Lunch CK. 2009. Primary production at Jasper Ridge Biological Preserve, in *Jasper Ridge Biological Preserve State of the Preserve Assessment*, Chiariello N (ed). Jasper Ridge Biological Preserve, Stanford University.

Primary production at Jasper Ridge Biological Preserve

Introduction

Primary production is the total amount of biomass produced directly by solar energy in an ecosystem; in most terrestrial ecosystems, this is very closely approximated by the total amount of biomass produced by plants. There are many factors that influence the efficiency with which plants convert solar energy into biomass–soil fertility, water availability, temperature, and species being some of the most important. However, to the extent that productivity is the net outcome of all these factors, it provides a useful integrated measure of biological activity in a given ecosystem. In addition, productivity and its limitations are of great interest to humans in certain ecosystems. When humans deliberately manipulate production, they generally aim to increase it, whether for the purpose of food, fuel, building materials, or, more recently, carbon storage. Understanding the controls on productivity has consequences for human economic purposes, while understanding the likely future trajectory of productivity will inform predictions of climate change and its feedbacks.

This review explores the magnitude of, and limitations to, primary production in a specific location, Jasper Ridge Biological Preserve (JRBP), which contains examples of nearly all of the plant communities of central coastal California. Some of these communities, such as redwood forest, are present only in fragmentary patches and have been little studied, whereas others, such as broadleaf forest, chaparral, and grassland, dominate the Jasper Ridge landscape. Of these three, the latter two have been the focus of most studies on productivity. The relative importance of various resources to primary production continues to be explored, building on many decades of research.

Although relatively little research at JRBP has involved regular monitoring of primary production, research at Jasper Ridge has contributed fundamental insights into controls on primary production, particularly within the fields of plant biology and physiology. Areas of research that have been influential on a very broad scale include the allocation and balance of carbon within plants (Mooney et al. 1972, Mooney and Chu 1974), the relationship between photosynthesis and leaf nitrogen content (Field and Mooney 1986), the tradeoffs between acquisition of different resources (Field et al. 1983), and the response of ecosystems to elevated CO_2 (Hungate et al. 1996, Shaw et al. 2002, and many more, see below).

It is difficult to compare the productivity of grasslands and woody vegetation at JRBP, because studies in the two ecosystem types have generally focused on different aspects of production. Although there has been substantial work in both systems on phenology (the timing of growth and activity), chaparral studies have primarily explored growth and carbon uptake at the leaf level, while most of the grassland studies have investigated whole-ecosystem production. Nonetheless, the limited overlapping work suggests that annual net primary production (NPP) is of roughly similar magnitude in both ecosystems. Remote sensing studies find that on sandstone substrates, both types of ecosystem achieve the same peak normalized difference vegetation index (NDVI), the most commonly remotely sensed proxy for photosynthetic biomass (Gamon et al. 1995, Garcia 2003). However, NDVI is fairly insensitive when leaf area index (LAI, the ratio of leaf area to ground area) is greater than two, which it is at the peak of the season in both of these ecosystems (Gamon et al. 1995).

Woody vegetation: oaks and chaparral

Woody vegetation at JRBP varies substantially in stature and structure, from isolated oaks in grasslands to redwood stands to dense chaparral. Studies of productivity have focused on oaks, both inside and outside chaparral, and on a variety of chaparral species. The majority of the woody vegetation grows on non-serpentine soils, with evergreen forest primarily on sandstone-derived soils and chaparral primarily on greenstone-derived soils. However, there are several patches of serpentine chaparral and a few oaks on serpentine soils, and several studies have investigated these. With very few exceptions, studies of woody ecosystems at JRBP have concerned leaf- or plant-level photosynthesis and phenology, rather than whole-ecosystem measures. This choice of focus has generally been practical rather than philosophical, reflecting the limitations of both traditional remote sensing, mentioned above, and also eddy covariance techniques. Woody plant communities at JRBP generally occupy relatively steep terrain with complex topography and heterogeneous microclimates, so they are not well suited to eddy covariance measurement.

Tree and shrub species at Jasper Ridge vary widely in foliar phenology, with multiple examples of evergreens and both winter-deciduous and drought-deciduous shrubs. The evergreens and winter-deciduous species typically flush new leaves in the spring, and conduct the majority of their annual carbon uptake in the spring and early summer. Most evergreen oaks and shrubs maintain LAI greater than 2 throughout the year, so remotely sensed NDVI does not detect annual cycles in these species (Gamon et al. 1995, Garcia 2003). Drought-deciduous species do have detectable seasonal changes in canopy NDVI (Gamon et al. 1995), but winter-deciduous species often do not, probably due to a winter- and spring-active grass understory (Garcia 2003).

Nearly all precipitation falls between October and May, enforcing a November-to-June activity period for drought-deciduous shrubs. The only intensively studied drought-deciduous shrubs are *Lepechinia calycina* (Field 1983, Field and Mooney 1983) and *Mimulus aurantiacus* (formerly *Diplacus aurantiacus*; Mooney et al. 1980, Williams et al. 1985). In *Lepechinia*, specific leaf area (SLA, the ratio of leaf area to leaf mass; roughly, a measure of leaf thinness) declines over the course of the season. This "thickening" of leaves is due to both a decline in SLA over the lifetime of a leaf and to lower SLA in leaves initiated later in the season (Field and Mooney 1983). Photosynthetic rate per unit leaf mass (A_{mass}) declines over the season as well, from 240 nmol CO_2 g^{-1} s^{-1} in January to 90 nmol CO_2 g^{-1} s^{-1} in late May. This change spans approximately one-quarter of the global range in A_{mass}, which is 5 - 662 nmol CO_2 g^{-1} s^{-1} (Wright et al. 2004, Fig. 1). Due to concurrent changes in SLA, photosynthesis per unit leaf area does not change during the season. Nitrogen content declines with leaf age, but leaf age is confounded with canopy position. Younger leaves of *Lepechinia* are generally in higher light than older leaves, and N is distributed preferentially to high-light leaves, increasing overall carbon uptake by the canopy (Field 1983).

The phenology of leaf traits in *Mimulus* follows a different pattern from that in *Lepechinia* (Mooney et al. 1980). *Mimulus* retains a few terminal leaves through the summer, despite losing the majority of leaves. The retained leaves tend to be small and thick, with much lower N content than leaves present during the growing season. Even within the twig growth period, however, there is a tendency for leaf area, SLA, and percent N to peak in the early- to mid-season, roughly in March. On an area basis, leaf N content declines slightly throughout the growing season.
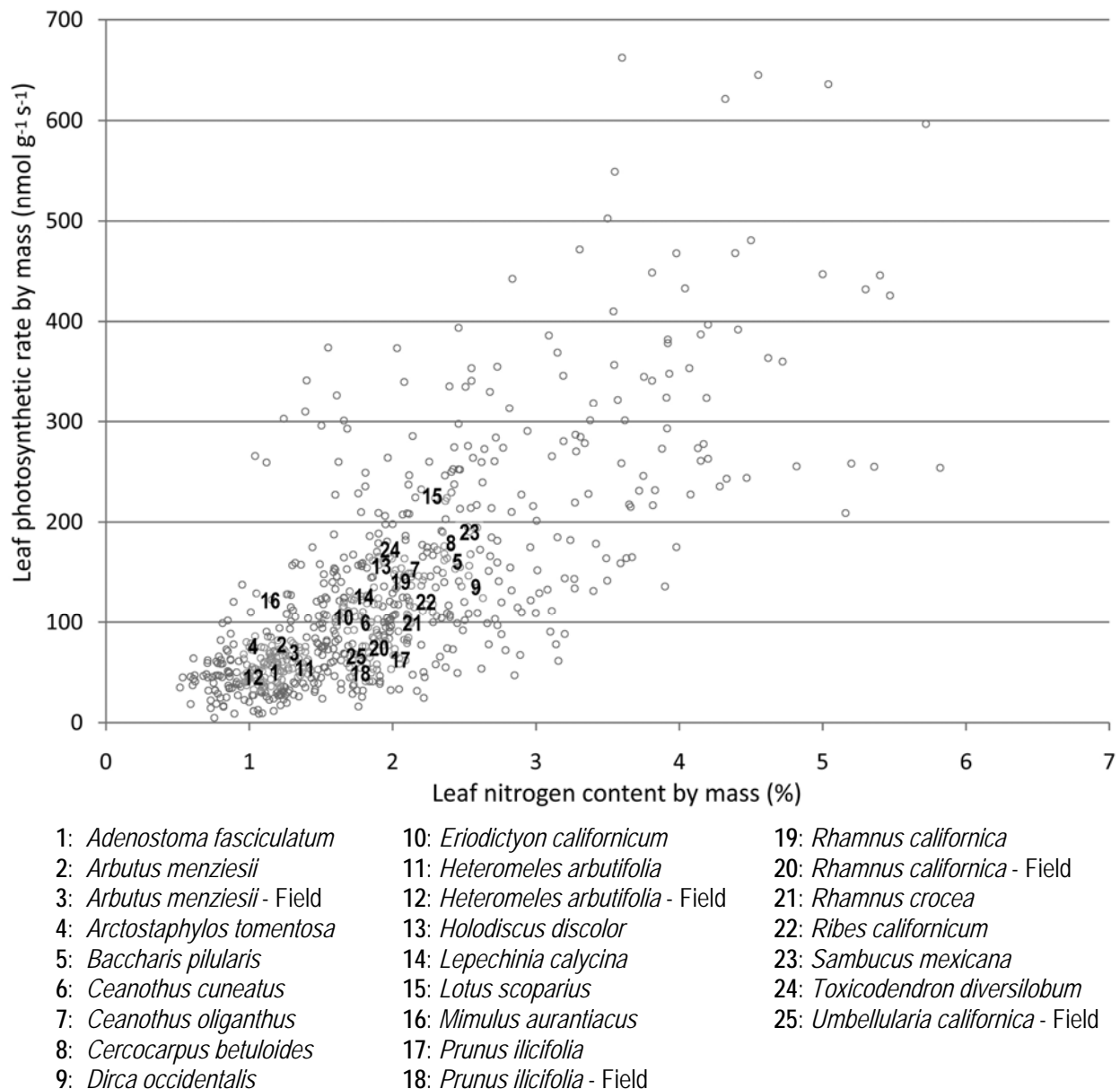
Figure 1. Photosynthetic rate versus leaf nitrogen content for 712 species worldwide. Values for 25 Jasper Ridge species are shown by numbers. Species marked "Field" in the legend are from Field et al. 1983, all others are from Ackerly 2004. (Adapted from Wright et al. 2004.)

Although precipitation ends predictably in April or May, spring- and summer-active species are more common than drought-deciduous species in JRBP woody vegetation. A comparison of four species that are dominant in serpentine chaparral found that all had a similar period of maximum stem elongation, roughly between April and July (Davis and Mooney 1986). This synchrony in growth occurred despite large differences across species in seasonal water use. Three of the four species showed marked declines in water potential (indicating increases in water stress) during the summer drought, with the magnitude of the stress being inversely

correlated with rooting depth. The fourth and most deeply rooted species, *Quercus durata,* maintained a water potential of about -0.4 MPa throughout the year, indicating that at least in some years it does not experience seasonal water stress (Davis and Mooney 1986). In *Heteromeles arbutifolia*, an evergreen shrub that was one of the species studied by Davis and Mooney, stem growth occurs mainly between June and September, peaking in July. New leaves are produced throughout the year, except in the fall, when most root growth occurs (Mooney and Chu 1974). Carbohydrate stored in leaves and bark showed roughly the opposite trend of stem growth, being lowest in the summer.

The coexistence of diverse phenological strategies within the single chaparral ecosystem has provided a fertile ground for study. Several experiments have used Jasper Ridge shrubs to test general hypotheses about the relationships among various plant traits, and the association of those traits with different growth strategies. In four evergreens, nitrogen use efficiency (NUE, photosynthetic rate per unit leaf nitrogen) and water use efficiency (WUE, the ratio of photosynthetic rate to rate of water loss) were inversely related, although a fifth species, *Heteromeles*, did not fit the trend (Field et al. 1983). The inverse correlation between NUE and WUE is consistent with a tradeoff between water and nitrogen use, in which increased opening of leaf stomata tends to increase both photosynthetic rate (greater carbon uptake for a given amount of nitrogen contained in the leaf) and transpiration (increased water loss). When measured across 20 chaparral species, including four of those used by Field et al. (1983), the negative relationship between NUE and WUE was maintained, but was not significant (Ackerly 2004). However, many physiological traits in those 20 species were associated with trends in leaf life span and minimum water potential (an indicator of rooting depth and/or water availability). Collectively, those traits defined a range of strategies for survival of summer drought. With respect to carbon uptake, photosynthetic rate was inversely correlated with leaf life span, such that leaves that persisted during the summer drought maintained lower photosynthetic rates throughout the year. Thus annual carbon uptake is likely to be more similar among different species than would be expected from leaf life span or photosynthetic rate alone (eg., Hollinger 1992, below).

The photosynthesis-nitrogen relationship in Jasper Ridge plants was the starting point for broad, global analyses of plant physiological traits (Field and Mooney 1986), and this approach has continued to expand (Wright et al. 2004). The positive correlation between photosynthesis and leaf N content (Field 1983, Field et al. 1983, Field and Mooney 1983) is a strong global pattern (Field and Mooney 1986, Wright et al. 2004, Fig. 1). The relationship between leaf life span and photosynthetic rate (Ackerly 2004) is also global (Wright et al. 2004). In an early survey of the photosynthesis-nitrogen relationship, all the JRBP evergreens were at the low end of the scale in both N content and photosynthetic rate, and had relatively lower photosynthetic capacity for their N content than most other species (Field and Mooney 1986). Evergreen sclerophylls outside of JRBP had trait values comparable to the Jasper Ridge species, suggesting that this is a characteristic of the growth type rather than the location. In a more recent analysis, the JRBP evergreens generally maintained their position at the low end of the scale, but the larger dataset makes it apparent that they are well within the global range of both N content and photosynthetic capacity (Wright et al. 2004, Fig. 1).

Maximum rates of leaf photosynthesis in oaks at JRBP are similar to those of the woody species studied by Field and Mooney (1983), and in oaks, total plant-level carbon balance has also been examined. Two comparisons between oak species have focused on *Quercus agrifolia* (Coast Live Oak) and *Q. lobata* (Valley Oak) (Hollinger 1992) and on *Q. agrifolia* and *Q. durata*

(Leather Oak) (Goulden 1996). Of these three species, only *Q. lobata* is deciduous. Annual gross photosynthesis was similar between *Q. agrifolia* and *Q. lobata* (Hollinger 1992). Their equivalence in annual carbon uptake was driven by two counterbalancing effects: longer leaf retention in *Q. agrifolia*, and higher photosynthetic rates in *Q. lobata* when it was in leaf. Based on modeling of canopy light interception and nitrogen content, neither species maintained the LAI that would have maximized production; *Q. lobata* fell especially short. *Quercus agrifolia* maintained higher WUE, both instantaneously and integrated over the season. However, in both species, transpiration exceeded rainfall within the dripline, suggesting that *Quercus* roots must occupy an area larger than their canopy, and that water availability may limit LAI. *Quercus durata* also had lower WUE than *agrifolia*, and in this study, too, total seasonal water use exceeded rainfall for both species (Goulden 1996). Maximum leaf photosynthesis (A_{max}) was similar between *Q. durata* and *Q. agrifolia*, but LAI was considerably higher in *Q. agrifolia*, 7.6 *vs.* 2.0. Total canopy carbon uptake was 1500 g C m^{-2} year^{-1} in *Q. durata*, 1900 g C m^{-2} year^{-1} in *Q. agrifolia*. It is possible that the trees chosen for photosynthesis measurements were unrepresentative in terms of canopy structure; litterfall traps beneath other trees suggested no difference in LAI (Goulden 1996).

It is striking that all three oak species apparently exploit water resources over a larger area than their canopies. If this is a general trend, it suggests that the classic Californian oak, isolated in a grassland, is heavily reliant on the inefficient water use and high drainage rates of that grassland system (see below); this may also explain how scattered oaks are able to survive in grasslands but not to form a denser woodland.

Grassland

In both sandstone and serpentine grasslands at Jasper Ridge, the timing of plant growth within a season is highly correlated with water availability. Seedlings germinate at the beginning of the rainy season in the fall, growth peaks in early to mid spring, and senescence occurs during May and June for most species. In both ecosystems there are a few species of summer-active annuals which flower in July and August and senesce the following fall. However, despite the coordination of growth with rainfall, on both substrates, annual evapotranspiration (ET) is well below rainfall. Estimates based on a model of weather years 1985-1994 indicated ET averaged two-thirds of incident precipitation in sandstone grasslands, the remaining third being lost to drainage or runoff (Jackson et al. 1998). On serpentine soils, ET was 40% of precipitation. These high drainage rates occur because rain often falls on already saturated soils in the winter. An eddy covariance study in the serpentine grasslands examined variation in water use over the course of the season, and found that ET is largely controlled by stomatal conductance early in the season, but by late spring evaporation dominates (Valentini et al. 1995).

The productivity of serpentine grasslands is consistently low relative to adjacent sandstone systems, although both vary considerably both in space and time. In grasslands the most common method of measuring NPP is wholesale harvest of aboveground plant material at the peak of the growing season, and occasionally harvest of roots, by soil coring, as well. Considering only studies that have used these methods, annual aboveground NPP in unfertilized serpentine grasslands varies from 55 to 145 g m^{-2}, while aboveground NPP in sandstone grasslands ranges from 200 to 610 g m^{-2}. For the minority of studies that have included root harvests, estimates of total NPP are about 150 g m^{-2} for serpentine soils, and 300 to 920 g m^{-2} for sandstone (Hungate et al. 1996, Shaw et al. 2002, Dukes et al. 2005). The timing of growth may also differ somewhat between the two soil substrates; in 1991 NDVI peaked in February in the

serpentine grassland and in April in the sandstone (Gamon et al. 1995). Part of this may be due to the influence of greater standing dead litter mass in the sandstone system (Gamon et al. 1995, Garcia 2003). However, in 1996, LAI of live biomass peaked about a month later in the sandstone than serpentine grassland (Lund 2002). The relatively larger proportion of forbs in the serpentine may also be an explanation; most of the forbs in this system flower and senesce earlier than the grasses.

Serpentine

Serpentine grasslands are distinctive in both community composition and productivity. The serpentine grasslands at Jasper Ridge are dominated by native annuals, both grasses and forbs, and a few perennial grasses. Naturalized European annuals vary in abundance as a function of water availability and disturbance, but are generally less abundant than in non-serpentine grassland (Hobbs et al. 2007, McNaughton 1968). The more recent invader *Centaurea solstitialis* (yellow star thistle) is also less successful in the serpentine ecosystem than on sandstone (Dukes 2001*a*, Dukes 2002). Leaf area index is low in serpentine grasslands, around 1 at the peak of the season (Valentini et al. 1995, Gamon et al. 1995, Lund 2002). Photosynthesis is correspondingly low, with midday net ecosystem C exchange peaking at 8 μmol m^{-2} s^{-1} in 1991 (Valentini et al. 1995). Integrating over gross photosynthesis in 1991, Valentini estimated NPP at 133 g m^{-2}. In assembled communities in microcosms in 1993-94, C exchange peaked at 4 μmol m^{-2} s^{-1}, and peaked earlier than corresponding sandstone microcosms (Fredeen et al. 1998).

Much of the work on serpentine ecosystems focuses on their unusually low productivity, and Jasper Ridge is no exception. It has been proposed that the unusually low Ca:Mg ratio and high heavy metal content of serpentine-derived soils reduces the productivity they can support (Harrison and Viers 2007, McNaughton 1968), but it appears that this is at best only a part of the explanation. Both serpentine species and European invaders grow successfully on serpentine soils when fertilized by macronutrients, and achieve production levels comparable to those on sandstone soils (Turitzin 1982, Chiariello and Field 1996, Joel et al. 2001). Production consistently responds to N and P addition, and rarely to any other manipulation. In a field experiment, serpentine grasslands increased production in response to both N and P, with N nearly doubling production, and the effects of N and P together were roughly additive (Turitzin 1982). There was no response of production to either Ca or K, although one species, *Bromus hordeaceus* (formerly *B. mollis*), responded to K when N and P were abundant. In a potted study, in which nutrients were added in greater quantities than in Turitzin's work, production increased 5-fold in response to fertilization with N, P, and K (Chiariello and Field 1996). Responses to each nutrient individually were not addressed. A mixed community of exotics and native species outproduced a purely native community on fertilized serpentine soil but not on unfertilized soil (Chiariello and Field 1996).

Although well-established at Jasper Ridge, limitation by N and P on serpentine soils may not be general. Harrison and Viers (2007) suggest that the strong response of serpentine grassland production to NPK is idiosyncratic to the San Francisco Bay Area, but a mechanism for this regional pattern is unknown.

In addition to soil nutrient availability, other factors whose influence on production in serpentine grasslands has been studied at Jasper Ridge include water availability, diversity, and elevated CO_2. Water availability may be somewhat lower on serpentine than sandstone soils, due to the rockiness and higher drainage rates on serpentine (Harrison and Viers 2007, McNaughton 1968). McNaughton (1968) established a series of plots on both substrate types, varying in aspect

and water availability. Northeast slopes were wettest and SW driest. McNaughton found that annual production across this gradient varied by a factor of three, with driest slopes having the highest productivity, and NW slopes the lowest. It should be noted that in this design, water availability was confounded with temperature and light availability, so it may be that high light and heat were driving this pattern rather than dryness. In addition, although production varied across the gradient, total standing biomass did not, so that NW slopes maintained a mass of standing dead litter three times as large as that on SW slopes.

Species richness also varied across the aspect gradient in McNaughton's (1968) study. Across the two substrate types, diversity was inversely correlated with productivity, but this was strongly influenced by the contrast between the two soils, sandstone grasslands being relatively species-poor and productive. Within the serpentine sites, diversity and productivity were positively correlated.

Over decadal time scales, there may be substantial variation in diversity. Long-term herbivore exclosure plots have been maintained since 1983 in the serpentine area at the top of Jasper Ridge (Hobbs et al. 2007, Hobbs and Mooney 1985). This study has targeted species composition and community dynamics rather than biomass, but an overview of the first 20 years of these exclosures has some suggestive points (Hobbs et al. 2007). There were several drought years early in the experiment, during which all annual grasses dropped in abundance to nearly zero, but they rebounded readily during later, wetter years. This was especially true of *B. hordeaceus*, one of the most abundant European grasses in the serpentine. Given that the annual grasses are often large contributors to total ecosystem biomass, this could have a strong impact on productivity. Species richness was also dependent on rainfall, being positively correlated with rainfall across all levels of herbivore access.

At the level of individual species, peak biomass is correlated with length of growing season, so that species that germinate early and senesce late achieve the highest peak biomass (Mooney et al. 1986). The pattern is largely driven by two clusters, the small, spring-flowering species and the larger summer-active species. This highlights the importance of summer-active species' influence on total ecosystem production in JRBP grasslands, because not only are they growing at a time when most species are dead, and thus are not in direct competition, but they are also potentially the largest contributors to biomass. When higher diversity is associated with the presence of these species, a positive relationship between diversity and production is likely.

Elevated CO_2 has consistently failed to alter production levels in serpentine grasslands at Jasper Ridge, except when nutrient availability is increased. In a field study with no nutrient additions, biomass did not change at elevated CO_2 (Hungate et al. 1996). In microcosms of assembled communities, aboveground biomass was nearly identical at elevated as at ambient CO_2, whereas when fertilized by N, P, and K, the effect of CO_2 was a 30% increase in ANPP (Chiariello and Field 1996). In the same communities, elevated CO_2 had no effect on net ecosystem C exchange at ambient nutrient levels (Fredeen et al. 1998). Fertilization, on the other hand, increased both the peak and the duration of C uptake, and elevated CO_2 in combination with fertilization increased peak C uptake even further.

To the extent that the uniqueness of serpentine grasslands derives from the poor productive potential of their soils, threats to serpentine systems are likely to be in the form of rising resource levels. Nitrogen pollution in particular has the potential to dramatically increase serpentine productivity, as it already has in less secluded places than JRBP (Harrison and Viers 2007). Increases in soil nutrient levels not only change productivity, but also enable invasion by more productive alien species. If rising CO_2 levels also contribute to invasion, it may become

increasingly difficult to preserve serpentine communities. Although Chiariello and Field (1996) found that exotic-containing communities were no more responsive to CO_2 than serpentine-only communities, the responses of more recent invaders are still largely unknown. Monocultures of *Centaurea solstitialis*, an invasive, summer-active thistle, on serpentine soils, increased in aboveground biomass by 70% in response to elevated CO_2 (Dukes 2002). When grown in communities, the CO_2 effect on *Centaurea* biomass was 69%, but was not significant. However, even at elevated CO_2, *Centaurea* biomass was 1300% greater in monoculture than in communities, suggesting that despite its high CO_2 response, this species is not a strong competitor on serpentine soils.

Non-serpentine grassland

Although Jasper Ridge has a Mediterranean-type climate and its sandstone and greenstone grasslands are often described as water-limited, rainfall is at best a mediocre predictor of annual production. JRBP sandstone grasslands formed one site in a multi-biome comparison across an order-of-magnitude rainfall gradient, in which Huxman and colleagues found a linear relationship between minimum annual rainfall and the corresponding aboveground net primary production (Huxman et al. 2004). The relationship became weaker and non-linear when all recorded years (wet and dry) were considered. On a site-by-site basis, annual production at the driest sites was tightly correlated with rainfall, while production at the wetter sites was better predicted by growing season temperature and previous year's production. Jasper Ridge fell at the cusp of this shift. Based on the cross-biome comparison, a site with JRBP's average precipitation would be expected to have higher productivity in wetter years than is observed. At least one other study has also found that rainfall is a poor predictor of production at JRBP (Dukes et al. 2005). However, consistent with the linear relationship across sites at minimum rainfall, Garcia (2003) found that NDVI in Jasper Ridge grasslands was most sensitive to rainfall in the lowest-rainfall year analyzed.

Variations in water availability within a year, rather than between years, do appear to explain some variations in growth. Based on differences in soil moisture driven by aspect, McNaughton (1968) found that both total biomass and annual production declined with water availability. When *Avena*, *Lolium*, and *Bromus* were monitored over three growing seasons in 1971-74, early-season growth was delayed by several months in all three species in 1972, when rain was scarce in the fall (Gulmon 1979). In early February, all three species were at least three times larger in 1973 and 1974 than in 1972. However, both *Lolium* and *Bromus* overcame the early-season growth deficit and ended the season at a biomass comparable to that reached in 1973 and 1974.

Attempts to connect production with diversity on non-serpentine grasslands have been of limited success. McNaughton (1968) found an inverse relationship between diversity and production on greenstone soils, while Dukes (2001*b*) found a weak positive correlation between species richness and production on sandstone. The former study was carried out in naturally occurring communities, with variations in diversity being associated with differences in aspect, while the latter was a potted study of assembled communities; this difference may explain some of the inconsistencies. Diversity may have other impacts on grasslands than productivity effects, however. When *Centaurea solstitialis* (yellow star-thistle) was introduced into assembled communities of varying species richness, increasing richness did not decrease the success of *Centaurea*, but it did decrease the negative impact of *Centaurea* on other species' productivity

(Dukes 2001*a*). Growth of yellow star-thistle when paired with another species was inversely related to the productivity of that species in monoculture.

Beginning in 1992, several multi-year experiments have explored the responses of sandstone grasslands to elevated CO_2, sometimes in combination with increases in the availability of other resources or environmental factors that are changing globally. This work was done primarily in a series of manipulative experiments, as follows: a system of open-top chambers at elevated and ambient CO_2, as well as unchambered controls, in sandstone and serpentine grasslands (OTC, 1992-1996); a set of microcosms of varying community composition, on both serpentine and sandstone soils, receiving elevated CO_2 and additions of N, P, and K (MECCA, 1992-1996); a free-air CO_2 enrichment system in factorial with increased temperature, nitrogen deposition, and precipitation in sandstone grassland (JRGCE, 1998-present); and a set of mesocosms of varying community composition, grown on sandstone monoliths, receiving elevated CO_2 and addition of N and P (MESO, 2005-07; data from this experiment remain unpublished, but I mention it here for reference). Results from the serpentine grasslands are discussed above.

Increases in growth in the sandstone grasslands at elevated CO_2 have ranged from moderate to nonexistent. In the OTC experiment, elevated CO_2 increased belowground production, but the aboveground change was not significant (Hungate et al. 1996). The belowground response may have been somewhat different than the estimate by Hungate and colleagues, which was made by soil cores. A more detailed examination of seasonal root growth suggested that soil cores at peak biomass underestimate total root growth by at least 50% in this system, and found no difference in total root growth between ambient and elevated CO_2 (Higgins et al. 2002). In addition, both root and heterotrophic respiration increased at elevated CO_2, so that the carbon cycle was accelerated throughout, and the increase in growth was unlikely to increase carbon sequestration (Hungate et al. 1996, Luo et al. 1996).

Several species responded in a positive, nonadditive manner to the combination of CO_2 and fertilization in the MECCAs, and no species was less responsive to CO_2 when grown on sandstone than on serpentine soil (Joel et al. 2001). The synergistic fertilization effects were driven by N; there was little response to P and K, which were applied together. In contrast, in the JRGCE, not only have CO_2 effects been low or even negative, but there have also been no positive effects of CO_2 combined with other resource manipulations (Dukes et al. 2005, Shaw et al. 2002). In 2000-01, the third growing season of treatment application in the JRGCE, elevated CO_2 reduced biomass when applied in combination with any of the other three treatments (Shaw et al. 2002), but this result was not consistent across years, and overall across 1998-2003 there was no effect of CO_2 on biomass (Dukes et al. 2005). Over the first five years of the JRGCE, the only one of the four treatments to have a consistent effect on production was N deposition, which increased growth by 20-40% (Dukes et al. 2005). The added precipitation treatment changed allocation patterns, decreasing the root-to-shoot ratio. This serves as a cautionary tale, since if only aboveground production had been measured, as in most of the studies reviewed here, this would have appeared as an increase in growth.

Growth responses to elevated CO_2 in the sandstone grasslands have consistently been outpaced by photosynthetic responses. Over two years (1992-93, 1993-94) in the OTC, photosynthesis in *Avena*, the dominant grass genus, increased by 70% and 50% at elevated CO_2 (Jackson et al. 1994, Jackson et al. 1995). In comparison, in these two years production changed by -13% and 40%, respectively (Luo et al. 1997). In a third year (1995-96), increases in photosynthesis in *Avena*, *Bromus hordeaceus*, and *Hemizonia congesta* averaged only 30%, and

in *Avena* the difference was nonsignificant (Lund 2002). The downward trend in the CO_2 effect over time suggests photosynthetic downregulation; variation in weather is also a possible explanation, but seems an unlikely one. Rainfall in the 1992-93, 1993-94, and 1995-96 growing seasons was 905, 433, and 780 mm respectively (Jackson et al. 1995, Lund 2002). The year with the largest increase in photosynthesis at elevated CO_2 was the first and wettest year, whereas in general, grassland systems respond most strongly to CO_2 in dry years (Morgan et al. 2004).

Various mechanisms have been proposed and studied to explain the much larger photosynthetic than growth response to CO_2. First of all, as mentioned above, in the OTC, root and heterotrophic respiration both increased at elevated CO_2 (Hungate et al. 1996). This was also the case in the MECCAs, in which increased respiration was sufficient to remove almost all of additional photosynthesis (Luo et al. 1996), and in the JRGCE, for at least the first three years (Moore 2005). This is also apparent from measurements of net ecosystem C uptake, which increased less at elevated CO_2 than leaf-level photosynthesis did (Fredeen et al. 1998, Lund 2002). In 1992-93 in the OTC, increases in *Avena* photosynthesis were offset by reductions in plant density (Jackson et al. 1994). Changes in phenology and growing season length have also been common (see below), and if the correlation between growing season length and biomass is viable for sandstone as well as serpentine species (Mooney et al. 1986, see above), then this could also have substantial impacts on production.

In a modeling analysis based on the OTC, shifts in a variety of parameters could explain the difference between photosynthetic and growth responses; there is no reason to expect only one factor to be at play. Modeled biomass could be reduced approximately to the observed level by increasing C allocation to roots, increasing leaf death rate, increasing non-structural C storage, or decreasing specific leaf area (Luo et al. 1997). There is some support for the latter two explanations, and only leaf death rate remains unstudied. Elevated CO_2 has had an inconsistent effect on root biomass in different experiments and in different years, but rarely increases it (Dukes et al. 2005, Higgins et al. 2002, Shaw et al. 2002, Hungate et al. 1996). Some evidence suggests that respiration per unit root may increase, so it is possible that allocation of C to roots increases without increasing biomass (Hungate et al. 1996, Moore 2005). Non-structural C content increased in response to elevated CO_2 in *Avena* but not in *Plantago* in the serpentine MECCAs (Chu et al. 1996). Specific leaf area has been found to decrease at elevated CO_2 in several species (Jackson et al. 1995, C. K. Lunch, unpublished data). Interestingly, the models that include reductions in SLA or non-structural carbon predict reductions in standing dead litter as well, which is the opposite of what has been observed.

A fairly consistent effect of elevated CO_2 across these experiments has been an increase in standing dead litter (Hungate et al. 1996, Chiariello and Field 1996, Dukes et al. 2005). Given the small effect of CO_2 on biomass, this is likely driven by changes in decomposability. Pinning down a more precise mechanism has been difficult. Dukes and Field (2000) found few direct effects of elevated CO_2 on litter decomposability. Instead, differences in decomposition rate were driven primarily by litter position, with standing litter decomposing much more slowly than litter in contact with soil. However, some studies have found decomposition effects through litter chemistry (Houlton and Field 2009). The feedback effects of increased litter mass on productivity remain uncertain; a number of recent studies explore this question, but do not yet resolve it. Early-season growth, as measured by NDVI, is delayed at elevated CO_2 in the JRGCE (Chiariello et al., in prep), while total biomass in MESO is reduced by the combination of CO_2 and litter (unpublished data). Increasing standing litter levels in an otherwise unmanipulated

grassland had no effect on biomass, but did change density and species composition (Amatangelo et al. 2008).

By far the most consistent effect of elevated CO_2 in JRBP grasslands has been a shift in the timing and magnitude of water use, with consequent shifts in phenology. Across several grassland ecosystems, including Jasper Ridge, a general pattern has emerged in which elevated CO_2 enables plants to stay active longer into drought periods. This occurs due to reductions in stomatal conductance when water is abundant, which leaves soil moisture high (Morgan et al. 2004). This pattern is more pronounced in dry than in wet years. In both the MECCAs and the OTC, this phenomenon manifested as a decrease in evapotranspiration (ET) throughout most of the growing season, followed by an increase in ET at the end of the season, as the plants remained active longer than those at ambient CO_2 (Field et al. 1997, Lund 2002). However, this comes at a cost in terms of drainage, since the water is saved mostly at times when it is already abundant and soils are at or near saturation. In a model of water budgets based on the OTC, elevated CO_2 decreased the proportion of incoming rainfall used in transpiration, but increased the proportion lost to drainage from a third to a half (Jackson et al. 1998).

Increases in water availability late in the season may favor summer-active species that otherwise are a minor component of the community; this was particularly apparent in the OTC, where *Hemizonia congesta* increased in abundance and biomass in response to elevated CO_2 (Lund 2002). By promoting the growth of summer annuals, elevated CO_2 may increase productivity indirectly, enabling the ecosystem to take up C during a time of year when it is currently mostly inactive. This effect appeared in a study of net ecosystem C exchange in the 1995-96 season in the OTC (Lund 2002). During January-April, both treatments were a sink for C, of 111.9 g C m^{-2} at ambient and 72.4 g C m^{-2} at elevated CO_2. But in June-August, when *Hemizonia* bolts and flowers, the ambient treatment was a source of 3.6 g C m^{-2} while the elevated CO_2 treatment was a sink of 39.1 g C m^{-2}.

It is likely, then, that the primary effects of CO_2 on sandstone grasslands will not be direct effects of CO_2 on plant physiology, but rather feedbacks through changes in turnover times and water availability. In particular, changes in community composition have the potential to induce substantial changes in carbon dynamics.

Conclusions and future directions

Over the years of study reviewed here, the emphasis of carbon cycle research at Jasper Ridge has shifted from a fairly eclectic approach to a more focused, in-depth exploration of a single ecosystem, the sandstone grassland. This shift has been driven largely by the various global change experiments, and has led to a thorough, though still developing, understanding of the processes driving this system. The global change work done on the serpentine grasslands has also enhanced understanding of that system and of its contrasts with the sandstone. However, other systems have received less attention, and are comparatively less well understood.

In particular, the woody systems have been relatively neglected in recent years. As noted above, several seminal studies on chaparral species were conducted in JRBP serpentine chaparral, but they have rarely been compared to other substrates. No studies have compared the productivity of woody species on serpentine and non-serpentine soils. Given the unexpected nature of the nutrient limitations on serpentine grasslands, this may be a fruitful area of research.

Most of the non-grassland research on productivity has been done in chaparral, but some other systems may be feasible for study. The large and growing marsh in the Searsville wetland,

for example, is likely to be an interesting place in terms of carbon dynamics, and may become even more interesting depending on the eventual fate of the dam.

In coming years the greatest changes to production and carbon balance in JRBP grasslands are likely to come not in the form of direct physiological changes, but as invasions and changes in community dynamics. Not only invaders, but also native, non-grassland species may be favored by global change. A new study currently underway in the JRGCE will address the possibility that global change may facilitate invasion and encroachment in the sandstone grassland system; the effects of such community shifts on carbon dynamics are largely unknown. Work at JRBP and elsewhere has already shown how vulnerable serpentine grassland communities are to the combination of invasion and resource addition. But the effects of various global changes and of invaders in other systems at Jasper Ridge are still unstudied. Since the non-grassland community types are not nearly as tractable for large-scale manipulations, novel approaches and monitoring will be needed to predict the future of these systems.

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