)</i>		101	106	84	84	108			107	111	96
<i>V. pubescens</i>	106	114	107	77	110	95	102	93	102	97	104
<i>V. sororia</i>	99	99	107	91	92	95	74	85	99	91	96
<i>V. striata</i>	122	114	110	105	110	110	103	93	109	109	110
<i>Zizia aurea</i>		139	114	107	110		101		119	90	
Average first-flowering/year	105	109	109	97	90	100	93	95	108	99	102

Table 1. Continued.

Species	1981	1982	1983	1985	1986	1987	1988	1989	1990	1991	1992
<i>Acer negundo</i>	94	98	92	89	91	94	94	93	90	90	81
<i>A. rubrum</i>	59	76	64	62	74	66	65	23	42	54	61
<i>A. saccharinum</i>	48	55	50	55	74	60		51	41	96	54
<i>Ajuga reptans</i>	115	107	100	89	96	101	93	98	76		109
<i>Achillea millefolium</i>	144	132	144	132	137	143	143	149	133	131	152
<i>Alliaria petiolata</i>		101	106	101	110	102	95		84	97	110
<i>Alnus serrulata</i>	58	70	72	68	81	64	72	51	42		61
<i>Amelanchier canadensis</i>	95	108	100	89	96	94	94	91	76	90	101
<i>Anemone quinquefolia</i>		107	113	89	96		93	91	91	96	102
<i>Anemone thalictroides</i>	102	94	116	101		94			78	104	96
<i>Anthoxanthum odoratum</i>	109	108	113	103	102	104	100	106	97	96	109
<i>Aquilegia canadensis</i>	101	103	114	96	109	101	100	98	87		
<i>Arisaema triphyllum</i>		111	113	102	95	116	107			110	
<i>Aronia arbutifolia</i>	109	122	130	104	109	109	107	115	91	104	116
<i>Asarum canadense</i>	108	114	104	102	95	102	100	98	91	110	116
<i>Asimina triloba</i>			130	110	109	116	107	115	104	104	116
<i>Barbarea vulgaris</i>		107	106	96	102	102	94		90	100	102
<i>Capsella bursa-pastoris</i>	87	95	92	94	96		72	63	50	83	100
<i>Cardamine hirsuta</i>	74	71	1	68	81	66	33	51	42	40	54
<i>Cercis canadensis</i>	94	108		100	95	104	97	98	76	96	
<i>Chelidonium majus</i>	109	114	130	110	109	109	107	106	118	110	116
<i>Chionanthus virginicus</i>	129	128	134	117	123	129	128	127	117	124	131
<i>Chrysogonum virginianum</i>	129			96	96	87	93	98	91	40	
<i>Cichorium intybus</i>	144	142	149	128	133	136	143	140	132	131	145
<i>Claytonia virginica</i>	79	83	50	69	69	80	73	70	52	40	
<i>Cornus florida</i>	109	114	110		109	111	97	115	104		116
<i>Corydalis flavula</i>	88	103	84	89	95	87	87		97	83	
<i>Dentaria laciniata</i>	85	85	79	73	89	87	87	85		62	96
<i>Dicentra cucullaria</i>	102	86	81	87	89	94			91	90	102
<i>Dirca palustris</i>	74	86	72	68	81	80	79	78	69	68	81
<i>Duchesnea indica</i>	83	7	72	69	102	87	87	77	51	33	96
<i>Epigaea repens</i>	85	107			103	102	87	98			
<i>Erigenia bulbosa</i>	60	68	64	69	76	77	73			53	
<i>Erodium cicutarium</i>	85	94	84	95	88	94	93	85	72	90	96
<i>Euonymus americanus</i>	136	142	149	124	130	136	142	140	126	131	137
<i>Fragaria virginiana</i>	101	107	106	75	96	122	100	106	76	40	109
<i>Galium aparine</i>		122		118		109	122	113	84	118	122
<i>Geranium maculatum</i>	101	114	113	110	95	109	100	106	90	104	116
<i>Glechoma hederacea</i>	74	84	79	75	88	73	87	91	76	75	96
<i>Hepatica americana</i>		86	9	69	74	87	72	78	50	83	96
<i>Houstonia caerulea</i>	94	115	92	96	98	102	107	120	97	100	116
<i>Ilex opaca</i>	128	132	131	119	127	129	134	131	120	121	132
<i>Kalmia latifolia</i>	136	135	146	124	130	136	142	140		131	145
<i>Lamium amplexicaule</i>	80	7	64	73	89	70			50	75	81
<i>L. purpureum</i>	81	94	36	61	81	73	73	63	50	40	61
<i>Lindera benzoin</i>	87	85	79	75	89	87	87	92		83	81
<i>Liquidambar styraciflua</i>	109	114	130	110	109	111	108	113	97	100	110
<i>Liriodendron tulipifera</i>	115	128	127	117	123	122	126	127	118	118	131
<i>Lonicera japonica</i>	136	107	142	128	137	141	142	140	127	132	145
<i>Maianthemum canadense</i>	109	122	127	117	137	129	121	120	118	117	123
<i>Melilotus officinalis</i>	123	128	133	138	129	135		135	123	129	137
<i>Mertensia virginica</i>	85	94	79	58	89	94	87	92	72	83	

Table 1. Continued.

Species	1981	1982	1983	1985	1986	1987	1988	1989	1990	1991	1992
<i>Nyssa sylvatica</i>	123	128	127	124	130	129	121	120	118	118	123
<i>Osmorhiza claytonii</i>	108		106	111	130	122		120		117	123
<i>Panax trifolius</i>	122	127	113	96	96	94	93	91	91	96	102
<i>Paulownia tomentosa</i>	122		126	131	118	120	121		112		131
<i>Phlox divaricata</i>	102	114	71	87	103	94	107	98	91	104	102
<i>P. subulata</i>	81	80	64	68	33	67	80	92		68	89
<i>Plantago lanceolata</i>	115	122	124	110	116	109	122	121	117	104	116
<i>Poa annua</i>	105	95	74	71	76	93	85	52	50	61	99
<i>Podophyllum peltatum</i>	108	122	130	111	109	111	107	115		104	116
<i>Polygonatum biflorum</i>	123	128	127	117	130	129	128	127	122	124	137
<i>Potentilla canadensis</i>	109	107	106	110	109	102	100		90	100	110
<i>Prunus serotina</i>	119	125	127	115	123	127	129	127	118	118	132
<i>P. serrulata</i>	119	117	102	106	105	98	100	97	92	99	108
<i>P. × yedoensis</i>	94	98	98	98	93	88	91	89		89	98
<i>Ranunculus abortivus</i>	94	101	106	96	96	87	87	85	97	96	102
<i>R. bulbosus</i>	122	127	100		113		95	106	90	90	109
<i>Rhododendron periclymenoides</i>	115	122	130	111	116	116	107	115	104	104	116
<i>Robinia pseudoacacia</i>	119	129	130	115	122	127	128	123	117	118	132
<i>Rumex acetosella</i>	112	114	92	117	114	101	108	106	118	110	116
<i>R. crispus</i>		149		120	137	128	142	124	123	121	134
<i>Salvia lyrata</i>	136	128		117	123	122	121	120	118	124	123
<i>Sanguinaria canadensis</i>	85	86	92	88	89	80	87	77		83	
<i>Sassafras albidum</i>	101	107	106	95	96	101	100	98	76	96	109
<i>Saxifraga virginiana</i>	85		79	110	89		95		80	96	102
<i>Sedum ternatum</i>	130	122	127	117	123	135		118	124	123	122
<i>Senecio aureus</i>		127	92	110	95	104	93	92	76	83	96
<i>Smilacina racemosa</i>	130	127	131	124	130	129	135	127	122	124	131
<i>Solanum dulcamara</i>	129	135	128	118	137	130	130	127	133		144
<i>Staphylea trifolia</i>	101	114	113	103	102	109	114	120			116
<i>Stellaria media</i>	53	7	1	61	74	61	39	34	40	33	61
<i>S. pubera</i>	108	107	79	96	88	94		106		96	102
<i>Taraxacum officinale</i>	71	7	1	1	76	46			28		54
<i>Toxicodendron radicans</i>	133	135	134	118	137	134		140	132	129	137
<i>Trifolium pratense</i>	115	122	127	110	116	114	121	123	118	110	131
<i>Trillium sessile</i>		94	106		95		85	110	102	107	106
<i>Tussilago farfara</i>	58	78	64	55	88	66	53	77	50		
<i>Ulmus americana</i>	54	68	64	59	76	64	67	62	51	56	65
<i>Uvularia perfoliata</i>	130		126		130	122	114	115		104	123
<i>Vaccinium corymbosum</i>	101	107	131	89	96	94	100	91	76	96	109
<i>V. stamineum</i>	123	128	134	124	123	136	135	120	122	124	131
<i>Veronica hederifolia</i>	74	80	78	76		67	73		48		
<i>Viburnum acerifolium</i>	143	142	134	124	130	129	135	134	126	131	137
<i>V. prunifolium</i>		114	130	103	109	116	107		97	104	116
<i>Viola bicolor</i>	88	94		89	89	88	87		76	83	96
<i>V. pubescens</i>		122	106		89		95		97	96	
<i>V. sororia</i>	88	93	92	89	88	87	87	89	76	76	96
<i>V. striata</i>			106	89	96			133		96	
<i>Zizia aurea</i>			84	73	95		121	120			102
Average first-flowering/year	102	104	100	96	103	102	102	102	90	96	109

Table 1. Continued.

Species	1993	1994	1995	1996	1997	1998	1999
<i>Acer negundo</i>	101	85	84	97	81	87	93
<i>A. rubrum</i>	68	73	69	67	61	39	44
<i>A. saccharinum</i>	66		57	56	53	52	44
<i>Ajuga reptans</i>	115	99	98	111		103	115
<i>Achillea millefolium</i>	150	141		140	120	122	142
<i>Alliaria petiolata</i>	105		97	104	95	95	93
<i>Alnus serrulata</i>	66	79	70	67	61		44
<i>Amelanchier canadensis</i>	102	95	94	96	88		94
<i>Anemone quinquefolia</i>	101	99	98	104	88	109	100
<i>Anemonella thalictroides</i>	97	99		90	88	74	98
<i>Anthoxanthum odoratum</i>	108	106	98	111	95	94	100
<i>Aquilegia canadensis</i>		105	105	111	95	94	100
<i>Arisaema triphyllum</i>	105	106	106	110	102	100	100
<i>Aronia arbutifolia</i>	115	113	112	118	102	101	113
<i>Asarum canadense</i>	108	106	95	108	95	100	98
<i>Asimina triloba</i>	115	106	105	111	95	101	100
<i>Barbarea vulgaris</i>	108	105	105	104	95	102	94
<i>Capsella bursa-pastoris</i>	96	93	85	104	88	59	93
<i>Cardamine hirsuta</i>	16		21	56	4	11	44
<i>Cercis canadensis</i>	109	102	99	111	94	91	95
<i>Chelidonium majus</i>	115	106	105	104		101	113
<i>Chionanthus virginicus</i>		120	126		123	115	133
<i>Chrysogonum virginianum</i>	101	113	98	122	102	101	100
<i>Cichorium intybus</i>	143	141	140	140	144	137	142
<i>Claytonia virginica</i>	67	92	78	84	67	45	79
<i>Cornus florida</i>	115	107	109	112	103	95	113
<i>Corydalis flavula</i>			98	104		81	93
<i>Dentaria laciniata</i>	94	92	85		75	74	93
<i>Dicentra cucullaria</i>	97	99	91	90	88	87	93
<i>Dirca palustris</i>	87				68	73	87
<i>Duchesnea indica</i>	65	93	85		66	47	23
<i>Epigaea repens</i>			92	112	95	80	93
<i>Eriogenia bulbosa</i>					75	66	93
<i>Erodium cicutarium</i>	94	99	85	90	88	87	93
<i>Euonymus americanus</i>	135			140	138	129	142
<i>Fragaria virginiana</i>	128	99		111	88	87	87
<i>Galium aparine</i>	107	128	119	125	124	108	128
<i>Geranium maculatum</i>	108	105	105	111	103	101	100
<i>Glechoma hederacea</i>	93	92		97	75	87	87
<i>Hepatica americana</i>	30	85	1	73	61	59	87
<i>Houstonia caerulea</i>		106	92		95	87	93
<i>Ilex opaca</i>	121	118	131	135	138	127	135
<i>Kalmia latifolia</i>	135	134	140	140	138	129	135
<i>Lamium amplexicaule</i>		92		97	68	14	79
<i>L. purpureum</i>	45	79	57	67	61	24	30
<i>Lindera benzoin</i>	93	85	78	91	68	81	87
<i>Liquidambar styraciflua</i>	109	107	106	119	110	101	114
<i>Liriodendron tulipifera</i>	127	120	126	125	123	108	128
<i>Lonicera japonica</i>	139	138	138	146	145	136	136
<i>Maianthemum canadense</i>	128	120	119	121	116	109	121
<i>Melilotus officinalis</i>	133	126	133	138	140	133	146
<i>Mertensia virginica</i>	100		84	90	75	66	87

Table 1. Continued.

Species	1993	1994	1995	1996	1997	1998	1999
<i>Nyssa sylvatica</i>		120	126	119	116	101	113
<i>Osmorhiza claytonii</i>	121	120	119	118	116	108	121
<i>Panax trifolius</i>	101		91	97	88	94	93
<i>Paulownia tomentosa</i>			112	125	103	114	121
<i>Phlox divaricata</i>	108	106	106	111	95	94	100
<i>P. subulata</i>	71	93		76	69	87	93
<i>Plantago lanceolata</i>	115	126	116	125	110	102	107
<i>Poa annua</i>		73	71	76	68	45	79
<i>Podophyllum peltatum</i>	115	113	112	118	109	101	114
<i>Polygonatum biflorum</i>		128	133	125	117	109	128
<i>Potentilla canadensis</i>	108	106	96	111	109	101	94
<i>Prunus serotina</i>	128	120	126	125	128		129
<i>P. serrulata</i>	121	109	106	113	99	96	111
<i>P. × yedoensis</i>	102	96	93	93	86	87	96
<i>Ranunculus abortivus</i>	100	99		104	88		93
<i>R. bulbosus</i>	100	106	84	118	81	24	114
<i>Rhododendron periclymenoides</i>	119	106	112	118	106	101	114
<i>Robinia pseudoacacia</i>		118	126	125	127	115	128
<i>Rumex acetosella</i>	115	113	112	126	117	109	
<i>R. crispus</i>	136	128	127	122	140	116	128
<i>Salvia lyrata</i>	128	120	126	125	123	109	121
<i>Sanguinaria canadensis</i>		92	77	76	60	74	79
<i>Sassafras albidum</i>		103	97	105	86	95	98
<i>Saxifraga virginienensis</i>						74	93
<i>Sedum ternatum</i>	120		113	122	116	105	142
<i>Senecio aureus</i>	107	106	91	112	88	87	94
<i>Smilacina racemosa</i>	128	120	133	132	130	122	128
<i>Solanum dulcamara</i>	131	135	127			114	136
<i>Staphylea trifolia</i>	121	113	113	118	109	108	100
<i>Stellaria media</i>	2		1	30	4	8	25
<i>S. pubera</i>		106	113	104	95	94	93
<i>Taraxacum officinale</i>	2		1	56	4	1	
<i>Toxicodendron radicans</i>	130	128	140	140	138	129	135
<i>Trifolium pratense</i>	121	113	113	125	117	115	121
<i>Trillium sessile</i>				110	102	100	94
<i>Tussilago farfara</i>	101	72	57	90	61	59	79
<i>Ulmus americana</i>	68		74	56	55	50	41
<i>Uvularia perfoliata</i>	115	99	113	118	117		128
<i>Vaccinium corymbosum</i>	108	105	96	104	95	87	94
<i>V. stamineum</i>		120	119	118	103	95	114
<i>Veronica hederifolia</i>	80		77		61	45	79
<i>Viburnum acerifolium</i>	128	120	133	132	130	122	128
<i>V. prunifolium</i>	115	113	113	118	103	101	107
<i>Viola bicolor</i>	97	99	85	104	88	87	93
<i>V. pubescens</i>	115			104	95		93
<i>V. sororia</i>	97	93	85	90	81	87	79
<i>V. striata</i>	108	106	98		89	94	100
<i>Zizia aurea</i>	108	113	98	125	75	81	87
Average first-flowering/year	103	107	99	107	94	89	100

** Cultivated, data obtained from <http://www.nps.gov/nacc/cherry/dates.htm>

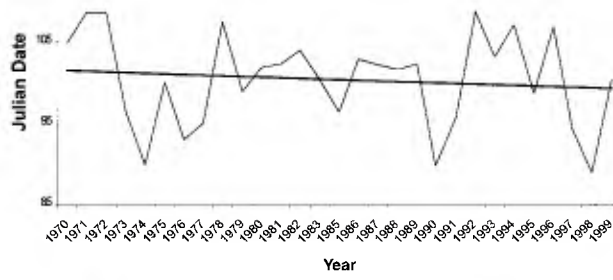
30-year period (Figure 1B; $F = 4.19$ at $P < 0.001$; $CI = 2.2$ at $P = 0.05$). The trends for the 89 earlier-flowering species taken individually range from -0.2 to -46 days, while those for the 11 later-flowering species range from $+0.3$ to $+10.4$ days. The 76 species of the 89 that individually exhibit a significant advance (Table 2) together show an average decrease of -5.6 days for the 30-year period ($F = 3.41$ at $P < 0.001$; $CI = 2.2$ at $P = 0.05$). Of these 76, *Duchesnea indica* (false strawberry) shows the greatest advance in flowering time, with a trend of -46 days ($CI = 12.45$ at $P = 0.05$, Figure 1C), whereas *Dicentra cucullaria* (Dutchman's-breeches) shows the smallest advance with a trend of -3.2 days ($CI = 2.67$ at $P = 0.05$, Figure 1C). Six (55%) of the eleven species show significant delays in first-flowering (Table 3); of these, *Lonicera japonica* (Japanese honeysuckle) has a trend of $+10.4$ days ($CI = 3.88$ at $P = 0.05$, Figure 1D), and *Osmorhiza claytonii* (sweet-cicely) has a trend of $+3.1$ days ($CI = 2.49$ at $P = 0.05$, Figure 1D). The 11 species exhibiting later first-flowering times are (* marks naturalized species): *Acer saccharinum*, **Ajuga reptans*, *Houstonia caerulea*, **Lamium amplexicaule*, **Lonicera japonica*, **Melilotus officinalis*, *Osmorhiza claytonii*, *Sedum ternatum*, **Solanum dulcamara*, *Stellaria pubera*, *Trillium sessile*.

From 1970 to 1999, the average T_{\min} for December–May, covering the recorded season of first-flowering, shows an increase of $+1.2$ °C ($CI = 0.35$ at $P = 0.05$) at College Park, Maryland (CP), and $+0.2$ °C at Washington, District of Columbia (DC) (Figure 2A). The monthly average precipitation for the six-month period at DC has increased $+0.6$ cm while it has decreased -1.1 cm at CP ($CI = 0.67$ at $P = 0.05$), (Figure 2B). After surveying the precipitation by month it appears that both stations show a decrease in precipitation during December (-0.7 cm for DC; -1.6 cm for CP), February (-0.2 cm for DC; -1.9 cm for CP), April (-0.6 cm for DC; -1.3 cm for CP), and May (-1.1 cm for DC; -0.8 cm for CP); whereas an increase in precipitation is seen in January ($+1.7$ cm for DC; $+0.2$ cm for CP) and March ($+1.8$ cm for DC and CP).

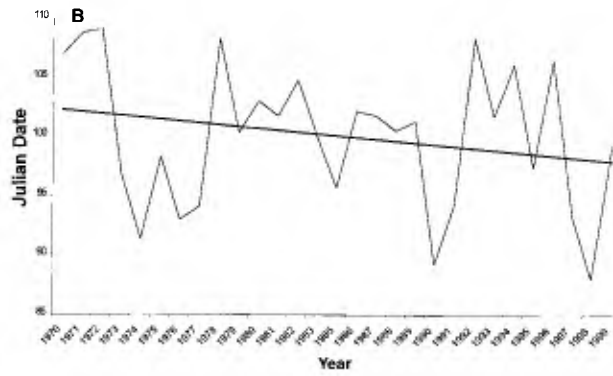
Average flowering time (in Julian date) per year of the 100 species shows a negative correlation with T_{\min} over the studied period (Figure 2A, $r = -0.58$ at $P = 0.01$ for DC; $r = -0.48$ at $P = 0.02$ for CP, Figure 3A), and a stronger negative correlation with T_{\min} for the 89 earlier-flowering species (Figure 3B; $r = -0.59$ at $P = 0.002$ for DC; $r = -0.53$ at $P = 0.01$ for CP, Figure 3B). No significant correlation was found between first-flowering and precipitation trends.

Although the onset of flowering in most plants is cued by photoperiodism, break of dormancy is triggered by temperature (Salisbury and Ross 1992). As the annual photoperiodic cycle presumably has not changed during the last 30 years, we must assume that other factors, such as temperature and precipitation, are causing earlier spring flowering. Our analysis suggests that trends toward earlier flowering are the result of a warming trend in the study area. This warming trend, $+1.2$ °C at CP, coincides with the global warming trend (Easterling et al. 1997). However, we cannot eliminate other causal factors not investigated by our study, such as CO_2 , as being

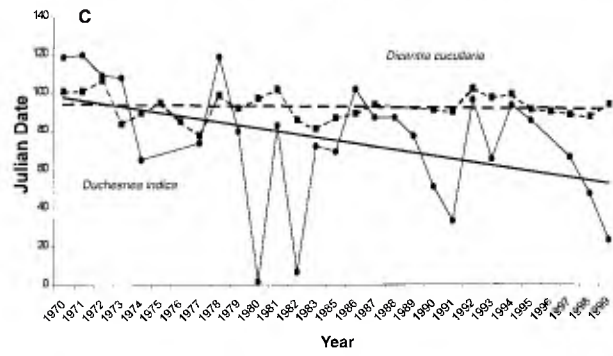
115 A



B



C



D

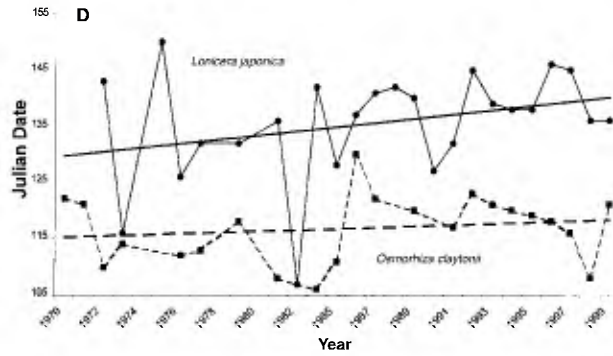


Figure 1. Average first-flowering times (Julian dates) for plants in the Washington, DC, area for 1970–1999. Bold line represents the trend and regular line indicates the average. (A) For all 100 plant species, (B) for 89 earlier-flowering plant species, (C) two species showing the most and the least advances in first-flowering: *Duchesnea indica* (solid lines) and *Dicentra cucullaria* (dashed lines), (D) two species showing the most and the least delays in first-flowering: *Lonicera japonica* (solid lines) and *Osmorhiza claytonii* (dashed lines).

Table 2. Species with statistically significant advances (in days) of first-flowering.

Species	Advance in flowering in days	SD	CI	No. of years on record
<i>Acer negundo</i>	9.06	6.88	2.59	27
<i>A. rubrum</i>	19.13	14.54	5.29	29
<i>Achillea millefolium</i>	11.79	9.05	3.87	21
<i>Alliaria petiolata</i>	11.00	7.53	2.90	26
<i>Alnus serrulata</i>	11.34	15.21	6.08	24
<i>Amelanchier canadensis</i>	6.39	6.62	2.90	20
<i>Anemone quinquefolia</i>	15.49	8.42	3.52	22
<i>Anemonella thalictroides</i>	8.37	9.21	3.69	24
<i>Anthoxanthum odoratum</i>	19.38	7.39	3.16	21
<i>Aquilegia canadensis</i>	17.70	10.07	3.95	25
<i>Arisaema triphyllum</i>	10.78	6.18	2.42	25
<i>Aronia arbutifolia</i>	19.77	10.00	4.18	22
<i>Asimina triloba</i>	14.35	8.14	3.13	26
<i>Barbarea vulgaris</i>	3.27	7.31	2.93	24
<i>Cardamine hirsuta</i>	41.74	24.55	9.09	28
<i>Cercis canadensis</i>	9.05	9.79	3.76	26
<i>Chelidonium majus</i>	14.63	7.29	3.20	20
<i>Chionanthus virginicus</i>	7.49	5.96	2.33	25
<i>Chrysogonum virginianum</i>	31.09	20.07	8.20	23
<i>Cichorium intybus</i>	8.24	6.17	2.64	21
<i>Claytonia virginica</i>	8.45	13.11	4.95	27
<i>Cornus florida</i>	7.18	8.17	3.08	27
<i>Corydalis flavula</i>	10.75	8.60	3.44	24
<i>Dicentra cucullaria</i>	3.19	7.07	2.67	27
<i>Dirca palustris</i>	15.99	9.08	3.98	20
<i>Duchesnea indica</i>	45.95	32.39	12.45	26
<i>Eriogenia bulbosa</i>	15.10	15.31	6.40	22
<i>Erodium cicutarium</i>	4.81	6.74	2.45	29
<i>Fragaria virginiana</i>	19.89	18.76	7.50	24
<i>Geranium maculatum</i>	10.83	7.46	2.81	27
<i>Glechoma hederacea</i>	9.65	11.09	4.18	27
<i>Hepatica americana</i>	23.51	24.21	8.97	28
<i>Ilex opaca</i>	7.23	6.75	2.70	24
<i>Kalmia latifolia</i>	7.72	6.88	2.75	24
<i>Lamium purpureum</i>	39.31	20.29	7.52	28
<i>Lindera benzoin</i>	6.39	8.51	3.15	28
<i>Liquidambar styraciflua</i>	8.72	7.00	3.07	20
<i>Liriodendron tulipifera</i>	10.18	7.81	2.84	29

Table 2. Continued.

Species	Advance in Flowering in days	SD	CI	No. of years on record
<i>Maianthemum canadense</i>	4.94	6.45	2.83	20
<i>Mertensia virginica</i>	17.25	11.40	4.30	27
<i>Nyssa sylvatica</i>	35.50	10.72	4.48	22
<i>Panax trifolius</i>	17.29	10.46	4.28	23
<i>Paulownia tomentosa</i>	4.23	8.05	3.22	24
<i>Phlox subulata</i>	11.99	14.62	5.73	25
<i>Plantago lanceolata</i>	16.77	8.17	3.41	22
<i>Poa annua</i>	20.40	20.72	8.47	23
<i>Podophyllum peltatum</i>	9.04	7.00	2.59	28
<i>Polygonatum biflorum</i>	13.10	7.93	3.48	20
<i>Potentilla canadensis</i>	8.04	6.76	2.70	24
<i>Prunus serrulata</i>	5.70	7.94	3.18	24
<i>P. × yedoensis</i>	6.97	5.88	2.18	28
<i>Ranunculus bulbosus</i>	26.97	21.61	8.83	23
<i>Rhododendron periclymenoides</i>	15.31	8.43	3.24	26
<i>Robinia pseudoacacia</i>	5.70	6.69	2.57	26
<i>Rumex acetosella</i>	7.06	10.02	4.19	22
<i>R. crispus</i>	18.81	10.11	4.43	20
<i>Salvia lyrata</i>	13.66	7.78	3.25	22
<i>Sanguinaria canadensis</i>	10.66	7.86	3.08	25
<i>Sassafras albidum</i>	6.58	8.10	3.06	27
<i>Senecio aureus</i>	8.65	12.59	4.75	27
<i>Smilacina racemosa</i>	3.61	5.13	1.97	26
<i>Staphylea trifolia</i>	4.78	6.92	2.83	23
<i>Stellaria media</i>	14.53	25.69	9.69	27
<i>Taraxacum officinale</i>	20.21	29.67	11.87	24
<i>Toxicodendron radicans</i>	5.41	6.71	2.87	21
<i>Trifolium pratense</i>	8.29	6.01	2.45	23
<i>Uvularia perfoliata</i>	7.64	8.50	3.73	20
<i>Vaccinium corymbosum</i>	25.80	13.45	5.89	20
<i>V. stamineum</i>	12.96	10.88	4.26	25
<i>Veronica hederifolia</i>	14.73	14.00	5.72	23
<i>Viburnum acerifolium</i>	14.26	6.38	2.80	20
<i>V. prunifolium</i>	9.03	7.77	2.99	26
<i>Viola bicolor</i>	9.27	9.23	3.69	24
<i>V. sororia</i>	11.67	7.65	2.79	29
<i>V. striata</i>	13.62	10.50	4.39	22
<i>Zizia aurea</i>	20.07	17.78	7.79	20

SD – standard deviation; CI – confidence interval.

important in regulating spring flowering. Likewise, we are unable to explain why 11 species exhibit later first-flowering times. At this time, we have compelling evidence that the rise in the average minimum temperatures (T_{\min}) is contributing to earlier flowering in 89 of the 100 species investigated. Our results are consistent with other studies showing that changes in air temperature have advanced the average annual

Table 3. Species with statistically significant delays (in days) of first-flowering.

Species	Delay in flowering in days	SD	CI	No. of years on record
<i>Acer saccharinum</i>	6.66	14.66	5.53	27
<i>Ajuga reptans</i>	9	10.19	4.47	20
<i>Houstonia caerulea</i>	6.89	13.46	5.08	27
<i>Lonicera japonica</i>	10.41	9.70	3.88	24
<i>Osmorhiza claytonii</i>	3.13	5.95	2.49	22
<i>Trillium sessile</i>	4.38	6.16	2.58	22

SD – standard deviation; CI – confidence interval.

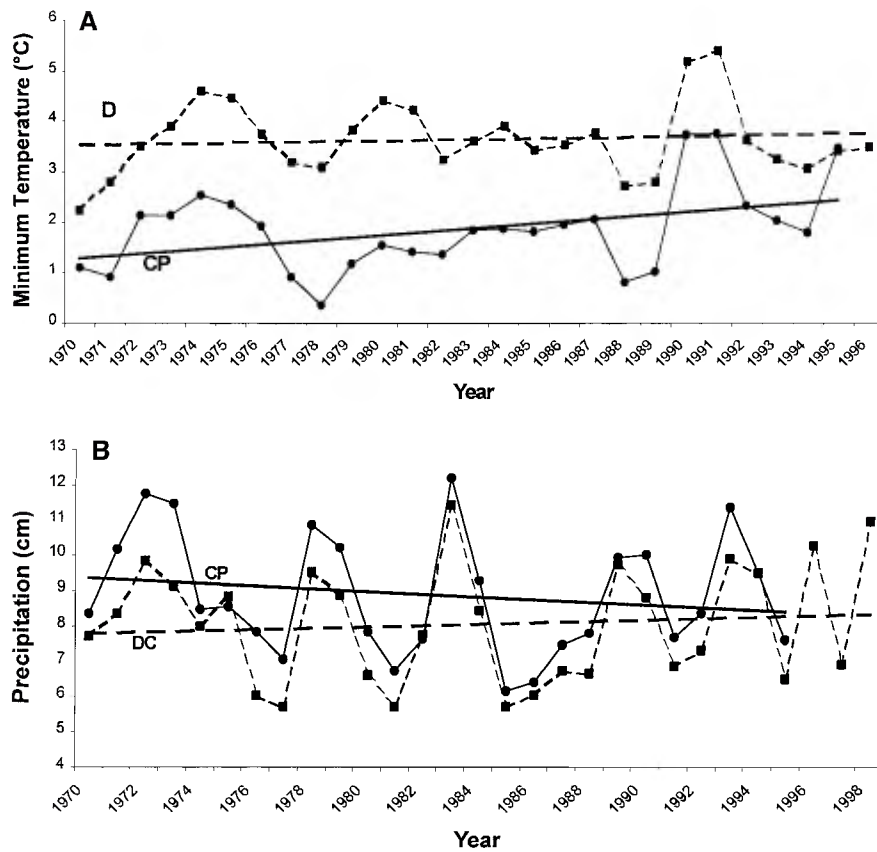


Figure 2. Climate data and their trends for Washington, DC (DC), and College Park, Maryland (CP), for 1970–1999. Solid lines with circles represent CP averages, and dashed lines with squares indicate DC averages. (A) Average minimum temperature (T_{\min}) for 6 months (December–May). Trend line equation: $y = 0.0456x + 1.2342$ (CP); $y = 0.0077x + 3.5331$ (DC). (B) Average precipitation for the same period. Trend line equation: $y = -0.039x + 9.402$ (CP); $y = 0.0188x + 7.788$ (DC).

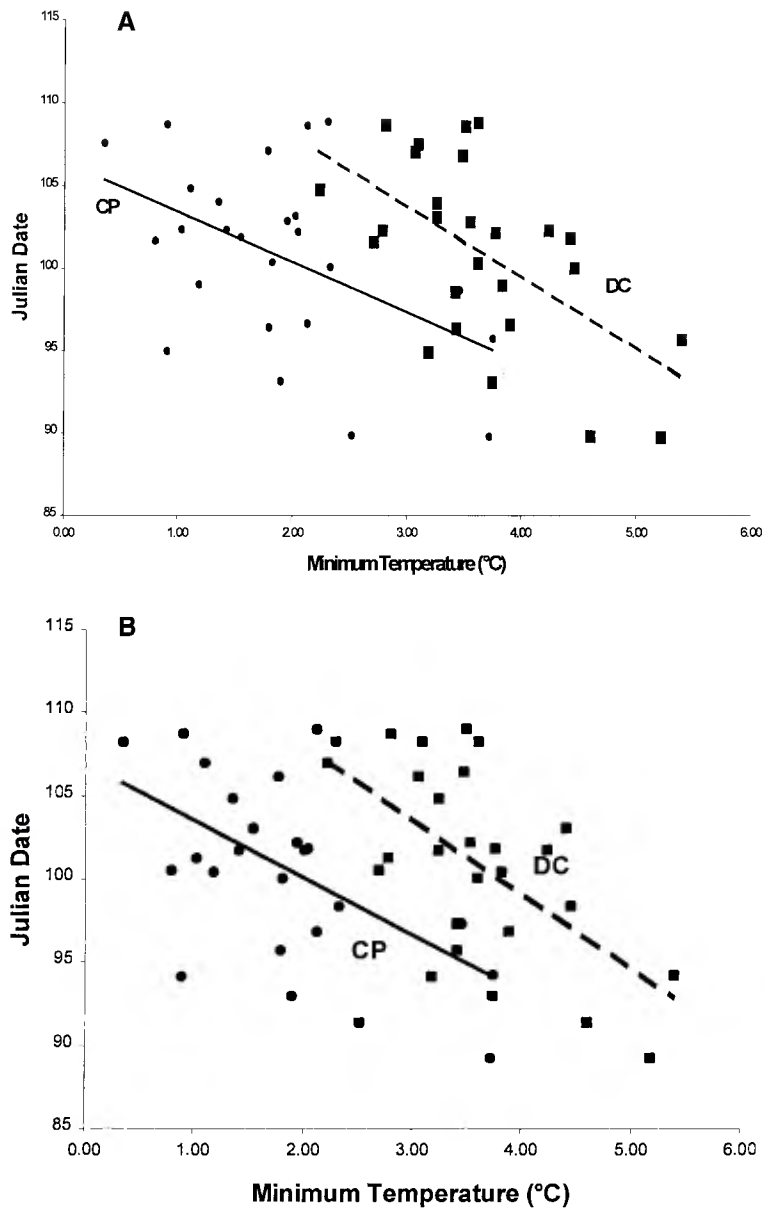


Figure 3. Correlation between average first-flowering dates and average T_{\min} (December–May) for DC and CP. Solid lines represent CP and dashed lines indicate DC regression trends; circles indicate CP averages and squares indicate DC averages. (A) All 100 species. (B) 89 earlier-flowering species.

growing season by six days in Europe and that warmer temperatures and higher CO_2 levels have promoted summer plant growth, thereby advancing the season by seven days in northern latitudes (Menzel and Fabian 1999).

Possible consequences of the warming and earlier-flowering trends should be investigated. Previous studies of our database (Shetler and Wiser 1987) showed that the earliest non-cultivated plants to flower in the Washington Area are predominantly naturalized introductions, such as common chickweed (*Stellaria media*), dandelion (*Taraxacum officinale*), and henbit (*Lamium amplexicaule*). They can exploit the slightest bit of warmth during the cold season to bloom quickly. The warming trend yielding milder winters is likely to favor increasingly the naturalization of exotic species. The introduced element already appears to constitute about 40% of the local flora (Shetler and Orli 2000), and clearly it has been rising steadily over the years.

Spring ephemerals require a tight synchrony with their pollinators, and the effects of earlier flowering on this relationship should be studied. Are the insects keeping pace? Likewise, the synchrony of the flowering cycles of the ephemerals with canopy closure needs examination. Of practical consequence is the earlier flowering of wind-pollinated trees and shrubs, which starts the season for allergy-sufferers earlier. Finally, there is the Cherry Blossom Festival in Washington DC, each spring. On average the two principal species, *Prunus serrulata* (Kwanzan cherry and other varieties) and *P. yedoensis* (Yoshino cherry), bloom 6 and 7 days earlier, respectively, than they did in 1970. This has major tourist implications, as predicting peak-flowering becomes more and more problematic.

Acknowledgements

We thank the more than 125 persons who contributed first-flowering dates through the years, especially Aaron Goldberg and the late John J. Wurdack; and Jacques Cayouette, Lee-Ann Hayek, Tom Hollowell, Harold Robinson, and Gene Rosenberg for comments that improved the manuscript.

References

- Alward RD, Detling JK and Milchunas DG (1999) Grassland vegetation changes and nocturnal global warming. *Science* 283: 229–231
- Chapin FS, Shaver G, Giblin A, Nadelhoffer K and Laundre J (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694–711
- Easterling DR, Horton B, Jones PD, Peterson TC, Karl TR, Parker DE, Salinger MJ, Razuvayev V, Plummer N, Jamason P and Folland CK (1997) Maximum and minimum temperature trends for the globe. *Science* 277: 364–367
- Houghton JT, Meria Filho LG, Callender B and Harris N (eds.) (1995) *The Science of Climate Change*. Cambridge University Press, Cambridge
- Kartesz JT (1994) *A Synonymized Checklist of the United States, Canada, and Adjacent Greenland*, 2nd edn. (2 vols.) Timber Press, Portland, Oregon
- Melillo JM (1999) Climate change: warm, warm on the range. *Science* 283: 183–184
- Menzel A and Fabian P (1999) Growing season extended in Europe. *Nature* 397: 659
- Salisbury FB and Ross CW (1992) *Plant Physiology*, 4th edn., Wadsworth Publishing Company, Belmont

- Shetler SG and Orli SS (2000) Annotated Checklist of the Vascular Plants of the Washington–Baltimore Area. Part I. Ferns, Fern Allies, Gymnosperms, and Dicotyledons. Smithsonian Institution (National Museum of Natural History, Department of Botany), Washington, DC
- Shetler SG and Wiser SK (1987) First flowering dates for spring-blooming plants of the Washington, DC, area for the years 1970 to 1983. *Proceedings of the Biological Society of Washington* 100: 993–1017